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CRETACEOUS ANURANS FROM CENTRAL ASIA

BY

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With 14 plates and 32 text-figures

Zusammenfassung

Mehrjährige Grabungen an verschiedenen zentralasiatischen Fundplätzen, die paläogeographisch den Südwestrand des alten asiatischen Kontinents markieren und Albium- bis Campanium-Alters sind, erbrachten unter anderem zahlreiche Anurenreste. Bemerkenswert ist, daß diese Amphibien Teil einer Fauna sind, die auch marine Wirbeltiere enthält. Dies wird mit ihrer Konservierung in Kanalablagerungen erklärt. Die Kanäle verbanden vermutlich Lagunen mit strandnahen Bereichen und enthielten je nach Fließrichtung Salz-, Brack- oder Süßwasser. Das Material besteht aus isolierten Einzelknochen. Die Formenvielfalt einzelner Knochen (speziell Maxillaria, Squamosa, Urostyle) an jedem Fundort läßt vermuten, daß die kreidezeitliche Froschfauna dieses Gebietes bereits bemerkenswert vielfältig war. Ein Teil des Materials, das auf *Gobiates* und neu beschriebene, verwandte Formen bezogen werden kann, zeigt Merkmale sowohl der Leiopelmatidae als auch der Discoglossidae. Die Merkmalskombination der Gruppe, die Übergangsmerkmale zwischen beiden Familien zeigt, erlaubt es, eine eigene Familie Gobiatidae vorzuschlagen. Der verbleibende Teil des Materials läßt sich den Discoglossidae zuordnen. Das relativ reiche Material erlaubt, sowohl einige evolutive Trends innerhalb der Gobiatidae und der Discoglossidae zu erkennen als auch einige phylogenetische Aspekte dieser Familien zu beurteilen.

Schlüsselwörter: Amphibia – Anura – Kreide – Zentralasien.

Abstract

Several years of excavations at nine central Asian sites, which paleogeographically represent the southwestern margin of the ancient Asian continent and which are of Albian to Campanian age, yielded, among others, numerous anuran remains. It is noteworthy that these amphibians are parts of assemblages comprising also marine vertebrates. This is explained by their preservation in channel deposits; the channels presumably connected coastal basins and contained salty, brackish or fresh water, depending on the direction of the water flow. The material consists mostly of isolated bones. The variety of single bone types (especially maxillaries, squamosals, and urostyles) at each locality suggests that the Cretaceous anuran fauna of this region was considerably diverse. The material that can be referred to *Gobiates* and newly described related forms displays characters of both Leiopelmatidae and Discoglossidae. The nature of this group, which differs by its character combination from both the families but displays transitional features between them, justifies to consider it a separate family, the Gobiatidae. The remaining material may be referred to the Discoglossidae. The relatively large amount of material allows to discern some evolutionary trends within the Gobiatidae and Discoglossidae and to determine some phylogenetic relations of these families.

Key words: Amphibia – Anura – Cretaceous – Central Asia.

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Introduction

The earliest fossil record of true anurans is *Vieraella herbstii* from the Early Jurassic (Liassic) of Patagonia (Reig 1961, Casamiquela 1965). Presence of frogs, without closer determination, is reported from the Early Jurassic of Arizona (Gaffney et al. 1989: 289). A frog of the family Discoglossidae is mentioned by Evans et al. (1988: 551) from the Middle Jurassic (upper Bathonian) of England (first reported by Freeman 1979); it was recently described under the name *Eodiscoglossus oxoniensis* (Evans et al. 1990). *Notobatrachus degiustoi* is of Late Jurassic (Tithonian) age and comes from Argentina (Stipancic & Reig 1955, Reig 1957, Casamiquela 1961). *Vieraella* displays structural resemblances with contemporary discoglossids and leiopelmatids, and *Notobatrachus* can be allocated to the latter family (Estes & Reig 1973: 18, 24). Other Late Jurassic anurans are from Wyoming – *Eobatrachus agilis* (see Marsh 1887 and Moodie 1912, 1914) with claimed relations to Aglossa or to the Discoglossidae (Reig 1957, Hecht & Estes 1960), and *Comobatrachus aenigmatis* (Hecht & Estes 1960). *Eodiscoglossus santonjae* with discoglossid affinities (Melendez 1957, Hecht 1970, Vergnaud-Grazzini & Wenz 1975, Estes & Sanchíz 1982b), *Montsechobatrachus gaudryi* (Vidal 1902) of indeterminate relations, and *Neusibatrachus wilferti*, assumed to have affinities to the Palaeobatrachidae and/or the Ranidae (Seiffert 1972), all are from the Late Jurassic of Spain (see also Gomez Pallerola 1979, who used the name *Montsechusbatrachus* for the second form). Review of Jurassic anurans with further references may be found in Estes & Reig (1973). The latter authors questioned the omosternum referred to the Ranidae, from the middle Jurassic of France (Seiffert 1969); they even suggested non-anuran nature of this element. A hitherto undescribed anuran with supposedly discoglossid affinities is known from the Jurassic of Portugal (Krebs, pers. comm. 1981). Another anuran, announced as a new, undescribed taxon, was preliminarily reported from the Upper Jurassic (Kimmeridgian) of Utah-Colorado, USA (Chure et al. 1989). Several bones of undescribed anurans, also of the late Jurassic age, from Wyoming, USA are noted by Prothero (1981), and by Ensom (1988) from England. Newly discovered Late Jurassic anurans from the Dinosaur National Monument (Morrison Formation) are currently studied by Dr. Amy Henrici.

The Cretaceous records are more numerous. Among the earliest is *Wealdenbatrachus jucarensis* from the Hauterivian-Barremian of Spain (Fey 1986, 1988). It is said to have discoglossid affinities. Pipid tadpoles (*Shomronella jordanica*) were reported from the Early Cretaceous (? Hauterivian) of Israel (Estes et al. 1978). *Cordicephalus gracilis*, *C. longicostatus*, and *Thoraciliacus rostriceps* are adult pipids of Barremian age, also from Israel (Nevo 1968). Pipids were found also in the Middle (Baez & Calvo 1989) and Late Cretaceous (Santonian-Campanian) of Argentina (*Saltenia ibanezi*; Reig 1959, Baez 1981) and Late Cretaceous (early Senonian) of Niger (*Xenopus* sp.; Vergnaud-Grazzini, in de Broin et al. 1974, Rage 1981; another form of the same provenance is not yet described genus; see Baez & Rage 1988). Vergnaud-Grazzini (in op. cit.) has also indicated some ranids from the same locality; however, Rage (1984) has denied this familial assignment. Besides, there is also an undescribed Early Cretaceous (Neocomian) anuran from Las Hoyas, East-central Spain (Estes, pers. comm. 1986, and Sanchíz, pers. comm. 1991). Abundant anuran material is reported, without determination, from the late Early Cretaceous of Cameroon (Flynn & Brunet 1989). Some anuran remains with discoglossid and unknown affinities from the Albian of Texas were described by Winkler et al. (1990; see also Murry et al. 1989). Aptian anurans (not determined but at least two taxa) were found also in Malawi (Jacobs et al. 1990). Anurans from the early Late Cretaceous are preliminarily reported from Utah (Eaton et al. 1988). A Late Cretaceous anuran from Montana and Wyoming (Lance Formation) identified earlier (Estes 1964: 54, fig. 27c) as ascaphid was later transferred to discoglossids and described as *Scotiophryne pustulosa* (Estes 1969). Similarly, the material of the same provenience identified as cf. *Barbourula* sp. (Estes 1964: 55–57, figs. 28a, b, 29b; Estes et al. 1969: 14) was later (Estes & Sanchíz 1982a) described as *Palaeobatrachus occidentalis*. Other Lance Formation anurans have been questionably referred to the pelobatid frog *Eopelobates* (Estes 1964: 57–60, Estes et al. 1969, Estes 1970: 315–316; Estes & Sanchíz 1982a). Other anurans of the same age are discoglossid *Paradiscoglossus americanus* (Estes & Sanchíz 1982a) and *Theatonius lancensis* of uncertain relations but distinct from the Discoglossidae and Pelobatidae (Fox 1976). *Gobiates leptocolaptus* and *G. khermeentsavi* are discoglossids from Campanian deposits of the Gobi Desert (Borsuk-Białynicka 1978, Špinar & Tatarinov 1986). Other forms were described from the Late Turonian to Coniacian deposits of central Asia by Nessov (1981, 1988), namely *Eopelobates sosedkoi, Kizylkuma antiqua, Aralobatrachus robustus*, and *Itemirella cretacea* (late Albian and early Cenomanian anurans from the same region were also mentioned). A questionable record of the Leptodactylidae from the Late Cretaceous of Peru was noted by Sigé (1968). Material tentatively referred to that family is known also from the Late Cretaceous of Bolivia (De Muizon et al. 1983), and another leptodactylid was reported from the Late Cretaceous of Brazil and Argentina (Baez 1985, 1987, Baez & Peri 1987, 1989). Unidentified Late Cretaceous (most probably Campanian) pipids and leptodactylids were reported also from Patagonia (Bonaparte 1986). Isolated and fragmentary bones belonging to four types of anurans referred to the Discoglossidae and tentatively (two fragmentary ilia) also to the Pelobatidae were described by Sahni et al. (1972) from the Middle Campanian of Montana, USA. Sahni et al. (1982, 1983), Gayet et al. (1984), and Sahni (1984) reported an anuran claimed to be a pelobatid (assignment based on the ilium, a small fragment of maxillary, and the distal section of humerus), and an anuran maxillary fam. inc. sedis from India (Cretaceous/Tertiary boundary). However, probably the same anuran material (the uppermost Maastrichtian, India), is mentioned without explicite determination by Prasad & Sahni (1988), and determined as discoglossid by Prasad & Rage (1991). Hitherto undescribed Late Cretaceous anurans are known also from Zaire (Estes, pers. comm. 1986). Recently, the late Cretaceous discoglossids and palaeobatrachids were reported from Spain (Astibia et al. 1990).

In addition to the noted Cretaceous forms, abundant, though fragmentary and disarticulated in great majority, material was recovered from various localities in central Asia by one of us (L.A.N.). Its stratigraphic range is from the Albian to Santonian or early Campanian, thus spanning about 20–25 million years. The material consists mainly of isolated bones which add to the information provided by the articulated skeletons described by Borsuk-Białynicka (1978) and Špinar & Tatarinov (1986). Moreover, the present material suggests that the Cretaceous anuran fauna of central Asia was much more diverse than previously believed.

Abbreviations used in text and illustrations

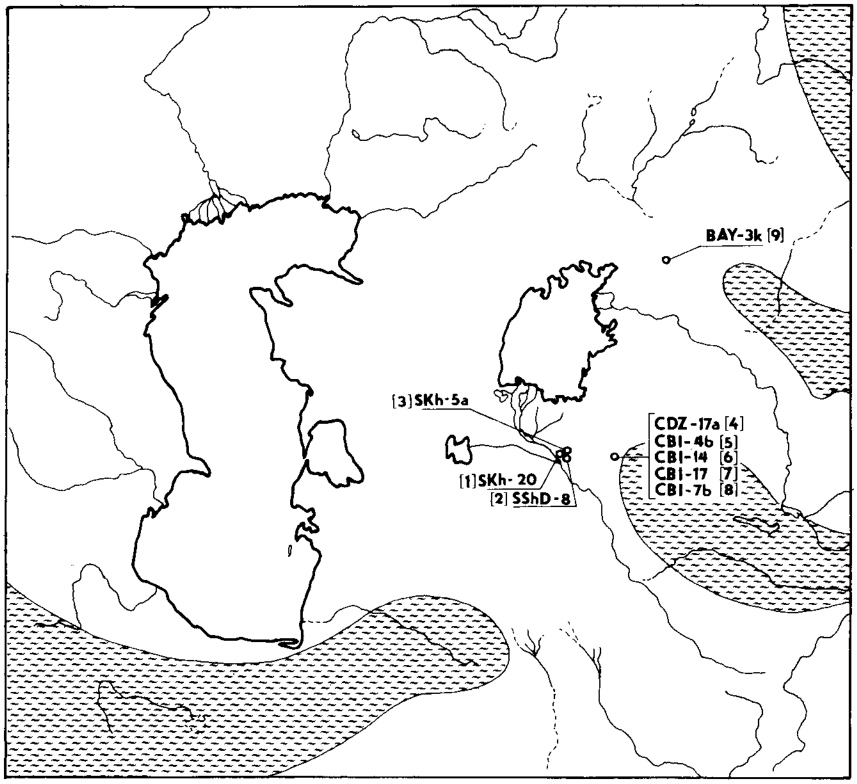
LU-N	Nessov's collection at the St. Petersburgh University
DPFNSP	Collection of the Department of Palaeontology, Faculty of Natural Sciences, Prague
PIN	Paleontological Institute, Moscow
ac	acetabulum
ala	agger limitans anterior
aoi	ala ossis ilii
c	centrum
ch	caput humeri
ci	crista ilii
cl	crista lateralis
cm	crista medialis
cn	carina neuralis
co	collum ilii
coc	condylus occipitalis
cp	crista parotica
cpc	crista paracoronoidea
el	epicondylus lateralis
em	epicondylus medialis
es	extremitas spatulata
fc	fossa condyloidea
fcv	fossa cubitalis ventralis
ffrp	articulation facet for the frontoparietal
fm	facies maxillaris

fo	foramen ovale
fp	foramen prooticum
fs	articulation facet for the squamosal
gpb	groove for the palatoquadrate bar
gr	groove
ld	lamina dentalis
lh	lamina horizontalis
mo	margo orbitalis
na	neural arch
nc	neural canal
pal	processus palatinus
pa	pars ascendens
pc	processus coronoideus
pd	processus dorsalis
pds	processus descendens
pdsp	prominentia ducti semicircularis posterioris
pf	processus frontalis
poz	postzygapophysis
ppd	processus posterodorsalis
ppl	processus posterolateralis
ppo	processus postorbitalis
pt	processus transversus
pz	processus zygomaticus
pzm	processus zygomatico-maxillaris
rms	orifice of the canal for the ramus maxillaris superior
rna	rudiment of neural arch
rnc	rudiment of neural canal
rp	ramus paroticus
rv	recessus vaginiformis
scM	sulcus pro cart. Meckeli
svj	sulcus venae jugularis
ts	torus superior

Material and Methods

The material comes from the following sites (Text-fig. 1):

1. Khodzhakul Lake (Karakalpak AR, SW Kizylkum Desert) (Chodzhakul Lake in Nessov 1988). Excavation site SKh-20 (between the road Nukus-Turtkul and Amu-Darya River, N of dried up Khodzhakul Lake). Middle or



Text-fig. 1. Geographic position of sites with fossil anurans described in the present paper, and approximate distribution of the sea and dry land in contemporary central Asia during the Late Cretaceous (after Sinitsyn 1966). Complete account of localities of Cretaceous anurans in the CIS may be found in Nessov (1988 b, fig. 1). Figures in parentheses correspond to those in the chapter Material and Methods. The shore line of Aral Sea corresponds to the situation before 1979.

Middle or upper part of the Khodzhakul Formation. Late Albian age based on chondrichthyans *Eoanacorax dalinkevichiusi* (Anacoracidae) and *Paraisurus* sp. (Cretoxyrhinidae). Associated flora and fauna: Coniferales, Angiospermae, Gastropoda, Bivalvia, Ammonoidea, Malacostraca, Selachii, Batoidea, Holocephali, Holostei, Teleostei, Anura, Caudata, Chelonia, Lacertilia, Crocodylia, Dinosauria, Aves, Mammalia. Coll. nos. LU-N 1/1 – 1/3. Collected in 1978 and 1982.

2. Sheikhdzheili (SW Kizylkum Desert) (Sheichdzheili in NESSOV 1988). Excavation site SShD-8 (4km SE from SKh-20, near the Sheikhdzheili Hill). Upper part of Khodzhakul Formation (14m above the level of Skh-20). The age is based on (1) the maximum sea regression in the interval between the late Albian small transgression and the late Cenomanian to early Turonian great transgression, and (2) the absence of teeth of *Ptychodus* (Selachii), present in the region only from the late Cenomanian to Senonian, and absence of the genus *Scapanorhynchus* (Selachii) that appeared in the region only in the late Cenomanian. Consequently, the most probable age is an early Cenomanian. General faunal composition is similar to that in SKh-20, but some species, genera, and even some families are different. Coll. nos. LU-N 2/4 – 2/45. Collected in 1980 and 1982.

3. Khodzhakulsay (SW Kizylkum Desert) (Chodzhakulsay in NESSOV 1988). Excavation site SKh-5a (about 2km N from the line SKh-20 – SShD-8). Stratigraphically near SShD-8. Age is early Cenomanian. Rich vertebrate fauna similar by its generic and specific composition to that in SShD-8. Coll. no. LU-N 3/46.

4. Dzhyrakuduk (Uzbekistan, Bukhara District, central Kizylkum Desert) (incorrect spelling Dzharakhuduk and Dzharakuduk was used by A. K. Rozhdestvensky, though A.D. Arkhangelsky used correct spelling already at the beginning of this century). Site CDZ-17a, stratigraphically 26 m above the base of the Bissekty Formation (previously termed Taikarshin Beds). Based on the Anacoracidae (Selachii), the age is late Turonian. Vertebrate assemblage composed of all gnathostome classes and more than 50 families. Coll. nos. LU-N 4/47 – 4/91. Collected in 1977 and 1982.

5. Dzhyrakuduk. Excavation sites CBI-4b and CBI-4v. Middle part of the Bissekty Formation, 48–50 m above its base. Age is Coniacian. Associated flora and fauna: Angiospermaephyta, Bivalvia, Crustacea, Chondrostei, Holostei, Teleostei, Amphibia, Chelonia, Lacertilia, giant pterosaur *Azhdarcho*, Dinosauria (various Theropoda, Sauropoda, Ankylosauridae, Hadrosauridae, Ceratopsidae, ? Hypsilophodontidae), Aves (Enantiornithidae, Ichthyornithidae, and Zhyraornithidae), Mammalia. Vertebrate assemblage consists of more than 60 families. Coll. nos. LU-N 5/92 – 5/259. Collected in 1979, 1980, and 1981.

6. Dzhyrakuduk. Excavation site CBI-14 (about 800 m E of CBI-4b). Middle part of the Bissekty Formation, about 55 m above its base. Based on *Ptychocorax aulaticus* (Selachii), the age is Coniacian. Associated fauna: Coleoptera (Curculionidae, Hydrophilidae) and Hymenoptera, and the richest Cretaceous vertebrate assemblage hitherto found in Eurasia. It is composed of elasmobranchs *Polyacrodus, Hybodus, Myledaphus, Sclerorhynchus, Ptychotrigon, Scapanorhynchus, Eostriatalamia,* and *Brachaelurus*, Lepisosteidae, Amiidae, Teleostei (Albulidae, Ichthyodectidae, etc.), Caudata, six genera of the chelonians (Macrobaenidae, ? Chelydridae, Lindholmemydidae, Adocidae, Trionychidae), Agamidae, Scincomorpha, Anguimorpha, Pterosauria, Dinosauria (both latter groups similar to CBI-4b), Aves (e. g. representatives of two families of the Ichthyornithiformes), Mammalia (Deltatherididae, Mixotheridia, Proteutheria, Condylarthra). Altogether about 60 vertebrate families. Coll. nos. LU/N 6/260 – 6/442. Collected in 1980, 1984, and 1985.

7. Dzhyrakuduk. Excavation site CBI-17 (about 200 m W of CBI-14). Approximately 10 m above the level of CBI-14. Middle or upper part of the Bissekty Formation, Coniacian. This faunal complex is very rich but slightly different from that in CBI-14 (e. g. some Selachii, Teleostei, and mammals that are not present in CBI-14). Coll. nos. LU-N 7/443 – 7/461. Collected in 1980.

8. Dzhyrakuduk. Excavation site CBI-7b (3.5–4 km E of CBI-4b). Upper part of the Bissekty Formation, Coniacian (or transitional to Santonian; judging from a single tooth of cf. *Parapalaeobates*, Batoidei). Faunal complex: all classes of the Gnathostomata except birds. Coll. nos. LU-N 8/462 – 8/495. Collected in 1979.

9. Baybishe (Kazakhstan, Kzyl-Orda District, Kalmakerchinsky region, N of the lower Syr-Darya River, 130–135 km NNW of the village of Dzhusali). Excavation site BAY-3k. Middle or upper part of the Bostobe Formation, late Santonian-? Campanian on clear evidence of increasing aridity. This vertebrate assemblage appears to postdate that known for the lower Santonian of W. Fergana (Kansai, Isfara, Kizylpilyal, Zamuratsho), but the site itself is located underneath the layers deposited during the late Campanian great transgression in this region. The vertebrates include Batoidea other than those at Dzhyrakuduk, one shark species (also different from that at Dzhyrakuduk),

'ganoid' fishes (except Lepisosteidae that apparently disappeared in central Asia), Caudata (two species that are obviously different from that at Dzhyrakuduk), Chelonia of the same genera that are at Dzhyrakuduk, one genus of the Crocodylia (different from that at Dzhyrakuduk), Dinosauria (Hadrosauridae, Tyrannosauridae, etc.). Coll. no. LU-N 9/496. Collected in 1982.

The material consists of isolated and fragmentary skeletal elements; complete bones are very scarce. On the average, the richest sites yielded one anuran per 100–600 kg of sediment. All sites are in arid areas, with scarce vegetation, which allows intensive wind corrasion. Sandstones containing animal remains are considerably friable due to small clay content and absence of calcium-carbonate cement (this is associated with the semihumid climate of the Albian to Coniacian in the region and slightly acidic conditions in the course of deposition of the sediments). Wind corrasion causes sand grains to be blown away, whereas larger inclusions such as bones, teeth, sandy and siltstone nodules, Fe concretions, and pebbles of light aleurolites and clays stay essentially in place, concentrate, and form the surface layer. If such inclusions are not numerous in the sandstone (i. e. they do not protect the surface as in stone desert or in hammada and thus do not prevent further corrasion), the final concentration of bone, teeth, coprolites, gastrolites, etc. on the surface may become several times higher than the original concentration within the layer. Dry screening of matrix located below patches of the highest surface concentration of vertebrate remains yielded the best material.

As a rule, anuran remains are found together with those of the Lepidotidae (known in the region from the Aptian to Cenomanian), Lepisosteidae (late Turonian to Coniacian), and other 'ganoid' fishes (Santonian to early Campanian), which are characteristic of brackish and fresh waters. Even better chances of finding anurans are at sites that yield amiid remains, which are characteristic of standing, calm waters. At several dozen Cretaceous localities where anurans and salamandrids have been found together, remains of the latter group are several times more numerous. This allows to use them as an indicator of the potential for finding anurans.

As to the depositional environment in which Cretaceous anurans of central Asia have been found, one can say that the principal fossiliferous sediments are sandstones and/or siltstone nodules in sandstones, usually of limnic or tidal marsh origin. The colour of all of them is chiefly greyish yellow or (rarely) pink. If they are of Albian to Coniacian age, they as a rule do not contain calcium-carbonate cement, but in those of Santonian to early Campanian age some amount of such cement is rather usual. Anuran bones are mainly found in lenticular sandstone bodies, that are almost entirely devoid of clay and aleurite particles. Almost all mollusc shells in these sandstones are usually dissolved (only sandy fillings and rare phosphatized mantle, leg, and gill remains are preserved). The sandstone lenses are usually more-or-less cut into the basement (Text-fig. 2C), or form a loose basement cover (Text-fig. 2 D). Laterally, they finger out at a short distance. Their width varies from several meters to tens or several hundred meters, and their length attains probably several hundred meters (it is difficult to follow them along their long axis at outcrops). Where these fossiliferous layers are cut into the basement, they are more-or-less of symmetrical cross-section. Several such lenses may be superposed, resulting in a complex surrounded by rocks in which vertebrate fossils are rare.

Beside bone, these sandstone lenses and tongues contain teeth and calcified cartilage, a great amount of phosphatic fish and crustacean coprolites, blobs of hard and phosphatized clay with fragments of plant detritus, and three-dimensionally preserved insects and crayfishes (in which chitin is completely replaced by calcium phosphate). At some sites (especially at Dzhyrakuduk) one can find even the above noted soft parts of bivalves, and insect eggs in fissures of the fossil wood.

Characteristic for occurrences of Cretaceous anurans in central Asia is that they are always accompanied by salamanders (which dominate) and by teeth of euryhaline sharks and rays, as well as brackish-water osteichthyans (strictly marine fishes are not common). Vertebrate remains within the lens-like bodies are usually not accumulated in layers and are not sorted by size. This suggests that the fossiliferous sandstones, judging by their structure, were deposited rather quickly.

The total number of the specimens is 496 (including e. g. parts of the braincase, urostyles, maxillaries, and squamosals), however, a considerable number of them (mainly fragments of long bones) bear no diagnostic characters and are thus indeterminate. Bones were assembled taxonomically on such features as morphology, sculpture, size, and stratigraphy. As a basis for systematic assignment were taken the maxillaries because they were the most numerous in the material, and at the same time they best (in the material available) reflect taxonomic differences.

Taphonomy

The large amount of phosphatized animal remains and the presence of phosphate clay indicate high concentration of phosphate ions in the water of the reservoirs, or at least in the water content of the sediment. Phosphates were permanently concentrated due to their removal from biotic circulation. This in turn caused favourable life conditions for organisms with phosphatic skeletons, as well as conditions for formation of new phosphatic coprolites. Ecosystems that included anurans were apparently open to a considerable degree. Influx of phosphates into such ecosystems (judging from composition of vertebrate fauna) took place in the course of upwelling that was caused by the estuary-type water circulation (SHOPF 1982). This upwelling was stronger in the Albian to Coniacian and became much less pronounced in the Santonian to early Campanian.

A considerable amount of phosphates and phosphate ions near the bottom of the water column and especially in the solutions that filled the sediments, and the buffering action of the phosphate ions in these solutions, ensured preservation of tiny morphological details on the phosphatized anuran remains against dissolution by organic and inorganic acids that circulated freely through the sand. This contrasts with the type of fossilization of amphibian bones in loams, where they are protected against chemically aggressive solutions by means of isolation afforded by small loam particles. If the above mentioned chemical condition (the buffering action of phosphate ions) is taken into account, the oryctocoenosis of phosphatized remains might be similar to taphocoenosis (i.e. there was no chemical decomposition in the course of diagenesis). The acidity of waters within the deposits, no doubt, reached high levels, which is evidenced by the complete dissolution of calcium-carbonate shells at most of the noted localities and by either total absence or only a very low content of calcium-carbonate cement in not just certain strata but whole units containing vertebrate-bearing horizons.

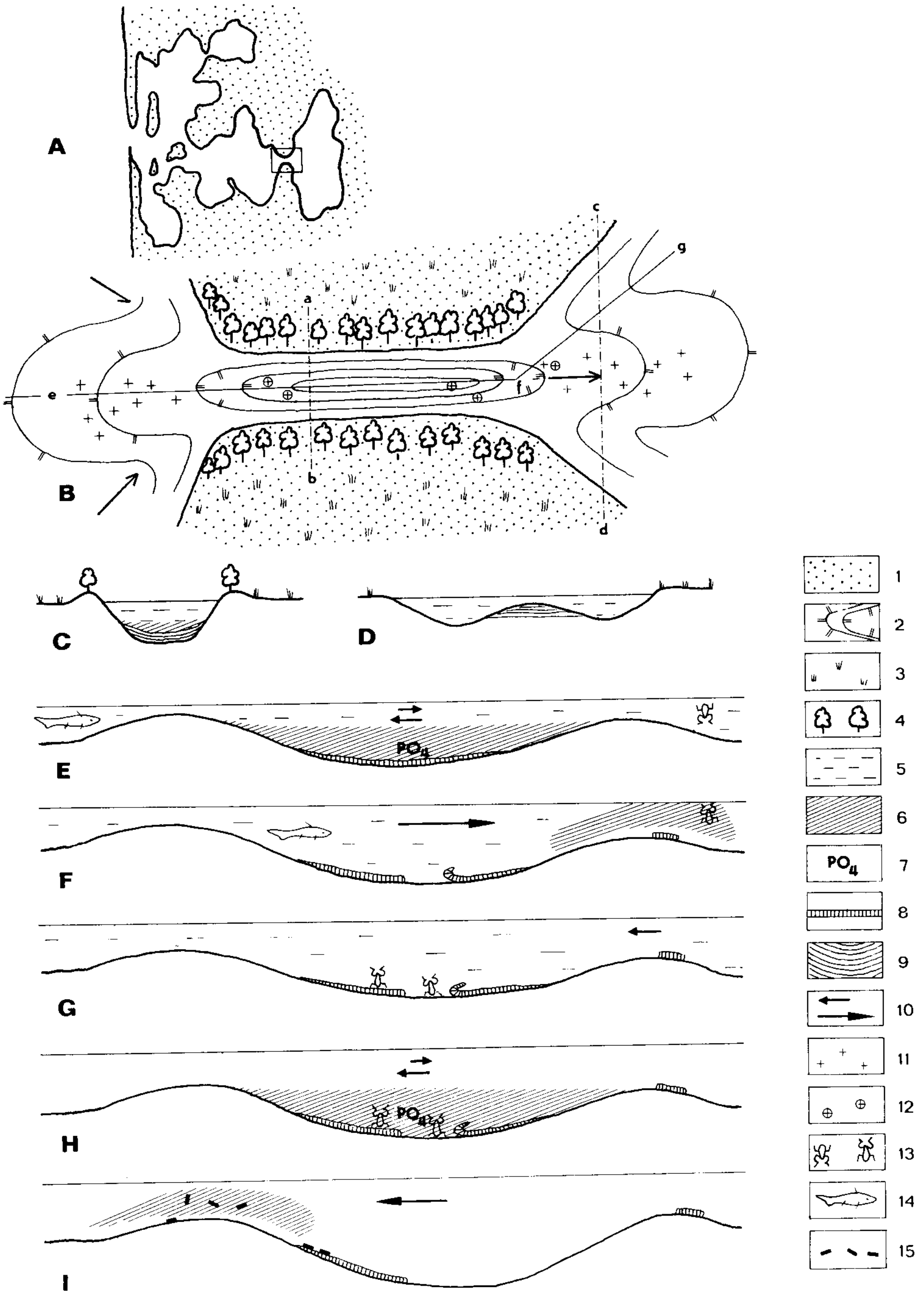
Analysis of geological, taphonomical, autecological, and biogeocoenotic data derived from the Cretaceous anurans and other vertebrates found at our localities (see Text-fig. 1) suggests the presence of channels (Text-fig. 2 B) connecting large basins that presumably were of complex shapes (Text-fig. 2 A). One may also assume differences in salinity of the neighbouring basins, the degree in either basin having been different from the normal fresh and marine waters. Winds blowing mostly along the long axis of a channel caused an inflow-outflow effect so that water level in both basins alternately fluctuated. The difference between water levels on opposite sides of the system was dependent on atmospheric pressure, speed of atmospheric low-pressure displacements, size and depth of the basins, shape of the coastline, shape of the bottom, presence and location of islands, etc. According to observations made by one of us (L. A. N.), the inflow-outflow effect in deep channels that connect shallow Khanka and Lebekhe Lakes (Far East of Siberia) results in a difference of water level reaching 1m, and the velocity of water flow in the axial part of the channels can reach ca. 2 m per second. Another example is the shallow eastern part of the Finnish Bay in the Baltic Sea, where sea-level fluctuations exceed 2 m.

If such channels were relatively short (up to several hundred meters, which is estimated for one channel at Dzhyrakuduk) and inflows and outflows were fast, the channels became deeper than the adjacent basins. Consequently, they were the deepest part of the system (Text-figs. 2 B, C). Similar morphology of the bottom may be observed in the Khanka Lake system.

In the SW and central Kizylkum Desert such channels were oriented, judging from the channel deposits, from NE to SW or from ENE to WSW, i.e. approximately perpendicular to the ancient sea shore. In the NW and SW Fergana, as well as in the NE Aral Sea region, the principal direction of the paleochannels was from N to S. One would assume that, owing to the Earth's rotation, water flow in such channels should cut their right bank and bar deposits should accumulate along the opposite bank. However, because wind causes one-way movement of water and after it ceases to blow water flows back due to gravitation, the resulting erosion (and deposition) affecting both banks is approximately even. As a result, such a N to S-oriented channel, in contrast to a similarly directed river, does not display unilateral deposition. At the same time, back-and-forth flows (both approximately the even) suppress the formation of meanders.

Channels that exhibit this behaviour produce deposits whose cross-section is usually bilaterally symmetrical (Text-fig. 2 C). Similar may be deltaic deposits that are, however, usually more or less asymmetrical due to uneven back-and-forth flows which cause scour of deposits and subsequent formation of meanders.

In the moderate-wind periods of the year (most likely these were the warmest seasons) one should assume some stratification of water in such interbasin channels (Text-fig. 2 E). The upper layers could have been rather warm, with moving water and normal oxygen content. In contrast, the deep-water layers could have been cold, with temperatures corresponding to those of the surface layers during the coldest season, or even lower, and immobile. The immobility of deep water was caused by its isolation from the upper layers. Plant and animal remains in the form of detritus were transported into the shallow basins via the deeper channels and partly accumulated there. The accumulation of organic detritus, weak exchange between the deep and surface waters, and oxidation of organic matter have resulted in a lower oxygen content and sometimes in the presence of hydrogen sulphide in the deep layers. Under such conditions phosphate ions could migrate, partly also into the deposits, so giving rise to greasy and sticky phosphate clay which is often found as fossilized (i. e. hard) small lumps, layers, or crust on the larger vertebrate remains.



Peculiar situation developed in the channel and its vicinity as a result of the first strong inflow after a long period of stable weather with zero or only weak wind (Text-fig. 2 F). Because of this current, bottom layers of cold, oxygen-deprived water moved from the deep channel into the shallow basin with warm water. Thermophilous and especially gill- and skin-respirating organisms undoubtedly died of thermal shock and the sudden decrease in oxygen content of the water. In such situations, soft parts of invertebrates could have been quickly phosphatized (Martinson et al. 1986); this phosphatization was favourably influenced by lower solubility of calcium compounds at higher temperatures.

As W, SW, and S from today's Kizylkum Desert, Fergana, and NE Aral Sea region was a sea with normal salinity in the Cretaceous (Sinitsyn 1966), the movement of relatively salty water from the sea towards limans (and farther into their fresh-water bays and adjacent marshes) no doubt caused very unfavourable conditions even for those animals that usually do not suffer much from limited increase of salinity, e. g. amphibians. Subsequent drop in water level caused transport and partial capture of amphibian remains in the deep channels between basins (Text-fig. 2 G).

During heavy rainstorms that caused movement of fresh or brackish water in the channels toward the sea, and also during strong winds that suddenly moved the deep, cold, and hypoxidized water from the channels into the more salty, larger but shallower basins, sharks, rays, and actinopterygians which normally inhabit relatively salty water (Albulidae, Aspidorhynchiformes, etc.) or which are thermophilous, could not survive. If after reversal of the current conditions were favourable, their bodies accumulated in the deep channels similarly to amphibians. Following strong inflow-outflow currents, bodies of various vertebrates rose to the surface and were thrown on the banks where they attracted birds, pterosaurs, carnivorous deltatheriids, mammals, and large numbers of insects which in turn attracted insectivorous lizards, small proteutherian mammals, and anurans. Further strong inflow-outflow currents could have caused the death of all these animals, with subsequent accumulation of their remains in the limited area of channel deposits.

This may explain the accumulations of Cretaceous anurans in central Asia (Nessov 1981, Nessov & Udovichenko 1986, Nessov 1988 a), which are part of rather unusual oryctocomplexes. These assemblages consist of a considerable number of brackish-water and marine sharks and rays (Hybodontidae, Sclerorhynchidae, Hypolophidae, some Scapanorhynchidae, and many others; total of 12–20 genera), as well as of typically fresh-water organisms (amphibians, some teleosts, and abundant amiids, gars, and other 'ganoid' coastal fishes). This composition indicates situations that were lethal for marine, brackish- and fresh-water animals, and to some extent also for terrestrial ones.

Strong current in the channel, the cause of which was the inflow-outflow phenomenon, did not affect only living organisms but also caused transposition of macerated and disarticulated remains of anurans and other vertebrates accumulated on the bottom of deeper channels into the adjacent parts of shallow basins. These areas of final burial of the remains were situated on the main axis of the channel, close to both ends (Text-fig. 2 B).

Text-fig. 2. Possible model of inter-basin channel on the basis of which it might be possible to explain assemblages of fresh-water, brackish-water, and marine vertebrates mentioned in the list of the localities (see chapter Material and Methods). A – Position of the inter-basin channel in the hypothetical continental bay. B – The channel with the adjacent parts of basins and dry land. Lines of equal depth mark the shape of bottom. C – Section through the channel marked by line a–b in B. D – Section through that part of the basin which is adjacent to the channel, marked by the line c–d in B. E – Section through the channel and the adjacent part of the basins (in the condition not affected by strong winds), marked by the line e–f–g in B. F – Dying of some aquatic amphibians caused by invasion of cold water with low oxygen and some hydrogen sulphide content, as well as by increase of salinity in the basin and adjacent marshes. G – Accumulation of amphibian remains in the deep parts of the channel, and their subsequent disarticulation. H – Re-establishing of the stratification similar to that in E. I – Rapid transposition of the disarticulated amphibian and other vertebrate remains from the channel to the adjacent shallows, due to the strong inflow and outflow currents. Explanations: 1 – dry land; 2 – lines of equal depth; 3 – marshes; 4 – trees on the cheniers; 5 – water with rather high oxygen content; 6 – water with low oxygen and possibly some hydrogen sulphide content; 7 – presence of phosphate ions, concentration of which is mainly due to their import from deeper and larger neighbouring basins with higher salinity, and due to biogenetic concentration; 8 – bottom clay and aleurite with high content of phosphate ions; 9 – deposits formed by sedimentation in the course of subsidency of the depositional area (see C) and by transportation of channel deposits in the neighbouring part of the basin (see D); 10 – stream directions (size of arrows indicates their velocity); 11 – area of prevailing accumulation of tiny vertebrate remains; 12 – area of accumulation of large vertebrate remains; 13 – anurans and other fresh-water animals (living are on the left, dead ones on the right); 14 – sharks of the families Hybodontidae and Polyacrododontidae, and other brackish water and marine animals; 15 – disarticulated vertebrate remains.

As the hitherto known central Asian localities of Cretaceous anurans in Kazakhstan and Uzbekistan lie in areas that underwent compensational sinking, some of the channel deposits are arranged in multi-story complexes. Among other things, they can be regarded as evidence of relative positional stability of such channels in the course of time.

Many channel deposits of Devonian age in the Baltic states, St. Petersburgh District, and Spitsbergen, of Late Permian and Triassic age in the Ural region (e.g. EFREMOV 1950), of Middle and Late Jurassic age in Kirghizia, and of Cretaceous age in central Asia, Kazakhstan, Mongolia, China, Canada, and USA (see e.g. KOSTER 1987, BEHRENSMEYER 1988) that are characterized by symmetrical cross-sections, and presence of both fresh-water, brackish water, and some marine animals, could have arisen in a similar way. If so, they should not be termed 'deltaic deposits'.

Systematic Part

Anura RAFINESQUE, 1815

Gobiatidae fam. n.

Genus typicus: *Gobiates* ŠPINAR et TATARINOV, 1986

Diagnosis: Vertebral centra amphicoelous, with or without notochordal canal. Neural arches may or may not roof neural canal dorsally; if they join one another, they are imbricate. Articulation between sacrum and urostyle bicondylar. Free ribs (at least on the 2nd and 3rd vertebrae). Sacral vertebra with scarcely expanded transverse processes.*) Frontoparietal paired. Maxillae and praemaxillae dentate. Quadratojugal present. Epicondylus lateralis humeri absent, fossa cubitalis ventralis basically triangular in shape. Crista femoris prominent, close to proximal end of bone; it recalls more *Ascaphus* than any other of contemporary discoglossids.

Remark: Since all urostyles in the material bear proximally one or two pairs of transverse processes, it may be assumed that some of them belong to *Gobiates* or *Gobiatoides* gen. n. and, consequently, that this character (presence of at least one pair of transverse processes on the urostyle) may be included among those that are important for the diagnosis of the family. However, this can be confirmed only by finding a complete vertebral column.

Relations to other families: Gobiatidae agree with Leiopelmatidae in having amphicoelous centra, sometimes with notochordal canal (ectochordal vertebrae sensu GRIFFITHS 1963). They share with the Discoglossidae imbricate neural arches and bicondylar articulation between the sacrum and urostyle. The following characters are shared with either of these two families – free ribs, paired frontoparietal, tooth-bearing maxillae and praemaxillae, and most probably urostyl with at least one pair of transverse processes proximally. The characters shared with neither family are narrow sacral diapophyses (however, see the footnote above), and absence of the lateral epicondylus on the humerus. It is obvious that Gobiatidae display characters typical for both Leiopelmatidae and Discoglossidae. Possible phylogenetic relations of all the three groups are briefly discussed below (see chap. Discussion). They differ from all other families in having a complex of these characters: amphicoelous centra, sometimes with a notochordal canal, scarcely expanded sacral diapophyses, and probably at least one pair of transverse processes proximally on the urostyle.

Genus *Gobiates* ŠPINAR & TATARINOV, 1986

1978 *Eopelobates* – BORSUK-BIAŁYNICKA, p. 58
1981 *Eopelobates* – NESSOV, p. 71
1981 Hitherto undescribed form from Mongolia – ROČEK, p. 117
1986 *Gobiates* ŠPINAR & TATARINOV, 1986 – ŠPINAR & TATARINOV, p. 114

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*) However, as indicated by a hitherto undescribed anuran from the Late Cretaceous of the Gobi Desert (Text-fig. 18 A, F, G), with amphicoelous vertebrae and all other diagnostic features of the Gobiatidae (except for expanded sacral diapophyses), the sacral diapophyses might also be expanded similarly to the Discoglossidae (if it would turn out that this anuran belongs to the Gobiatidae; its taxonomic status is currently being studied by Z. V. ŠPINAR and L. P. TATARINOV).

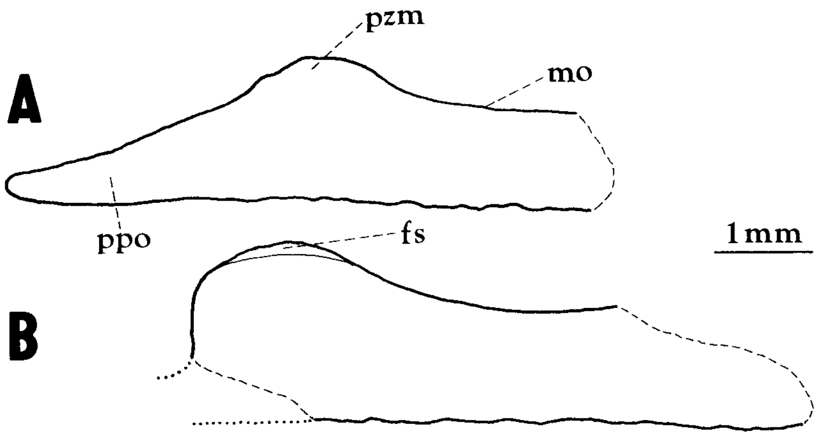
Species typica: *Gobiates sosedkoi* (NESSOV 1981).

Diagnosis (after ŠPINAR & TATARINOV 1986, amended): Irregular pit-and-ridge sculpture on frontoparietals, squamosals, maxillae, and nasals. Maxillary with only moderately concave margo orbitalis. Proc. zygomaticus squamosi not continued anteriorly by flange for articulation with pterygoid. Lamella alaris squamosi delimited from proc. posterolateralis by an elevated ridge, and not meeting frontoparietal. Frontoparietals paired, with a fontanelle between their anterior sections. Vertebrae amphicoelous, sometimes with preserved notochordal canal.

Remark: Early Cretaceous (Comanchean) material of maxillae described by WINKLER et al. (1990: 105, fig. 7C), namely SMU 72156 and 72168-72170, most probably belongs to *Gobiates*. This can be inferred from the presence of pitted sculpture and morphology of the medial surface of the bone.

Geological age: ?Early Cretaceous (Comanchean) to Late Cretaceous (Coniacian).

Geographical distribution: Central Asia, ?North America.



Text-fig. 3. *Gobiates*, right maxillaries in outer iew. A – *Gobiates bogatchovi* sp.n., holotype (LU-N 5/107; see also Pl. 1, fig. 2). B – *Gobiates dzhyrakudukensis* sp.n.; holotype (LU-N 6/341; see also Text.fig. 4; Pl. 1, fig. 3).

Gobiates sosedkoi (NESSOV, 1981)

1981 *Eopelobates sosedkoi* NESSOV, p. 71
1986 *Gobiates khermeentsavi* ŠPINAR & TATARINOV, p. 114.

Holotypus: ZIN, PHA No K77-5, collections of the Department of Herpetology, Zoological Institute of the Russian Academy of Sciences, St. Petersburgh. Posterior part of the right frontoparietal. Figured in NESSOV 1981, pl. XII, fig. 14, and in NESSOV 1988, pl. XIV, fig. 1.

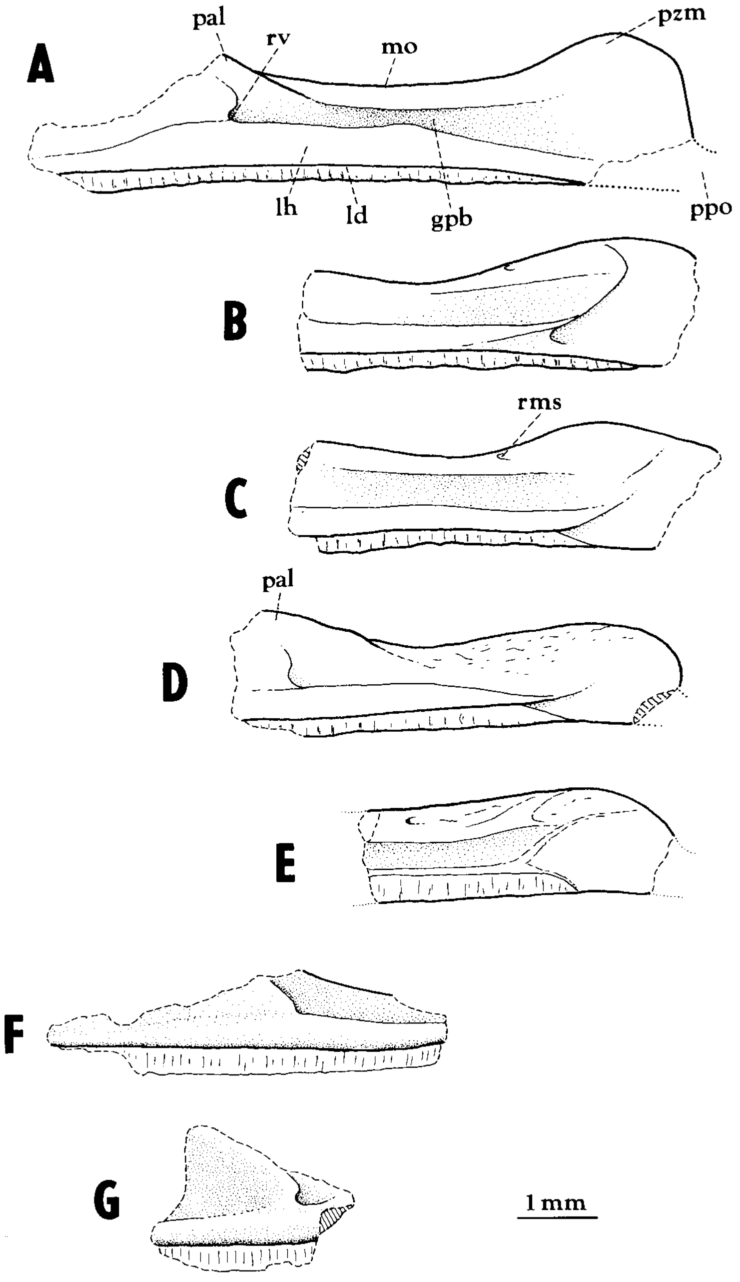
Locus typicus: Dzhyrakuduk (CBI-4v), central Kizylkum Desert, Uzbekistan.

Stratum typicum: Coniacian, middle part of the Bissekty Formation.

Diagnosis (Špinar & TATARINOV 1986, amended): Maxillo-squamosal suture comparatively short (ratio between maximum antero-posterior length of lamella alaris and length of the suture is 3.3); perpendicular line constructed from posterior end of maxillo-squamosal suture cuts dorsal margin of the lamella alaris anterior to its proc. dorsalis.

Geographical occurrence: Kizylkum and Gobi Deserts, Asia.

Remark: *Gobiates 'khermeentsavi'* is considered conspecific with *G. sosedkoi* because of (a) same shape of the posterolateral part of the frontoparietal, (b) same type of conspicuously pitted sculpture in the holotype of *G. sosedkoi* (frontoparietal) and the maxillary of the holotype of *G. 'khermeentsavi'*; although the sculpture of the frontoparietal in both type specimens is slightly different, certain variation of this character is to be expected (compare e. g. the sculpture of the frontoparietal, maxillary, and squamosal in the holotype of *G. 'khermeentsavi'*; ŠPINAR & TATARINOV 1986, fig. 3 A, B). However, it should be noted that present authors did not come to an unequivocal concensus in this respect, and that conspecifity of both forms is accepted only by one of them (Z.R.).



Text-fig. 4. *Gobiates*, right maxillaries in inner view. A – *Gobiates dzhyrakudukensis* sp. n. Composite reconstruction on the basis of LU-N 6/341 and 5/140. B – *Gobiates fritschi* sp. n., holotype (LU-N 5/143 – see also Pl. 1, fig. 7). C – *Gobiates tatarinovi* sp. n., holotype (LU-N 6/405 – see also Pl. 1, fig. 5). D – *Gobiates* cf. *G. sosedkoi* (NESSOV, 1981) (LU-N 5/129 – see also Pl. 1, fig. 1). E – *Gobiates furcatus* sp. n. , holotype (LU-N 5/165; reversed for comparison). F – cf. *Gobiates* (LU-N 5/145). Middle section of the bone. G – cf. *Gobiates* (LU-N 8/472). Middle section of the bone.

Gobiates cf. *G. sosedkoi* (NESSOV, 1981)

(Text-figs. 4 D, 5 G; Pl. 1, fig. 1)

Material: Maxillary LU-N5/129 (Text-fig. 4 D; Pl. I, fig. 1); squamosal LU-N5/111 (Text-fig. 5 G).

Description: Maxillary dentate, with the sculpture on the outer surface consisting of shallow pits separated by rounded ridges (the nature of sculpture is the only difference from the holotype of *G. sosedkoi*, the sculpture of which is conspicuously pitted). The proc. zygomaticomaxillaris only vaguely discernible above the level of the lowermost part of the margo orbitalis, however, its posterior margin is rather steep. The proc. postorbitalis is broken off but it is obvious that its proximal section was slender. The surface of the margo orbitalis is rough, the rugosity spreading also onto the inner surface of the bone. Hence, there is no distinct ridge parallel to the margo orbitalis on the inner surface of the bone. The lamina horizontalis has a broadly rounded margin in its section underneath the anterior limit of the orbit, however, it is tapering posteriorly and thus becoming sharp at its margin. Its posterior termination is rather abrupt because it disappears short distance after it turns posterodorsally. There is a shallow but distinct indentation in the groove, for the cartilaginous proc. maxillaris anterior, termed the recessus vaginiformis (sensu GAUPP 1896: 51). The posterior termination of the tooth row is approximately at the level where the lamina horizontalis turns posterodorsally.

The lamella alaris squamosi bears pit-and-ridge sculpture on its outer surface. The contact facet of the processus zygomaticus was straight, so that contact surfaces of the squamosal-maxillary suture well correspond with one another. Also the margo orbitalis squamosi is confluent with that of the maxillary. It should be noted that the squamosal is displaced relative to the maxilla and partly embedded into matrix in the specimen PIN 31/42/2 described by ŠPINAR & TATARINOV (1986). Moreover, it is better illustrated in their figs. 1 C and 2 A than in fig. 3 B. The inner surface of the lamella is smooth (except for the ramus paroticus that adjoined the crista parotica, and the proximal part of the proc. posterolateralis that are, however, both damaged, so that their original extent cannot be estimated).

Gobiates bogatchovi sp. n.

(Text-fig.3 A; Pl.1, fig.2)

Holotypus: Posterior part of the maxillary and praearticular, with quadratojugal-quadrate complex and pterygoid (the latter without its ramus interior), all bones more or less articulated. LU-N5/107 (Text-fig. 3 A; Pl. 1, fig. 2).

Locus typicus: Dzhyrakuduk, CBI-4b.

Stratum typicum: Late Cretaceous, Coniacian, middle part of the Bissekty Formation.

Derivatio nominis: In honour of V. V. BOGATCHOV, pioneer in search and study of fossil anurans in the Russia.

Diagnosis: Proc. zygomaticomaxillaris maxillae distinct, therefore margo orbitalis moderately concave. Quadratojugal and quadrate fused. Tooth row exceeds the level of the posterior end of the lamina horizontalis.

Material: Posterior section of the maxillary, LU-N4/48.

Description: Maxillary dentate, with prominent though rounded proc. zygomaticomaxillaris; consequently, the margo orbitalis is moderately concave. The processus postorbitalis is long, gradually tapering posteriorly. The outer surface of the bone is covered by a pit-like sculpture which is absent on the distal part of the proc. postorbitalis. Although the margo orbitalis is rather sharp, it is paralleled on the inner surface by a distinct mound. The medial margin of the lamina horizontalis is similarly rounded, and the lamina itself is similarly prominent; consequently both structures delimit a distinct groove for cartilaginous palatoquadrate bar at the section adjacent to the orbit, the width of which approximately equals that of both mounds. The posterior termination of the lamina horizontalis cannot be observed in the type specimen because it is obscured by the articulated ramus maxillaris pterygoidei. As the latter process is flattened and fixed to the medial surface of the maxillary obliquely (not horizontally), one may suppose that the posterior termination of the lamina is shaped correspondingly.

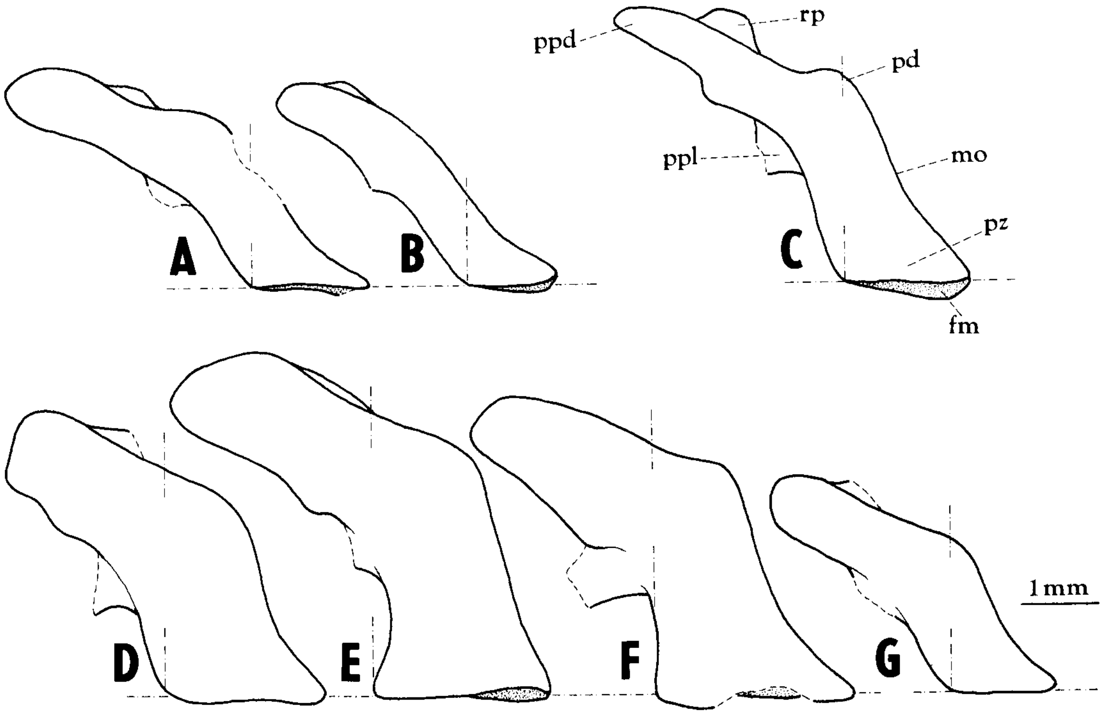
The pterygoid has a moderately convex and ventrally turned margin between its ramus maxillaris and ramus posterior (termed the margo mandibularis). The canal for the palatoquadrate bar is manifested on the ventromedial surface of the ramus maxillaris by a rounded ridge. The compressed anterior margin of this ramus is directed posterodorsally from the orifice of the mentioned canal, parallel to the anterior margin of the proc. zygomaticomaxillaris maxillae.

The quadratojugal and quadrate are fused with each other, the former as comparatively short rod attached to the maxillary by an oblique suture, the latter as transverse element with distinctly concave articular facet for the lower jaw. The tip of the proc. posterolateralis squamosi is present though slightly displaced from its original position, however, bearing no diagnostic features.

The posterior part of the praearticular is slightly displaced medially. It is only moderately S-shaped, if viewed in ventral aspect.

The maxilla LU-N4-48 (its preserved posterior part) recalls morphologically that of the holotype, however, it is of Late Turonian age. Its lamina horizontalis is gradually lowering posteriorly, and continues as a very indistinct ridge posterodorsally on the inner surface of the bone. No doubt this ridge indicates an articulation with the pterygoid.

Geological age: ? Late Turonian – Coniacian.
Geographical distribution: Central Asia.



Text-fig. 5. *Gobiates*, lamellae alares squamosi in outer view. A, B – *Gobiates asiaticus* sp. n. (LU-N 6/370, holotype – see also Pl. 5, fig. 5; 5/125 – see also Pl. 5, fig. 1). C – *Gobiates kizylkumensis* sp. n., holotype (LU-N 6/363 – see also Pl. 5, fig. 4). D–F – *Gobiates spinari* sp. n. (LU-N 5/139, 5/178, 5/137, holotype). G – *Gobiates* cf. *G. sosedkoi* (LU-N 5/111 – see also Pl. 5, fig. 2). Horizontal and vertical lines show proportions of the lamella. E and F reversed for comparison.

Gobiates dzhyrakudukensis sp. n.

(Text-figs. 3 B, 4 A; Pl. 1, figs. 3, 4)

Holotypus: Posterior part of the maxillary with the proc. postorbitalis broken off. LU-N6/341 (Text-fig. 3 B, Pl. 1, fig. 3).
Paratypoid: LU-N6/357; 5/140.
Locus typicus: Dzhyrakuduk, CBI-14.
Stratum typicum: Upper Cretaceous, Coniacian, middle part of the Bissekty Formation.
Derivatio nominis: After the name of the excavation site.

Diagnosis: Posterior margin of proc. zygomaticomaxillaris maxillae vertical; margo orbitalis maxillae paralleled on inner surface of bone by a ridge which is much less developed than lamina horizontalis; tooth row terminates at level of posterior end of lamina horizontalis.

Description: Maxillary toothed, with pit-like sculpture on its outer surface. The sculpture is more pronounced posteriorly than anteriorly. The proc. zygomaticomaxillaris moderately prominent, with its posterior margin vertical; consequently, the proc. postorbitalis is slender and its dorsal margin is not a straight continuation of that in proc. zygomaticus squamosi. The margo orbitalis is slightly concave, delimited by rounded ridges both externally and internally. The surface between both ridges is almost flat, slanting medially. In the lowermost section of the surface there is a foramen for a branch of the r. maxillaris superior; after passing a short distance in the bone the nerve appears on its outer surface as the r. cutaneus maxillaris. The outer orifice of this canal is in the bottom of one pit of the described sculpture. The lamina horizontalis, if compared with the ridge delimiting medially the margo orbitalis, is much more robust, rounded, and its medial margin is within a short section bent dorsally. Consequently, the groove for the palatoquadrate bar is deep and partly closed. The lamina horizontalis gradually disappears posteriorly, similarly to the tooth row; both terminate approximately at the same level. The recessus vaginiformis is well developed.

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.

Gobiates fritschi sp. n.

(Text-fig. 4 B; Pl. 1, fig. 7)

Holotypus: Posterior part of the right maxillary, with the proc. postorbitalis and posterior part of the proc. zygomaticomaxillaris broken off. LU-N5/143 (Text-fig. 4 B; Pl. 1, fig. 7).
Locus typicus: Dzhyrakuduk, CBI-4b.
Stratum typicum: Upper Cretaceous, Coniacian, middle part of Bissekty Formation.
Derivatio nominis: In honour of ANTONÍN FRIČ, a Czech paleontologist from the end of nineteenth century.

Diagnosis: Tooth row exceeds level where lamina horizontalis turns posterodorsally; edge for articulation with r. maxillaris pterygoidei very distinct.

Description: Maxillary dentate, the sculpture regularly pitted on the whole preserved outer surface of the bone. The proc. zygomaticomaxillaris only moderately prominent. On its upper margin is a groove-like facet for the lamella alaris squamosi. The margo orbitalis is broad and smooth in dorsal view, rather rounded in cross-section. The inner orifice of the canal for a branch of the r. maxillaris superior is large and situated in the posterior part of the margo orbitalis. The outer orifice of the canal is large too, located close below the margo. The lamina horizontalis is much more prominent than the inner margin of the margo orbitalis which is indistinct and rounded. Consequently, the groove for the palatoquadrate bar is shallow and wide, open. Posteriorly, the lamina is gradually tapering and turning posterodorsally towards the top of the proc. zygomaticomaxillaris, thus limiting posteriorly the mentioned groove. The lamina does not reach the top of the processus but it turns anteriorly, surrounding thus posterior termination of the ridge that is parallel to the margo orbitalis. As that part of the maxillary which is posterior to the mentioned prolongation of the lamina horizontalis is comparatively thin, the lamina borders here a distinct indentation. Its edge served for articulation with the r. maxillaris pterygoidei. The tooth row continues posteriorly behind the level where the lamina horizontalis turns posterodorsally.

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.

Gobiates tatarinovi sp. n.

(Text-fig. 4 C; Pl. 1, figs. 5, 6)

Holotypus: Posterior part of the right maxillary with the proc. postorbitalis broken off. LU-N6/405 (Text-fig. 4 C; Pl. 1, fig. 5).
Locus typicus: Dzhyrakuduk, CBI-14.
Stratum typicum: Upper Cretaceous, Coniacian, middle or upper part of the Bissekty Formation.
Material: Maxillary, LU-N5/124.
Derivatio nominis: After L. P. TATARINOV, co-author of the genus *Gobiates*.

Diagnosis: Ridge for articulation of maxillary with ramus maxillaris pterygoidei gradually lowering and ultimately disappearing; margo orbitalis delimited medially by an edge.

Description: Maxillary dentate, the proc. zygomaticomaxillaris very low and widely convex in lateral view. The sculpture is indistinct, with shallow pits. The margo orbitalis is bordered both medially and in lesser degree also laterally by sharp ridges; its surface is flat and slanting inwards. The lamina horizontalis is well prominent, with rounded margin. The groove for the palatoquadrate between the lamina and the edge delimiting medially the margo orbitalis is deep. The lamina horizontalis turns posterodorsally in its posterior section, gradually lowering and then disappearing. The tooth row terminates posteriorly at about same level where the lamina horizontalis turns posterodorsally. The specimen LU-N5/124 is similar in shape and proportions but is smaller, with only signs of sculpture on its outer surface; besides that, the ridge delimiting medially the margo orbitalis is not as pronounced as is the case with the holotype (consequently, the groove for the palatoquadrate bar is not so deep). These differences may be ascribed to developmental variation.

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.

Gobiates spinari sp. n.

(Text-fig. 5 D–F; Pl. 5, figs. 3, 6, 7)

Holotypus: Left squamosal with the proximal section of the proc. posterolateralis. LU-N5/137 (Text-fig. F; Pl. 5, fig. 7).
Locus typicus: Dzhyrakuduk, CBI-4b.
Stratum typicum: Upper Cretaceous, Coniacian, middle part of the Bissekty Formation.
Material: Left squamosal, LU-N5/178; probably also right squamosal, LU-N5/139.
Derivatio nominis: After Z. V. Špinar, Czech paleoherpetologist and co-author of the genus *Gobiates*.

Diagnosis: Maxillo-squamosal suture straight and comparatively long (ratio between the maximum anterior-posterior length of lamella alaris and the length of the suture is 2.4–2.7); posterior margin of lamella alaris squamosi perpendicular to maxillo-squamosal suture; perpendicular line constructed from the posterior end of maxillo-squamosal suture cuts dorsal margin of lamella alaris posterior to its proc. dorsalis.

Description: The shape of the lamella alaris squamosi may be seen in Text-figs. 5 D–F. Its outer surface is covered by heavy pit-and-ridge sculpture. The proc. dorsalis is well developed, nearly rectangular in shape. The proc. posterodorsalis is rounded, and distinctly bent outside. The ventral margin of the lamella bears a distinct outgrowth posterior to the basis of the proc. posterolateralis. Contact surface with the maxillary is formed by a groove along the whole length of the proc. zygomaticus by means of which it was fixed on the postorbital part of the maxillary. The proximal part of the proc. posterolateralis in the holotype has a rounded ridge running down on its posterolateral surface. Squamosal LU-N5/139 is similar in most characters but differs in not having the proc. posterodorsalis bent outwards.

Remark: It was impossible to associate squamosals of this form with the maxillae of other species of *Gobiates* because of combination of following characters: different shape of the maxillo-squamosal suture, not corresponding shape of the margo orbitalis, and larger size. This is the reason why these squamosals are considered belonging to a separate species, different from those described on the basis of the maxillaries.

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.

Gobiates asiaticus sp. n.

(Text-fig. 5 A, B; Pl. 5, figs. 1, 5)

Holotypus: Lamella alaris of the right squamosal. LU-N6/370 (Text-fig. 5 A; Pl. 5, fig. 5).
Locus typicus: Dzhyrakuduk, CBI-14.
Stratum typicum: Upper Cretaceous, Coniacian, middle part of Bissekty Formation.
Material: Right squamosal, LU-N5/125.

Diagnosis: Differs from all other forms of *Gobiates* by its lamella alaris which is very slender (ratio between its maximum length and the length of the squamoso-maxillar suture is 3.62 and 3.69, respectively). Perpendicular line from the posterior end of the mentioned suture cuts the anterodorsal margin of the lamella anteriorly to the top of the proc. dorsalis.

Description: The lamella alaris squamosi is covered by irregular pit-and-ridge sculpture. The posterior end of the lamella is arch-like. The proc. dorsalis is widely rounded, approximately corresponding to the posteroventral margin of the lamella. This margin does not bear any outgrowth, and does not form any distinct border between the lamella and the proc. posterolateralis. That part of the lamella which is adjacent to the squamoso-maxillar suture is the widest, due to concave margo orbitalis. The contact surface with the maxillary is in the form of a groove widening anteriorly, or flat (LU-N5/125). The margo orbitalis can continue as a rounded ridge on the inner surface of the lamella, parallel to its anterodorsal margin (see Pl. 5, figs. 1 b, 5).

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.

Gobiates kizylkumensis sp. n.

(Text-fig. 5 C, Pl. 5, fig. 4)

Holotypus: Lamella alaris of the right squamosal, LU-N6/363 (Text-fig. 5 C; Pl. 5, fig. 4).
Locus typicus: Dzhyrakuduk, CBI-14.
Stratum typicum: Upper Cretaceous, Coniacian, middle part of Bissekty Formation.
Derivatio nominis: After the name of the region.

Diagnosis: Proc. dorsalis prominent, the posterior moiety of the lamella more slender than the anterior one.

Description: The lamella alaris squamosi is covered by conspicuously pitted to groove-like sculpture. There is no distinct border between the lamella and the proc. posterolateralis. The posterior part of the lamella is comparatively slender, and bears a distinct outgrowth on its lower surface. The proc. dorsalis is prominent, asymmetrical in shape, and moderately bent medially. The contact surface with the maxillary is in the form of a groove, the medial margin of which is more extensive than the lateral one.

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.

Gobiates furcatus sp. n.

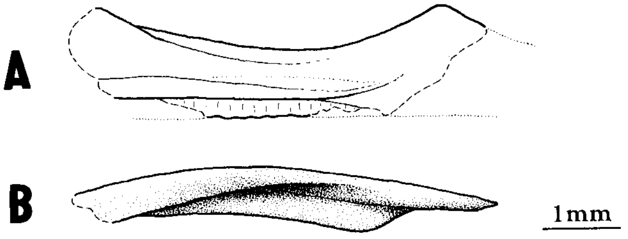
(Text-fig. 4 E; Pl. 1, fig. 11)

Holotypus: Posterior part of the left maxillary, LU-N5/165 (Text-fig. 4 E; Pl. 1, fig. 11).
Locus typicus: Dzhyrakuduk, CBI-4b.
Stratum typicum: Upper Cretaceous, Coniacian, middle part of the Bissekty Formation.
Derivatio nominis: '*furca*' (Lat.) means dichotomically splitted structure; refers to morphology of posterior termination of the lamina horizontalis.

Diagnosis: Lamina horizontalis maxillae thin and narrow; its posterior end bifurcates into two ridges – upper one continues posterodorsally, lower one delimits posterior section of tooth row. Tooth row exceeds posterior end of lamina horizontalis. Mound rimming margo orbitalis on its inner side is wrinkled, similar to inner surface of proc. zygomaticomaxillaris.

Description: The maxillary is dentate and its outer surface is covered by pit-and-ridge sculpture. The margo orbitalis is moderately concave; the proc. zygomaticomaxillaris is widely rounded and indistinctly prominent. The proc. postorbitalis, judging by its base, was thin. The margo orbitalis is paralleled on its inner size by a robust mound which delimits dorsally the groove for the palatoquadrate bar. In contrast to this mound, the lamina horizontalis is very thin and narrow. The mound is considerably wrinkled in the posterior part of the margo orbitalis and on the inner surface of the proc. zygomaticomaxillaris. The lamina horizontalis continues posterodorsally as a ridge that delimits ventrally the mentioned wrinkled area, as well as the groove for the palatoquadrate bar posteriorly. The wrinkled area is no doubt a contact surface for the pterygoid, and the groove on the edge of the proc. zygomaticomaxillaris is a contact facet for the lamella alaris squamosi. The tooth row exceeds the posterior termination of the lamina horizontalis. The orifice of the canal for a branch of the r. maxillaris superior is located on the inner surface of the margo orbitalis.

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.



Text-fig. 6. *Gobiatoides parvus* gen. et sp. n., holotype (LU-N 6/344). Right maxillary in medial (A) and dorsal (B) views (see also Pl. 1, fig. 10).

Gobiates sp.

Praesacral vertebrae

Type I – V3, with the praezygapophysis ground off and with the left transverse process broken off, LU-N6/348 (Text-fig. 7 A; Pl. 3, fig. 2). V6 or V7 (according to the inclination of the transverse process), LU-N5/183 (Text-fig. 7 E). The centrum of V3 is amphicoelous, with a wide notochordal canal. Although praezygapophyses are worn off, and also the posterior margin of the centrum and left transverse process are lacking, it is obvious that both neural arches fail to unify with one another; consequently, the neural canal has no roof. The postzygapophyses are partly preserved on the lower surface of the posterior free ends of the arches. The transverse processes were rather long, inclined slightly posteriorly, with the articular facet for the rib on their ends.

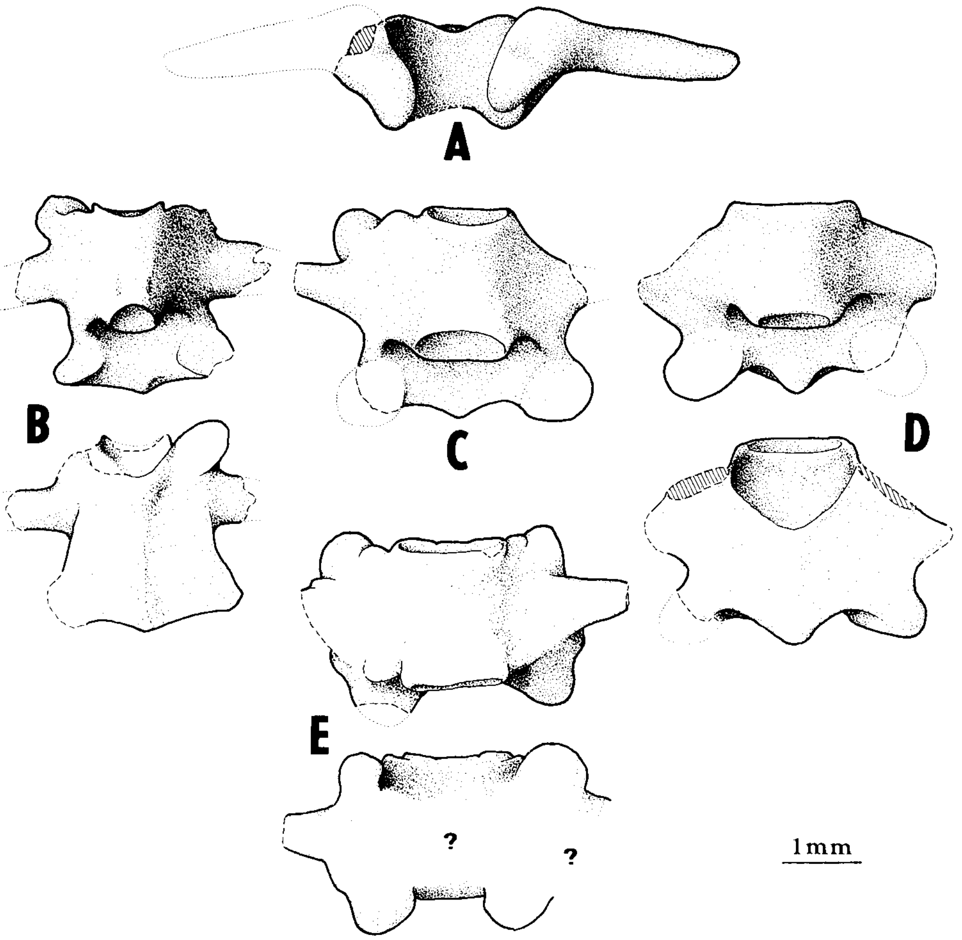
The centrum of the posterior praesacral vertebra is also amphicoelous, and spool-like (it is rather constricted in the middle), however, without notochordal canal. Although this vertebra is partly covered by sediment dorsally (the bone is so fragile that it cannot be cleaned) it is obvious that the neural arches do not join one another and therefore that the neural canal is not roofed dorsally. The distance between the praezygapophyses is longer than that between the postzygapophyses. This vertebra might be associated with the previous one on the basis of both their morphology and size; the absence of a notochordal canal can be dependent on the degree of development.

Type II – V3 or V4 (according to inclination of proximal section of the transverse process), LU-N5/239 (Text-fig. 7 B; Pl. 3, fig. 3). Centrum amphicoelous, with a narrow notochordal canal. Margins of both articular facets of the centrum are deeply concave in ventral view. The transverse processes seem to be slightly inclined posteriorly. The neural arches are imbricate, considerably exceeding the posterior extent of the centrum. Consequently, the vertebra is rather long. In dorsal view, there is a distinct ridge in the midline, confluent with a mound rimming the neural canal anteriorly. Posteriorly, it runs out in a blunt point. Both lateral margins diverge posteriorly, towards the zygapophyses.

Sacral vertebrae

Type I - LU-N5/191 (Text-fig. 14 A, Pl. 3, fig. 9). In ventral view, the centrum is posteriorly about twice as broad as anteriorly. The condyli are big and separated by a notch. Anteriorly, the centrum is concave. The neural canal is eliptical in shape, compressed dorso-ventrally. In dorsal view, the neural arches produce a rounded bump with ridges running anteriorly and posteriorly, as well as laterally. The antero-posterior diameter of the neural arches is shorter than that of the centrum; hence, the vertebrae are supposed to be non-imbricate. On the anterior margin of the proximal section of the proc. transversus is a sign of an outgrowth (similar to that in the sacral vertebra type II; see below).

Type II - LU-N5/246 (Text-fig. 14 B; Pl. 3, fig. 10). The centrum is moderately broadened posteriorly. The condyli are separated from one another by a deep notch. Anteriorly, the centrum is concave. Both neural arches produce a moderately developed proc. spinosus which has a shape of median ridge. The arches are thin both



Text-fig. 7. Praesacral vertebrae. A, B *Gobiates* sp. A – LU-N 6/348 (dorsal view; see also Pl. 3, fig. 2). B – LU-N 5/239 (ventral view above, dorsal view below; see also Pl. 3, fig. 3). C, D Gobiatidae indet. C – LU-N 5/231 (ventral view; see also Pl. 3, fig. 8). D – LU-N 5/201 (see also Pl. 3, fig. 4). E – *Gobiates* sp. , LU-N 5/183 (D and E ventral view above, dorsal view below; question marks indicate parts covered by matrix).

anteriorly and posteriorly (this is the main difference between the types I and II). However, in the middle of their antero-posterior diameter there is a robust mound running posterolaterally, representing distally the thickened part of the proc. transversus. On the anterior margin of the proximal section of the process (above the lateral wall of the neural canal) there is a pointed outgrowth directed anterodorsally. Medial to this outgrowth is a conspicuous depression. The distal section of the transverse process is moderately dilated and rounded on cross-section. There is a longitudinal groove on its dorsal surface.

Remark: Praesacral vertebrae are referred to *Gobiates* because of amphicoely and the presence of a notochordal canal (see Špinar & Tatarinov, 1986: 118, fig. 3 D), sacral vertebrae after the fact that they may be associated with amphicoelous ones, and because their morphology corresponds to that in praesacrals.

cf. *Gobiates*

Material: Fragment of the right maxillary, LU-N5/145 (Text-fig. 4 F).

Description: The maxillary is dentate, with faint pit-and-ridge sculpture on its outer surface. The lamina horizontalis is widely rounded, thinner along its attachment to the vertical part of the bone. It is not well delimited dorsally in its section anterior to the level of the recessus vaginiformis. The recess is delimited medially by a thin lamina that is well developed up to the margin of the fragment.

Material: Fragment of the right maxillary, LU-N8/472 (Text-fig. 4 G).

Description: The maxillary is dentate, with pitted sculpture on its outer surface. The lamina horizontalis has a shape of a rounded ridge. It is well defined though tapering towards the anterior, from the level of the recessus vaginiformis. There is a triangular depression anterior to the lamina delimiting medially the recessus vaginiformis.

Material: Anterior part of the right maxillary, LU-N8/473.

Description: The maxillary is dentate, the outer surface of its anterior part is almost smooth. The lamina horizontalis is well developed up to the anterior end of the bone; it is thin along its attachment to the vertical part of the bone, and wider and rounded along its medial margin.

Remark: This specimen might be associated with the same form as the previous one (LU-N8/472) according to the shape of the lamina horizontalis.

Material: Posterior part of the right frontoparietal, LU-N8/474 (Text-fig. 11).

Description: The dorsal surface of the bone, incl. its posterolateral part, is horizontal and flat, with irregular pit-and-ridge sculpture. Laterally, the dorsal surface of the bone produces vertical and slightly medially inclined lamina. The posterior section of the latter turns laterally and terminates on the ventral surface of the posterolateral outgrowth of the bone. This outgrowth bears a horizontal groove on its posterolateral margin, that can be a remnant of the canal for the occipital artery. The state of preservation does not allow to decide in what extent is the posterior part of the bone broken away, but the groove suggests that the bone could have been originally more extensive. The incrassatio frontoparietalis (sensu Jarošová & Roček 1982) is indistinct.

Remark: This frontoparietal is tentatively assigned to *Gobiates* on the basis of its sculpture.

Material: Sphenethmoideum, LU-N5/180 (Text-fig. 12 A; Pl. 12, fig. 2).

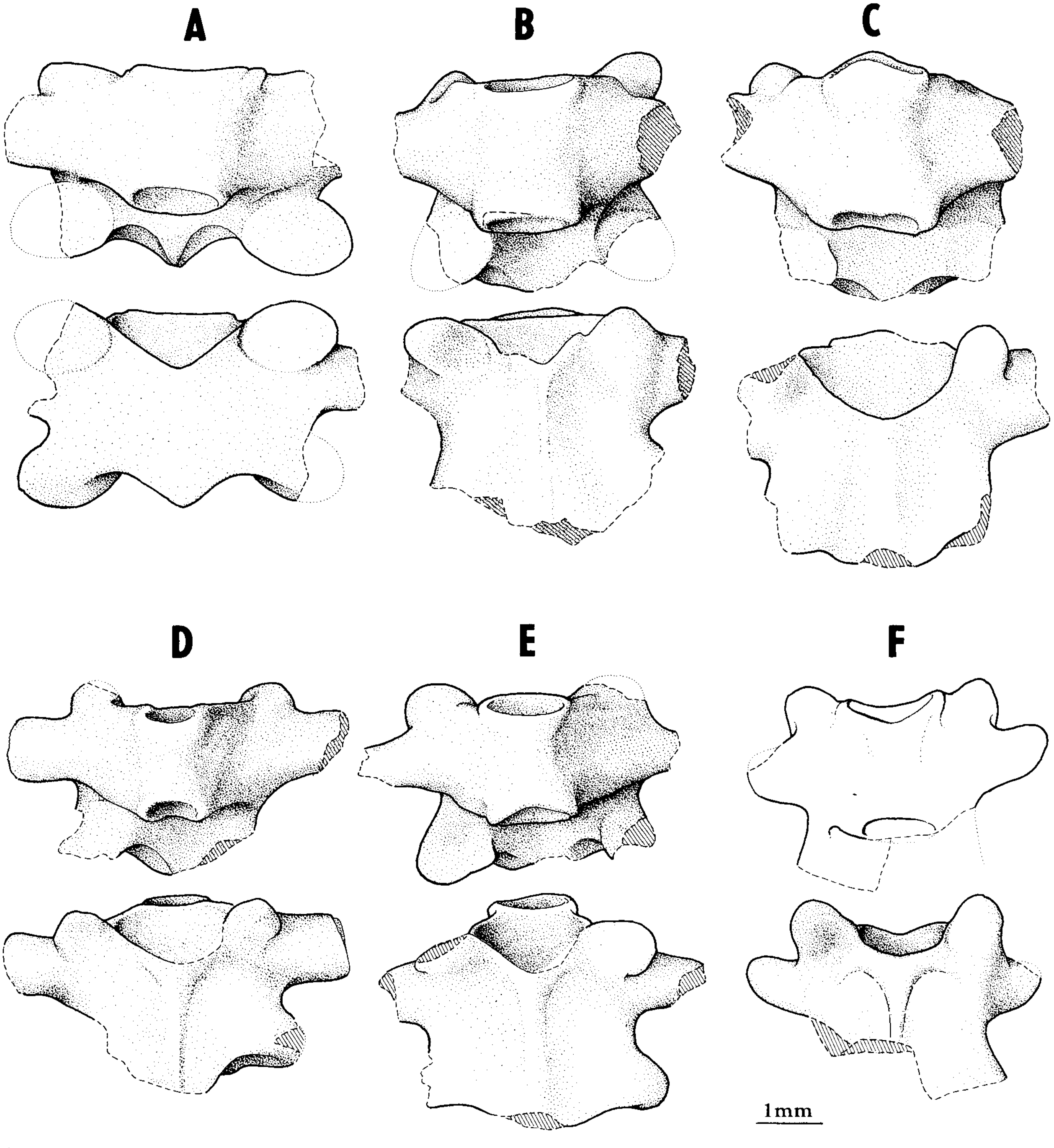
Description: On the dorsal surface of the bone there is a triangular area the surface of which is pitted along its margins and slightly raised. It was no doubt exposed on the surface of the skull (similarly to young *Pelobates*; see Băsoglu & Zăloglu 1964, fig. 15; Roček 1981, fig. 12). Its pitted sculpture corresponds to that on other dermal bones. Hence, sculpture is the main character on the basis of which this bone is tentatively assigned to *Gobiates*. Lateral parts of the bone that were covered by nasals are wrinkled (similarly to contact facets for the frontoparietal and squamosal in the prooticooccipital LU-N6/385; see below).

Material: Left prooticooccipitals, LU-N5/226 (Text-fig. 23 C), and 6/385 (Pl. 14, fig. 1).

Description: In contrast to the prooticooccipitals described as Discoglossidae indet. or cf. Discoglossidae, these are characteristic by a rounded prominentia posterior. The ridge delimiting contact area with the frontoparietal is only moderately developed. Both specimens have lateral part of the bone slightly indented (in LU-N6/385 considerably wrinkled, similarly to the facet for the frontoparietal); hence, this can be considered contact surface for the ramus paroticus squamosi. The sulcus venae jugularis is deep, oriented posterolaterally. Apart from proportions of the crista parotica, the bone rather recalls that in *Alytes*. Both prooticooccipitals are tentatively assigned to *Gobiates* on the basis of their typically wrinkled contact facets for dermal bones in LU-N6/385 which is same as in the sphenethmoideum LU-N5/180 (Text-fig. 12 A) which has pitted sculpture typical for the maxillaries of *Gobiates*.

Discussion of *Gobiates*

Seemingly, the number of species recognized within the genus *Gobiates* is rather high. However, if morphological diversity of those maxillaries that bear the diagnostic characters of *Gobiates* and that are approximately of the same size (so that growth and hence developmental variation are excluded) is taken into account, and if this diversity is based on such characters like maxillo-squamosal contact, extent of the tooth row, morphology of the inner surface of the bone, and in connection with the latter also the nature of the maxillary-pterygoid contact (so that distinct morphological types can be defined, without the possibility to derive one from another), then it may be concluded that these types most probably represent real specific variation. Considerable specific diversity within a single genus (*Gobiates*) might be caused by tropical semihumid climate of the Kizylkum area in the Coniacian, and large variety of biotopes near channels (see chap. Taphonomy). Besides the maxillaries, also squamosals were taken into account because they allow to deduce the shape of the proc. zygomaticomaxillaris



Text-fig. 8. Gobiatidae indet. Praesacral vertebrae. A – LU-N 5/192. B – LU-N 7/449. C – LU-N 6/324. D – LU-N 6/265 (see also Pl. 3, fig. 7). E – LU-N 5/241. F – 6/279 (ventral view above, dorsal view below; see also Pl. 3, fig. 6).

maxillae even in such cases when the maxillary itself is lacking. Only when squamosals could not be associated with any of maxillaries, they have been evaluated as separate species. It is not excluded that one of the above forms might be conspecific with *G. leptocolaptus* Borsuk-Białynicka, 1978; unfortunately this cannot be decided until the inner surface of its maxillary will be known.

Gobiates was probably one of dominant anurans in Asia during the Createaceous. This can be inferred from its diversification into considerable number of species, from its wide geographical distribution (excavation sites in Kizylkum and Gobi Deserts are separated by a distance of about 3000 km), and from its longevity (at least 25 million years).

If the anuran reported by WINKLER et al. (1990) is *Gobiates* then this would provide evidence for the distribution of this genus also in North America (see also p. 11).

Gobiatoides gen. n.

Species typica: *Gobiatoides parvus* sp. n.
Derivatio nominis: *Gobiatoides* means similar to *Gobiates.*

Diagnosis: Same as in type species.

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.

Gobiatoides parvus sp. n.

(Text-fig. 6; Pl. 1, fig. 10)

Holotypus: Middle part of the right maxillary. LU-N6/344 (Text-fig. 6; Pl. 1, fig. 10).
Locus typicus: Dzhyrakuduk, CBI-14.
Stratum typicum: Upper Cretaceous, Coniacian, middle part of Bissekty Formation.
Derivatio nominis: *'parvus'* (Lat.) means small; refers to its size.

Diagnosis: The margo orbitalis maxillae deeply concave. The bone very low at the level of the lowermost point of the margo. The margo paralleled on its inner side by a ridge coming from the proc. frontalis, and gradually disappearing towards the proc. zygomaticomaxillaris. The outer surface of the bone smooth.

Description: The maxillary is smaller than that in most *Gobiates* forms, and dentate. Its outer surface is smooth. The margo orbitalis is deeply concave, with a sharp ridge on its inner side, issuing from the proc. frontalis and disappearing towards the proc. zygomaticomaxillaris. Between this ridge and the lamina horizontalis there is a shallow groove for the palatoquadrate bar. The lamina has rounded margin, and is moderately tapering posteriorly. Its medial extent is approximately the same along the whole length of its preserved part. At the level of the anterior limit of the orbit it is covered dorsally by the proc. frontalis which is inclined medially. The canal piercing the margo orbitalis and appearing on the outer surface of the bone is located in the anterior part of the orbit. The tooth row terminates at the level of the posterior end of the lamina horizontalis.

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.

cf. *Gobiatoides*

Material: Right praearticular, LU-N5/120 (Text-fig. 24 A; Pl. 14, fig. 10); left praearticular, LU-N4/78 (Text-fig. 24 B; Pl. 14, fig. 9).

Description: Both are of approximately same size, differences are only in the posterior extent of the proc. coronoideus, and in the presence or absence of a ridge delimiting laterally the extremitas spatulata. Both elements correspond in size to the maxillary LU-N6/344 (holotype of *G. parvus*).

Gobiatidae indet.

Material: Praesacral vertebrae (although the material consists of vertebrae from various sections of the vertebral column, several principal types may be distinguished).

Type I – V6 or V7 (according to inclination of the transverse processes), LU-N5/231 (Text-fig. 7 C; Pl. 3, fig. 8; the specimen was destroyed in the process of taking SEM photographs). Centrum amphicoelous without notochordal canal (similarly to all other types described below), neural arches imbricate. Both praezygapophyses and postzygapophyses reach laterally approximately the same level.

Type II – LU-N5/201 (Text-fig. 7 D; Pl. 3, fig. 4). Centrum amphicoelous, neural arches imbricate. The vertebra is short and wide. Neural arches run out posteriorly in a distinct median outgrowth; as they are rather thick, the outgrowth separates here two lateral depressions facing posteriorly. If seen dorsally, there is a low median ridge on the roof of the neural canal. The anterior margin of this roof is distinctly concave, so that considerable part of the dorsal surface of the centrum is exposed, if an isolated vertebra is observed. The tips of the transverse processes are ground off, however, it is obvious that they were short and dorsoventrally compressed.

The following types are larger praesacral vertebrae.

Type III – LU-N5/192 (Text-fig. 8 A). Centrum amphicoelous, neural arches moderately imbricate. The vertebra is short and wide. Both prae- and postzygapophyses are comparatively large. The transverse processes were compressed dorsoventrally and obviously not very long. Neural arches run out posteriorly in a median process (continued downwards as a ridge separating two posteriorly facing depressions), whereas their anterior margin is deeply concave. The dorsal surface is smooth and flat, with no median ridge. This feature, besides the size of the vertebra, are the only characters that distinguish type III from the type II.

Type IV – LU-N7/449 (Text-fig. 8 B), LU-N5/241 (Text-fig. 8 E). Centrum amphicoelous, neural arches imbricate. The transverse processes oval in cross-section. The anterior dorsal margin of the neural arches is only moderately concave. There is a distinct median ridge on the dorsal surface. The praezygapophysis seems to be comparatively small.

Type V – V7 or V8 (according to inclination of the transverse processes), LU-N6/324 (Text-fig. 8 C). Basic features of this type correspond to those in the previous one. Differences are in the praezygapophyses that are directed straight anteriorly, and in the convex dorsal and ventral margins of the anterior articulation facet of the centrum.

Type VI – V3, LU-N6/265 (Text-fig. 8 D; Pl. 3, fig. 7). Centrum amphicoelous and markedly small. The neural arches imbricate and comparatively thick. A sharp median ridge terminates posteriorly in a point. The transverse processes are oval in cross-section. They seem to be thinner proximally. That of the right side is complete, with the articular facet for the rib. The praezygapophyses are comparatively small, whereas the postzygapophyses are large.

Type VII – Most probably V7 (according to complete left transverse process), LU-N6/279 (Text-fig. 8 F; Pl. 3, fig. 6). Centrum amphicoelous, neural arches imbricate. The transverse processes moderately compressed dorsoventrally. There is a median ridge on the dorsal surface, confluent with a mound rimming dorsally the anterior orifice of the neural canal. These motifs of the dorsal surface are sharply delimited from the indented lateral areas.

Other material of the praesacral vertebrae (too fragmentary to be assigned to a certain type): LU-N5/185 (may be perhaps associated with type I of *Gobiates* sp., i. e. with that having the roof of the neural canal absent), 5/227, 5/235, 5/249, 6/288, 6/424, 8/481, 8/483.

Material: Sacral vertebra, LU-N6/262 (Text-fig. 14 C).

Description:The anterior articulation facet of the centrum is concave. The transverse process distinctly compressed dorsoventrally, slightly dilated laterally, and moderately inclined posteriorly. If seen dorsally, there is a prominent transverse ridge (better developed than the median one). It, however, does not continue onto the dorsal surface of the transverse process. Instead, there is a smooth and flat area indented proximally, the delimitation of which recalls that of the praesacral vertebra type VII (see above). This character and its size permits one to associate both vertebrae as belonging to a single form.

Material: Left ilium, LU-N4/57; right ilium, LU-N5/93 (Text-fig. 25 C); left ilia, LU-N5/159 (Text-fig. 25 E), 5/169 (Text-fig. 25 B; Pl. 10, fig. 4), 5/195, 5/211, 6/284, 6/400 (Text-fig. 25 D; Pl. 9, fig. 5), 7/444 (Text-fig. 25 A; Pl. 11, fig. 1); middle section of the right ilium, LU-N8/476; left ilium, LU-N8/479.

Description: These tiny ilia morphologically recall those of *Alytes* (Pl. 11, fig. 3; see also SANCHÍZ 1984, figs. 83–85). Differences may be found mainly in the extent of the torus superior, and size of the bone.

Material: Left humerus, LU-N2/44 (questionably); right humerus, LU-N4/75; left humeri, LU-N4/90 (Text-fig. 31 C), 5/102 (Text-fig. 29 B), LU-N5/108, 5/113 (Text-fig. 31 D), 5/119 (Text-fig. 29 P); right humerus, LU-N5/133 (Text-fig. 29 E; Pl. 6, fig. 7); left humerus, LU-N5/142 (Text-fig. 29 G); right humerus, LU-N5/151 (Text-fig. 29 F); left humeri, LU-N5/160 (Text-fig. 29 N), 5/164 (Text-fig. 29 M), 5/167 (Pl. 11, fig. 8); right humeri, LU-N5/168 (Text-fig. 29 D), 5/174 (Text-fig. 29 K), 5/237, 6/293; left humeri, LU-N6/307 (Text-fig. 29 R), 5/212 (Text-fig. 29 O; Pl. 7, fig. 2); right humeri, LU-N5/237, 5/244 (Text-fig. 29 T; Pl. 7, fig. 3), 6/336 (Text-fig. 29 S; Pl. 7, fig. 1); left humerus, LU-N6/338 (Text-fig. 29 H; pl. 6, fig. 5); right humerus, LU-N6/358 (Text-fig. 29 C); left humerus, LU-N6/362; right humeri, LU-N6/372 (Text-fig. 29 J), 6/377 (Text-fig. 29 A; Pl. 6, fig. 2); left humeri, LU-N6/39LU-N4/90, 5/108, 5/113, 5/167, and 6/362 are described in the chap. Malformation.

Description: Text-fig. 29 illustrates variation of this bone in the Gobiatidae, as well as the principal diagnostic characters separating them from the Discoglossidae. All these humeri are characterized by the epicondylus medialis moderately developed, the epicondylus lateralis absent, the fossa cubitalis ventralis triangular in shape and pronounced to various degree, and the crista ventralis sharp and bent medially. However, within this variation range are also specimens (LU-N6/338, 6/410) that have their fossa cubitalis ventralis distinctly asymmetrical, and their crista ventralis continues towards the medial epicondylus. This feature recalls the condition in the Discoglossidae.

Material: Femurs, LU-N4/67, 5/109, 5/123 (Pl. 7, fig. 9), 5/250, 6/274, 6/352 (Pl. 7, fig. 5), 6/354 (Pl. 2, fig. 8), 8/464.

Description: Differences are in the shape and extent of the crista femoris – it is well developed though short, being triangular in lateral view (LU-N5/123, 6/352), or thin but distinct and longer than in previous two specimens (LU-N4/67, 5/109, 6/274), or rather robust and extensive, reaching up to the proximal end of the bone in LU-N8/464.

cf. Gobiatidae

Material: Centrum of the atlas with the neural arches broken off, LU-N6/436 (Text-fig. 19 A).

Description: In both ventral and dorsal views, the posterior articular cavity has deeply concave margins. The articulation facets for the occipital condyli are separated by a groove which continues as a shallow median depression onto the ventral surface of the centrum. There is a shallow pit in the midline, located at the same level as the similar one at the bottom of the neural canal; the latter is better pronounced. Lateral margins of the centrum diverge from their posteriormost ends. The neural arches were rather extended antero-posteriorly. This corresponds to the imbricate neural arches of *Gobiates* (ŠPINAR & TATARINOV 1986, fig. 3 E). However, it differs from *Gobiates* described by ŠPINAR & TATARINOV in having deeply concave margins of the posterior articular cavity of the centrum (op. cit., fig. 3 D). Because of this character, the specimen is assigned to the Gobiatidae only tentatively.

Material: Right coracoids. LU-N4/69 (Pl. 13, fig. 6) and 6/350 (Pl. 13, fig. 7).

Description: These elements are almost straight, only moderately convex ventrally. The glenoid fossa for the humerus is eliptical, not oval. This feature seems to prevent relationship to the Discoglossidae in which this fossa is circular in shape. Tentative assignment to the Gobiatidae is based only on their size corresponding to numerous gobiatid maxillaries (the smaller specimen might be associated with *Gobiatoides*, according to its size).

Material: Femurs, LU-N4/51, 5/194 (Pl. 14, fig. 3).

Description: Similar to LU-N6/123 and 8/352 determined as Gobiatidae indet., however, their crista femoris is low and not so close to the proximal end of the bone.

Discoglossidae GÜNTHER, 1859

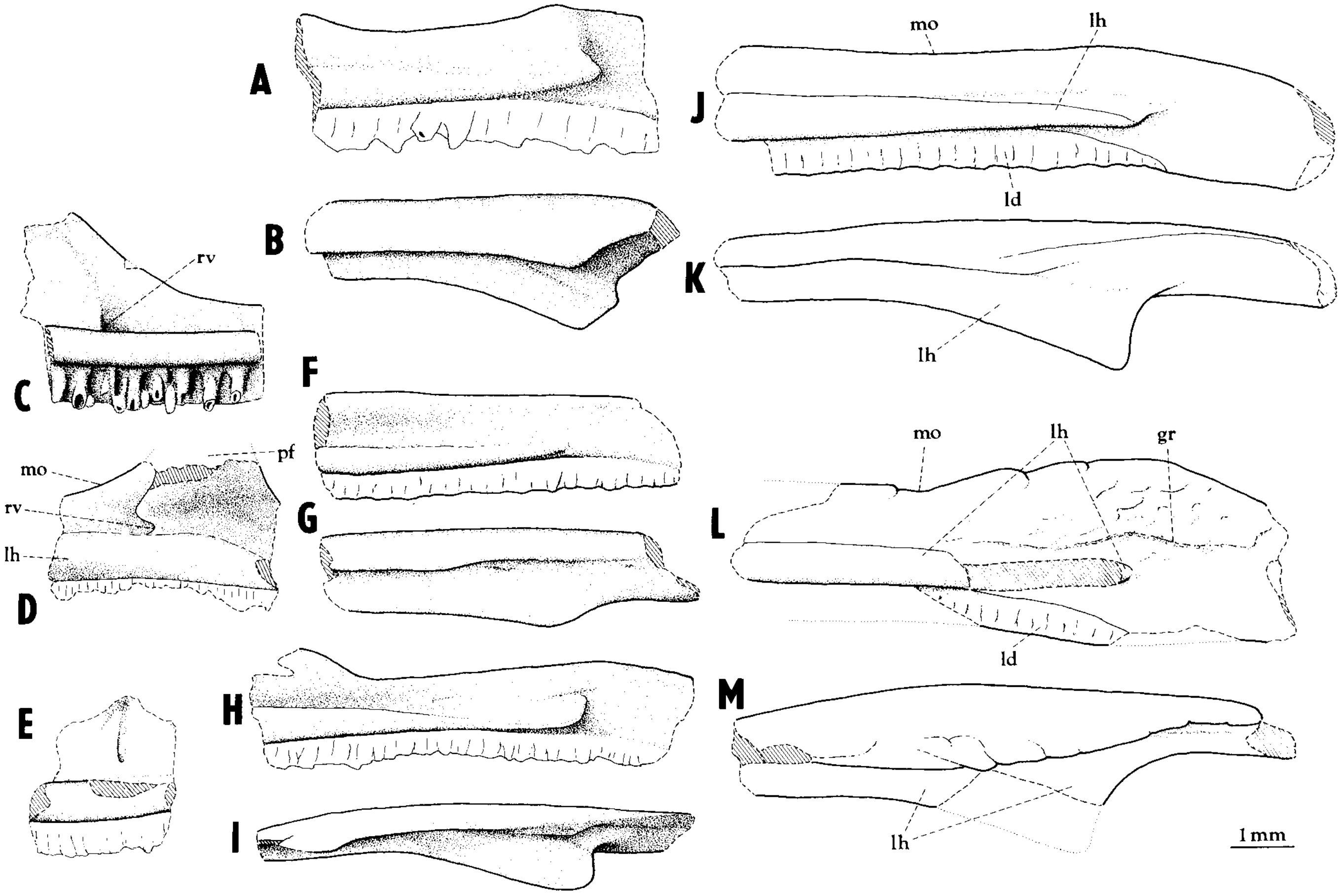
The material described below is referred to the Discoglossidae on the basis of dentate and mostly smooth maxillary, opisthocoelous vertebrae, bicondylar sacro-urostylar articulation, and morphology of the urostyle.

Genus *Kizylkuma* NESSOV, 1981

Species typica: *Kizylkuma antiqua* NESSOV, 1981.

Diagnosis (after NESSOV, 1981, amended): Outer maxillary surface smooth; lamina horizontalis maxillae thinner but more extensive posteriorly, its posterior termination abrupt; postorbital section of dorsal margin of maxillary only moderately exceeds level of margo orbitalis; tooth row terminating at level of posterior end of lamina horizontalis; fossa cubitalis ventralis humeri absent or shallow, both lateral cristae of humerus poorly developed.

Geological age: Late Turonian to Coniacian.
Geographical distribution: Central Asia.



Text-fig. 9. A, B – *Saevesoederberghia egredia* gen. et sp. n., holotype. Section of the right maxillary (LU-N 6/375) in inner (A) and dorsal (B) aspects. C – *Estesina elegans* gen. et. sp. n. (LU-N 6/335). Section of the right maxillary at the level of the anterior part of the orbit, in inner view. D – Anura indet. (LU-N 5/255). Section of the left maxillary in inner aspect. E – Discoglossidae indet. (LU-N 5/200). Section of the maxillary in inner aspect. F, G – *Procerobatrachus paulus* gen. et sp. n., holotype. Section of the right maxillary (LU-N 6/412) in inner (F) and dorsal (G) aspects. H, I – *Estesina elegans* gen. et sp. n. (LU-N 5/172). Section of the right maxillary in inner (H) and dorsal (I) aspects (see also Pl. 2, fig. 2). J, K – *Kizylkuma antiqua* Nessov, 1981 (LU-N 6/271). Right maxillary in inner (J) and dorsal (K) views. L, M – *Aralobatrachus robustus* Nessov, 1981 (LU-N 6/409). Right maxillary in inner (L) and dorsal (M) views.

Kizylkuma antiqua Nessov, 1981

(Text-fig. 9 J, K; Pl. 2, fig. 1)

Holotypus: ZIN, PHA No K77-10, collections of the Department of Herpetology, Zoological Institute of the Russian Academy of Sciences, St. Petersburgh. Left maxillary. Figured in Nessov 1981, pl. 12, fig. 17.

Locus typicus: Dzhyrakuduk (CBI-4v), central Kizylkum Desert, Uzbekistan.

Stratum typicum: Upper Turonian – Coniacian.

Material: Maxillaries LU-N5/105, 5/127 (Pl. 2, fig. 1), 6/271 (Text-fig. 9 J, K), 6/332, 6/398 (see also Nessov 1988, Pl. 14, fig. 9).

Description: The maxillary is low and elongated, bearing no sculpture on its outer surface. The postorbital section only slightly exceeds the horizontal level of the orbital margin. Whereas the postorbital dorsal margin is rather sharp, the margo orbitalis is widely rounded in its cross-section. Anterior to the orbit the dorsal margin is sharp again. The margo orbitalis is only slightly prominent medially, thus not roofing dorsally the palatoquadrate bar. The lamina horizontalis in its section anterior to the orbit is thick, moderately extensive and rounded; posteriorly it becomes thin and comparatively extensive. It terminates abruptly, approximately at a right angle. The tooth row terminates at the level of the posterior end of the lamina.

Geological age: Late Turonian to Santonian (Nessov 1981).

Geographical distribution: Central Asia.

cf. *Kizylkuma* NESSOV, 1981

Material: Humeri 5/95 (Pl. 7, fig. 8), 5/247 (Pl. 7, fig. 7), 6/319 (Pl. 7, fig. 6), 6/322, 6/423.

Description: The anterior surface of the humerus bears a longitudinal, prominent and rounded edge that is directed toward the medial epicondylus. Both medial and lateral cristae are short and narrow. The fossa cubitalis ventralis is either absent or very shallow. These humeri are tentatively assigned to *Kizylkuma* on the basis of their size.

The humerus LU-N2/43 (Text-fig. 31 A) that is similar to those just described, is obviously abberant. Its caput is not developed. It is described and illustrated in the chapter Malformations.

The ilium LU-N5/150 (Pl. 8, fig. 3) is tentatively assigned to *Kizylkuma* on the basis of its size and general morphology which deviates from that in *Aralobatrachus* at the degree similar to other bones (namely maxillaries). Its torus superior is large and widely arch-like, with a distinct bump on the lateral surface of its posterior half. The crista is developed only on the torus and for a short distance anterior to it. Further anteriorly the ala is oval in cross-section and slender. The acetabulum is a very shallow depression delimited only anteriorly by a short ridge. Its bottom is at the level of the surface of the pars descendens. Anterior as well as dorsal margins of the acetabulum are poorly defined so that the pars ascendens slants down into the acetabulum without a distinct border. If seen from the dorsal side, the pars ascendens considerably widens posteriorly.

Genus *Aralobatrachus* NESSOV, 1981

Species typica: *Aralobatrachus robustus* NESSOV, 1981.

Diagnosis (after NESSOV 1981, amended): Large-sized anuran (estimated length of the maxillary is about 18mm); outer surface of postorbital section of maxillary with horizontal grooves and/or groove-like rugosity, corresponding inner part of bone with irregular rugosity; there are transverse grooves on the dorsal margin of bone, within its posterior half; tooth row continues behind level of the posterior end of lamina horizontalis.

Geological age: Late Turonian – Coniacian.
Geographical distribution: Central Asia.

Aralobatrachus robustus NESSOV, 1981

(Text-figs. 9 L, M, 13 B, 15 A, B; Pl. 3, fig. 5, Pl. 4, fig. 6; Pl. 6, fig. 3; Pl. 8, fig. 4)

Holotypus: ZIN, PHA No 477-7. Collections of the Department of Herpetology, Zoological Inst. of Russian Acad. Sciences, St. Petersburgh. Middle section of the right maxillary. Figured in NESSOV, 1981, pl. 10, fig. 22.

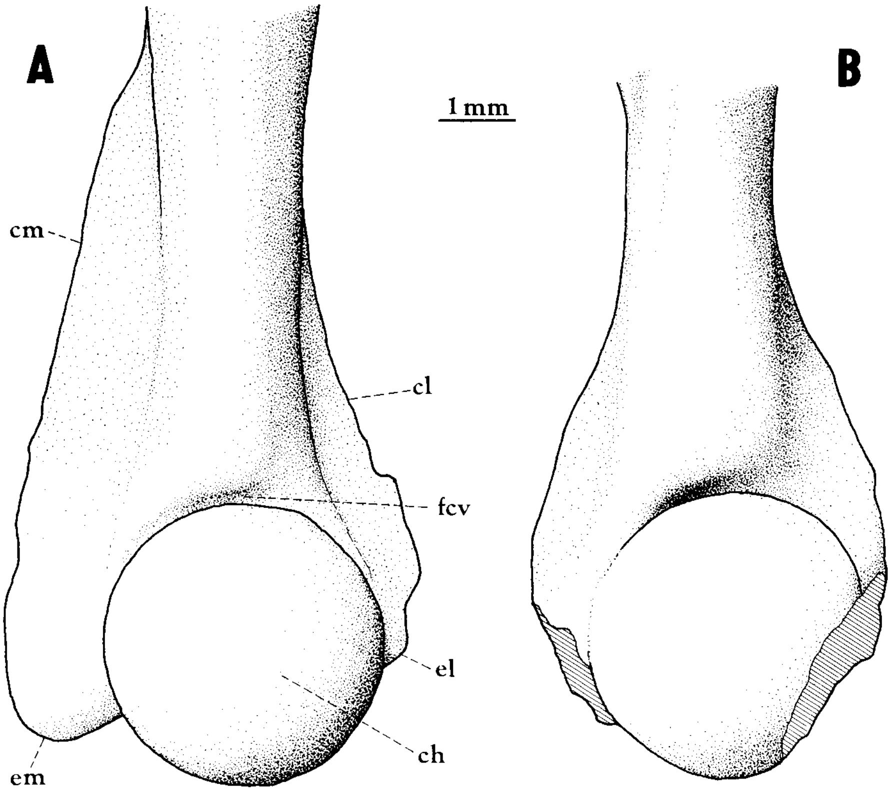
Locus typicus: Dzhyrakuduk, CDZ-17a, central Kizylkum Desert, Uzbekistan.

Stratum typicum: Upper Turonian, lower part of the Bissekty Formation.

Material: Maxillaries, LU-N6/353, 6/367, 6/409 (Text-fig. 9 L, M), 6/435, questionably also 6/314; V3, LU-N4/54 (Text-fig. 15 A; Pl. 3, fig. 5); urostyle, LU-N6/299 (Text-fig. 15 B; Pl. 4, fig. 6); humeri, LU-N6/343 (Text-fig. 10 B; Pl. 6, fig. 3), 6/419 (Pl. 6, fig. 1), 6/427, questionably also 6/296; ilia, LU-N5/130 (Text-fig. 13 B; Pl. 8, fig. 4), 7/452 (Pl. 8, fig. 6); ischia, LU-N5/128, 5/136).

Diagnosis: Same as in genus.

Description: The maxillary is a slender bone similar in its general shape to that in *Kizylkuma*. The margo orbitalis is not distinctly concave. The postorbital section of the bone bears on its outer surface horizontal grooves and/or a groove-like rugosity. The same part of the bone bears on its inner surface a similar though irregular rugosity. Grooves may run from inner to outer surface; hence, the dorsal margin of the bone is irregular. There is a distinct horizontal groove on the inner surface of the postorbital section of the bone in LU-N6/409. The groove gradually disappears above the posterior section of the lamina horizontalis. In LU-N6/435 is a distinct depression at the level posterior to the hind end of the lamina horizontalis, though sign of a groove running for a short distance anterior to the depression can be seen. In its anterior wall there is an orifice of a canal. Difference between both individuals in this character is atributable to individual variation. The lamina horizontalis is probably of the same shape and extent as in *Kizylkuma* (see Text-figs. 9 L, M). LU-N6/353 and 6/435 clearly show that the tooth row terminates posterior to the level of the hind end of the lamina horizontalis.



Text-fig. 10. Left humeri of (A) *Discoglossus sardus* (DP FNSP 1698, loc. Banyuls sur Mer, France), and (B) *Aralobatrachus robustus* (LU-N 6/343; see also Pl. 6, fig. 3), in anterior view.

The vertebrae are opisthocoelous. The proc. transversus of V3 (Text-fig. 15 A; Pl. 3, fig. 5) is perpendicular to the axis of the vertebral column. Its anterolateral part is thin and slightly extended with sharp margins, whereas its posterior and proximal part is thick with rounded margins. The centrum bears on its dorsal surface (i. e. at the bottom of the neural canal) a distinct median ridge.

The urostyle (Text-fig. 15 B; Pl. 4, fig. 6) bears a pair of transverse processes on its dorsal side, directed posterolaterally; their medial part is moderately extended dorsally, however, the parts do not fuse with one another to make the roof of the neural canal (seu canalis coccygeus Bolkay, 1919). Posteromedially to the proc. transversus there is a groove directed posterolaterally. There is a cavity within the urostyl, at the level of the vertebral centra.

Only the distal sections of the humeri (Text-fig. 10 B) are preserved, and both medial and lateral epicondyli are broken off. The maximum length of the bone can attain about 20mm. The proximal extents of the medial and lateral cristae are only slightly different. The fossa cubitalis ventralis is deep. The anterior surface of the bone is a prominent but rounded mound, distally directed towards the epicondylus medialis; consequently the fossa cubitalis is asymmetrical.

The ilium (Text-fig. 13 B) has moderately prominent torus superior that continues anteriorly as a sharp crista (within the extent of the preserved part of the bone). Laterally is a shallow depression at the level of the base of the torus. The dorsal margin of the pars ascendens is horizontal and widely rounded. Its lateral margin (taking part in the ischio-iliacal suture) continues anteriorly as a moderately prominent and rounded dorsal margin of the acetabulum. The interior of the acetabulum in its anterodorsal part is conspicuously depressed, whereas its margin is not much elevated (i.e., the agger limitans anterior is not prominent). On the other hand, the anterior part of the pars descendens is deeply depressed. If viewed dorsally, the pars ascendens considerably broadens towards its posterior.

The ischia LU-N5/128 bear no diagnostic features and are assigned to *Aralobatrachus* only on the basis of their size which corresponds to that of the ilia. The ischia LU-N5/136 are smaller but within possible variation range of *Aralobatrachus*. Towards the pars ascendens ilii they display clear signs of coalescence.

Geological age: Late Turonian-Coniacian.
Geographical distribution: Central Asia.

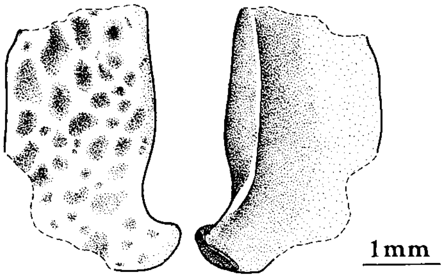
cf. *Aralobatrachus* NESSOV, 1981

Material: Left ilia, LU-N2/15 (Text-fig. 28 E; Pl. 8, fig. 2), 7/447 (Pl. 10, fig. 1).

Description: These ilia are similar to those in *Aralobatrachus*, however, their torus superior is not confluent with the crista ilii, their acetabulum is shallow and well delimited by a sharp ridge along whole its outlines, and it seems that the pars ascendens (although its tip is broken off) is not bent laterally. Also their size is smaller than that in *Aralobatrachus*. It is difficult to decide on the basis of the material at hand whether these differences are due to individual and/or developmental variation, or if they reflect real taxonomic status of the specimens. Similar situation is in LU-N5/210 (humerus).

Material: Praemaxillary LU-N5/158 (Pl. 1, fig. 9).

Description: As this specimen was destroyed in the course of taking SEM photographs, it can be associated with *Aralobatrachus* only on the basis of its size.



Text-fig. 11. cf. *Gobiates*. Right frontoparietal in dorsal (left) and ventral (right) views (LU-N 8/474).

Saevesoederberghia gen. n.

Species typica: *Saevesoederberghia egredia* sp. n.
Derivatio nominis: In honour of the Swedish paleontologist GUNNAR SÄVE-SÖDERBERGH, famous by his work on primitive tetrapods and the origins of the Anura.

Diagnosis: Same as in species.

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.

Saevesoederberghia egredia gen. et sp. n.

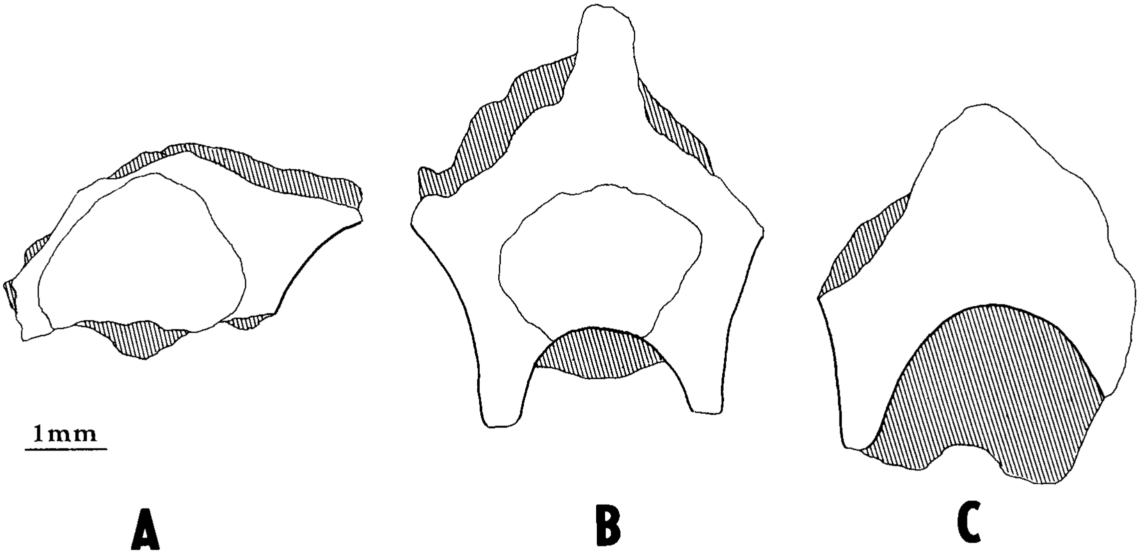
(Text-fig.9 A, B; Pl.2, fig.3)

Holotypus: Section of the right maxillary at the level of the margo orbitalis.LU-N6/375 (Text-fig.9 A, B).
Locus typicus: Dzhyrakuduk, CBI-14.
Stratum typicum: Upper Cretaceous, Coniacian, middle part of the Bissekty Formation.
Derivatio nominis: '*egredior*' (Lat.) means exceed; refers to the tooth row exceeding posterior termination of the lamina horizontalis.
Material: Left squamosal, LU-N5/178; probably also right squamosal, LU-N5/139.

Diagnosis: Similar to *Kizylkuma* tooth row exceeds posterior end of lamina horizontalis, and posterior end of margo orbitalis is marked by a distinct process directed medially. From *Itemirella* NESSOV, 1981 it differs by abrupt posterior termination of lamina horizontalis.

Description: The maxillary is dentate, and its outer surface is smooth.The margo orbitalis is moderately concave and is, including small process on its posterior end, slightly turned medially.The lamina horizontalis is narrow and widely rounded anteriorly, but extensive and thin posteriorly. There is no distinct groove for the palatoquadrate bar along the line of attachment of the lamina to the vertical part of the bone.Instead, the inner surface of the bone continues indistinctly into the dorsal surface of the posterior part of the lamina.From the posterior end of the lamina towards the mentioned process on the dorsal margin of the bone there is a distinct mound; posterior to it there is a depression which is also reflected on the dorsal margin of the bone (Text-fig.9 B).The tooth row continues behind the posterior termination of the lamina horizontalis.Teeth are comparatively robust.

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.



Text-fig. 12. Shape of sphenethmoids in dorsal view. A – cf. *Gobiates* (LU-N 5/180 – see also Pl. 12, fig. 2). B – Anura indet. (LU-N 7/448 – see also Pl. 12, fig. 1). C – Anura indet. (LU-N 5/141).

Procerobatrachus gen. n.

Species typica: *Procerobatrachus paulus* sp. n.
Derivatio nominis: *'procerus'* (Lat.) means slim; refers to the general shape of the maxillary.

Diagnosis: Same as in species.

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.

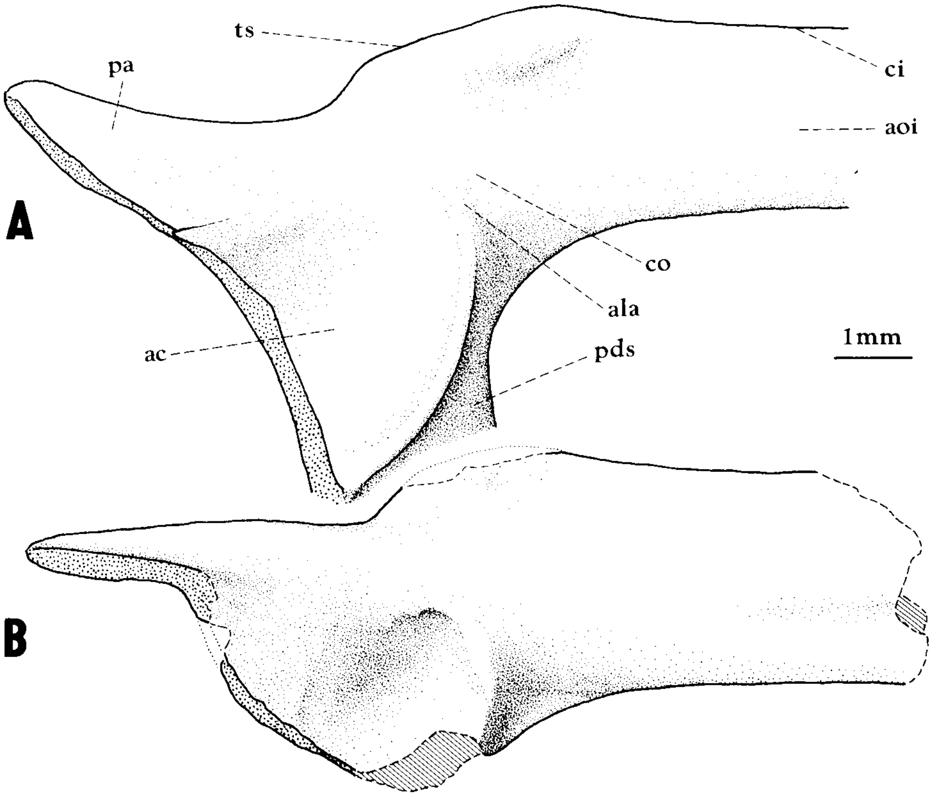
Procerobatrachus paulus gen. et sp. n.

(Text-fig. 9 F, G)

Holotypus: Section of the right maxillary comprising the posterior part of the lamina horizontalis. LU-N6/412 (Text-fig. 9 F, G).
Locus typicus: Dzhyrakuduk, CBI-14.
Stratum typicum: Upper Cretaceous, Coniacian, middle part of the Bissekty Formation.
Derivatio nominis: *'paulus'* (Lat.) means gradual; refers to posterior termination of the lamina horizontalis.

Diagnosis: Margo orbitalis and dorsal margin of posterior part of maxillary are straight, with no sign of proc. zygomaticomaxillaris. Lamina horizontalis only slightly extends medially, close to its posterior termination; the termination is gradual.

Description: The maxillary is dentate, its outer surface is smooth. In lateral aspect, the margo orbitalis is straight, as is the dorsal margin of the postorbital section. In dorsal view, only the margo orbitalis is slightly turned medially, whereas posterior to the level of the lamina horizontalis the dorsal margin of the bone is rounded. The lamina horizontalis is widely rounded (it is thin along its attachment and consequently it is almost cylindrical in cross-section). There is a groove for the palatoquadrate bar below the anterior part of the orbit, but posteriorly the upper surface of the lamina horizontalis is continuously connected with the inner surface of the vertical part of the bone. The lamina only slightly extends medially, and its posterior termination is indistinct. The tooth row exceeds far behind the lamina.



Text-fig. 13. Right ilia of (A) *Discoglossus sardus* (same specimen as in Text-fig. 10), and (B) *Aralobatrachus robustus* (LU-N 5/130 – see also Pl. 8, fig. 4), in lateral view.

Estesina gen. n.

Species typica: *Estesina elegans* sp. n.
Derivatio nominis: Named in honour of Richard Estes, an outstanding paleoherpetologist who died in 1990.

Diagnosis: Same as in species.

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.

Estesina elegans gen. et. sp. n.

(Text-fig. 9 C, H, I; Pl. 2, fig. 2)

Holotypus: Posterior part of the right maxillary. LU-N5/172 (Text-fig. 9 H, I; Pl. 2, fig. 2).
Locus typicus: Dzhyrakuduk, CBI-4b.
Stratum typicum: Upper Cretaceous, Coniacian, middle part of the Bissekty Formation.
Derivatio nominis: '*elegans*' (Lat.); refers to the morphology of the maxillary.

Diagnosis: Proc. frontalis maxillae well developed; lamina horizontalis widely rounded anteriorly, but thin and largely extended posteriorly; tooth row exceeds posterior termination of lamina horizontalis.

Material: Maxillaries, LU-N5/98 (Pl. 2, fig. 4), 5/251, 6/335 (Text-fig. 9 C).

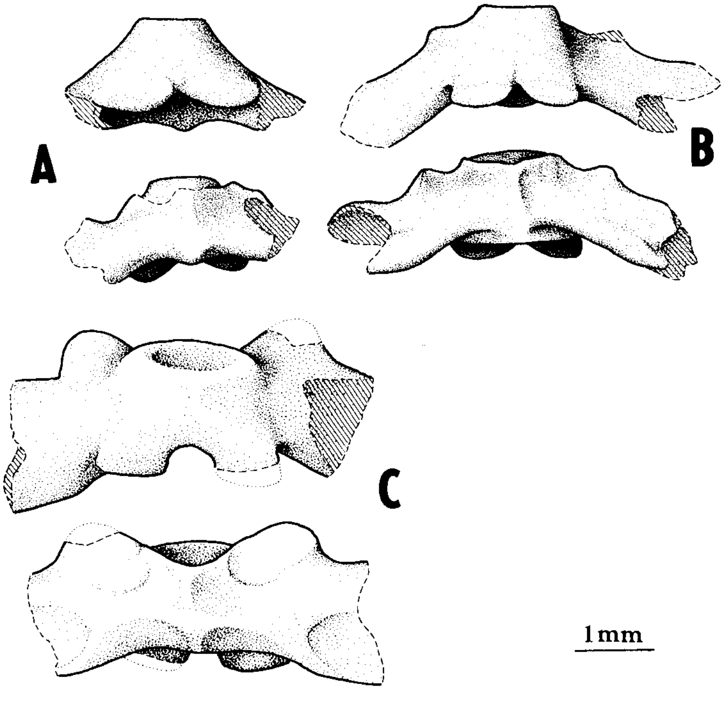
Description: The maxillary is dentate, low, with the proc. zygomaticomaxillaris indistinct and low. In contrast to the latter, the proc. frontalis is comparatively well developed. Consequently, the margo orbitalis is concave anteriorly but almost straight posteriorly. The outer surface of the bone is smooth. The lamina horizontalis is narrow at the level of the proc. frontalis, thin along its attachment to the inner surface of the bone but widely rounded along its free margin (hence, it is almost circular in cross-section). However, posteriorly it is thin, largely extended, and terminating arch-like. As the proc. frontalis is inclined medially, the inner surface of the bone and the lamina horizontalis form together a groove for the palatoquadrate bar. Posteriorly, this bar was housed in a shallow groove developed above the posterior termination of the lamina. The tooth row continues behind this termination. LU-N6/335 (Text-fig. 9 C) is similar in principal features, namely in the shape of the lamina horizontalis, but differs in size of the bone, size of the proc. frontalis, and position of the rec. vaginiformis relative to the margo orbitalis (compare Text-fig. 9 H and C). Whereas the first character may be atributed to ontogenetic variation, the latter two cast some doubts concerning the conspecific identity of LU-N6/335 and the holotype. LU-N5/98 (Pl. 2, fig. 4) corresponds with the holotype in shape of the lamina horizontalis and size of the bone. The lamina tapers towards the anterior, and also its medial extent decreases.

Geological age: Late Cretaceous, Coniacian.
Geographical distribution: Central Asia.

Discoglossidae indet.

Material: Section of the maxillary, LU-N5/200 (Text-fig. 9 E).

Description: Its outer surface is smooth, the lamina horizontalis is narrow, widely rounded. The main feature of this specimen is a vertical groove on the inner surface of the bone, that ventrally continues as a canal piercing the bone onto its outer surface.



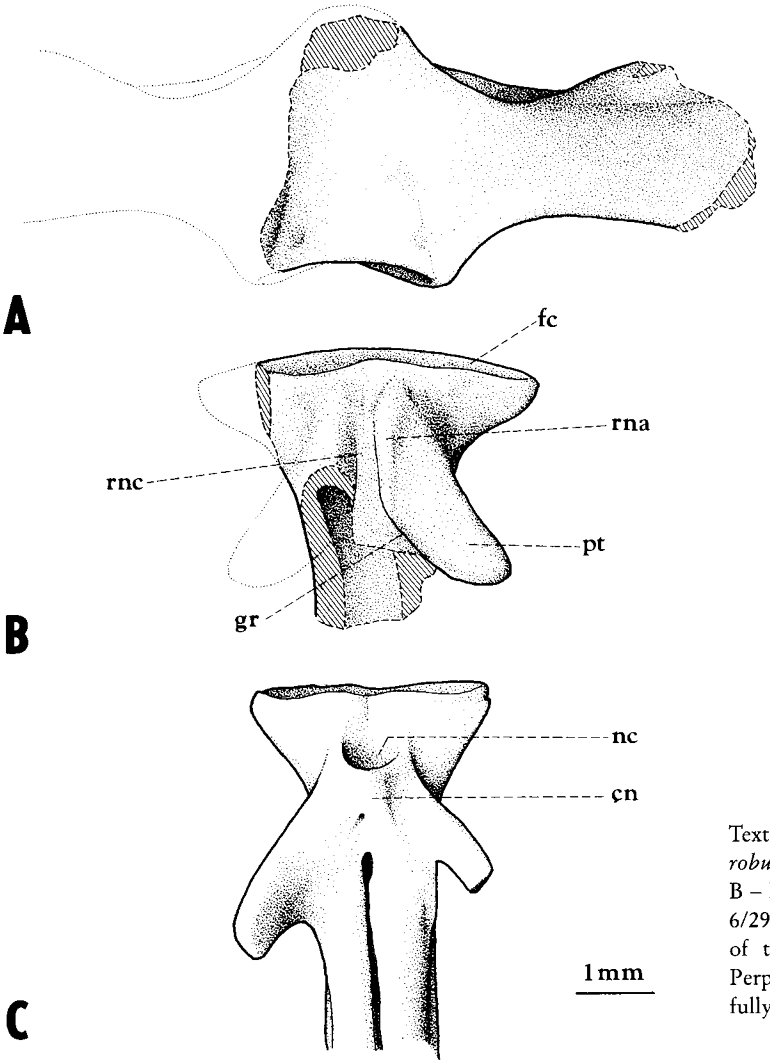
Text-fig. 14. Sacral vertebrae in ventral (above) and dorsal (below) views. A, B – *Gobiates* sp. (LU-N 5/191 – see also Pl. 3, fig. 9; 5/246 – see also Pl. 3, fig. 10). C – Gobiatidae indet. (LU-N 6/262).

Material: Right praearticular, LU-N 6/442 (Text-fig. 24C); left praearticular, LU-N 6/356 (Text-fig. 24D); right praearticular, LU-N 5/161 (Text-fig. 24E); right praearticular, LU-N 8/465 (Text-fig. 24F).

Description: All these praearticulars (except for LU-N 6/356 that is slightly smaller) are large, thus corresponding to the maxillaries illustrated in the Text-fig. 9. The differences between them are mostly in the morphology of the crista paracoronoidea (esp. its posterior termination) and in the depth of a depression between the crista and the medial margin of the proc. coronoideus. 6/442 and 6/356 are similar to one another in that the space between the crista and margin of the process is stepwise indented towards the posterior. In contrast, it is regularly groove-like shaped, with the medial margin of the proc. coronoideus turned dorsally in LU-N 5/161. Specimen 8/465 is similar to the previous one in that the depression between the medial margin of the proc. coronoideus and the crista paracoronoidea is deep. Consequently, the crista becomes a ledge on the inner concave surface of the widened posterior part of the bone. It is possible that LU-N 5/161 and 8/465 might belong to related forms.

Material: Centrum of the atlas with neural arches broken off, LU-N 6/317 (Text-fig. 19C).

Description: Neural arches were rather thin close to their bases. There is a shallow but distinct pit in the mid-line at the bottom of the neural canal. Both articular facets for the occipital condyli are separated by a narrow and shallow groove. Whereas the posterior part of the centrum is nearly cylinder-like, the lateral margins of its anterior moiety diverge towards the anterior. The basal parts of the neural arches are clearly visible in ventral view. In the midpart of the ventral surface there is a mound in the midline; its margins diverge anteriorly. The specimen is assigned to the Discoglossidae on the basis of thin neural arches and general shape of the centrum in ventral view (see Text-fig. 19D).



Text-fig. 15. A – Third praesacral vertebra of *Aralobatrachus robustus* (LU-N 4/54 – see also Pl. 3, fig. 5), in ventral view. B – Proximal part of urostyle of *Aralobatrachus robustus* (LU-N 6/299 – see also Pl. 4, fig. 6), in dorsal view. C – Proximal part of the urostyle in *Discoglossus pictus* (DP FNSP 6514; loc. Perpignan, France), in dorsal view (right proc. transversus not fully developed).

Material: Centrum of V3 with the right transverse process, LU-N 5/222 (Text-fig. 20).

Description: Centrum is opisthocoelous, with dorsal and ventral margins of the posterior articular facet distinctly concave. There is a well pronounced median ridge on both dorsal and ventral surfaces of the centrum, separating two deep depressions. The ridge on the bottom of the neural canal is more prominent and broadens anteriorly and posteriorly. The proc. transversi moderately dilate towards their distal end. The basis of the neural arches is elongated antero-posteriorly; hence, they were imbricate.

Material: Prooticooccipitals, LU-N 5/155 (Text-fig. 23B), 5/182 (Text-fig. 23A), 6/325 (Text-fig. 21A; Pl. 12, fig. 4), LU-N 6/431 (Text-fig. 21B; Pl. 12, fig. 5), 7/445 (Text-fig. 22). Probably also LU-N 7/459 (Text-fig. 21C) and 6/283 (Pl. 12, fig. 3).

Description: Assignment of these specimens to the Discoglossidae is based on laterally compressed prominentiae of the posterior semicircular ducts, typical of contemporary adult *Discoglossus* (they are less prominent and rounded in *Alytes* and *Bombina*), and on the presence of a foramen that probably served for the n. abducens (marked by "? VI" in Text-figs. 21 and 23B) piercing anterior wall of the otic capsule, at the medial end of the sulcus venae jugularis or slightly beneath it, also present in *Discoglossus* but lacking in *Alytes* and *Bombina*. LU-N 7/459 has such a foramen too, but the prominentia is broken off. This specimen is similar to LU-N 6/283, especially in the morphology of the condylar region; although the latter specimen comprises only the posterior wall of the otic capsule, its prominentia is well preserved, and considerably pronounced. The first two specimens agree with one another (and with LU-N 5/155) in their general shape and proportions, the second being distinguished by clearly delimited and rather wrinkled contact area for the frontoparietal. LU-N 7/459 differs from both of them in having the occipital condyli oriented more vertically, and by signs of pitted sculpture on the ventral surface. LU-N 5/182 and 6/431 have well developed facet for the frontoparietal, and horn-like prominentia with a ridge on its dorsal surface which is a continuation of a similar ridge on the frontoparietal. These characters are well developed in fully grown specimens of *Discoglossus*. By its size and morphology, the closest to *Discoglossus* is LU-N 7/445; judging from its size it might be associated with *Aralobatrachus* or other large discoglossids.

Material: Right scapula, LU-N 2/45 (Pl. 13, fig. 5).

Description: The bone is characteristic by a deep cleft between the pars acromialis and pars glenoidalis. This, as well as general proportions of the bone, recall those of *Latonia* (see e.g. ŠPINAR 1978: 298, pl. 68) and some specimens of *Discoglossus*.

Material: Left ilia, LU-N 6/291 (Text-fig. 28B; Pl. 9, fig. 9), 6/303 (Text-fig. 25F; Pl. 10, fig. 7); right ilium, LU-N 6/340 (Pl. 9, fig. 1); left ilium, LU-N 6/376 (Text-fig. 26A; Pl. 11, fig. 2); right ilia, LU-N 6/378 (Text-fig. 28F), 6/386 (Text-fig. 25H; Pl. 8, fig. 7), 6/403 (Text-fig. 26D); left ilium, LU-N 6/406 (Text-fig. 28C; Pl. 9, fig. 8); right ilium, LU-N 6/407 (Text-fig. 26C); left ilia, LU-N 6/421 (Text-fig. 28A), 7/450 (Pl. 10, fig. 5), 7/456 (Text-fig. 28D); right ilium, LU-N 8/463 (Text-fig. 26E; Pl. 8, fig. 5); left ilia, LU-N 8/468 (Text-fig. 25G; Pl. 10, fig. 2), LU-N 8/493 (Text-fig. 28G; Pl. 10, fig. 3).

Description: Remarkable is that the larger discoglossids come mostly from middle to upper part of the Bissekty Formation (Coniacian and transition to Santonian). Assignment to the Discoglossidae is based on the combination of following characters: the torus superior well developed, the pars ascendens directed postero-dorsally, the pars descendens well developed. LU-N 6/303 and 8/468 recall the corresponding element in *Alytes*.

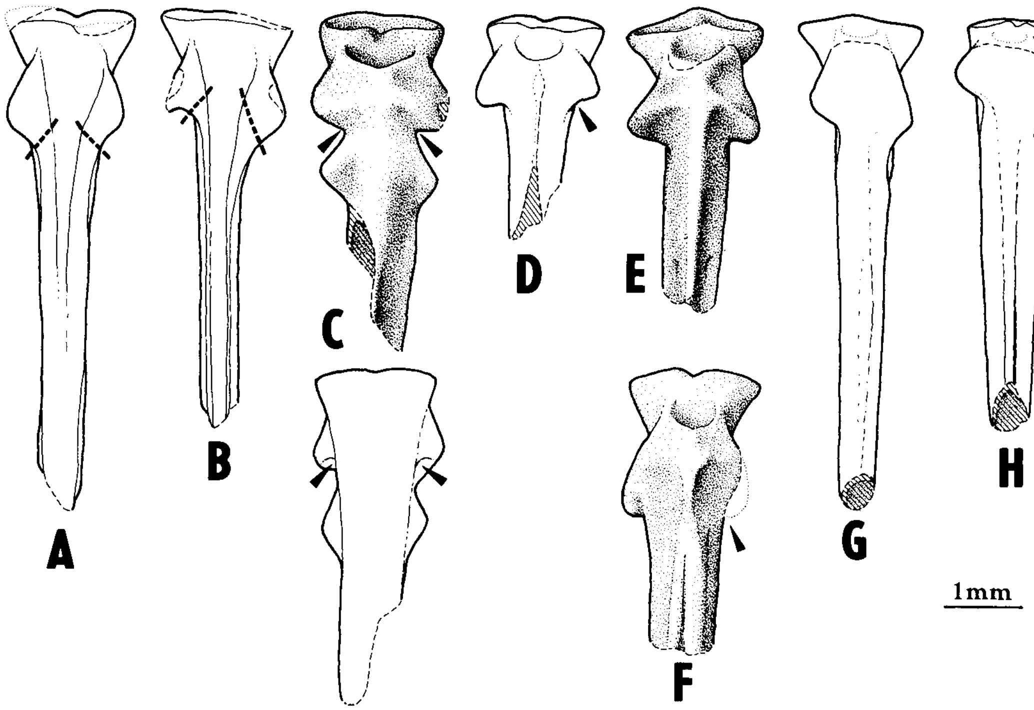
Material: Right humeri, LU-N 5/118 (Text-fig. 29U), 5/135 (Text-fig. 29I).

Description: These humeri are characteristic by the presence of both medial and lateral epicondyli, by the fact that the crista ventralis continues as a mound towards the medial epicondylus (and consequently that the fossa cubitalis ventralis is open laterally), and that the cristae medialis and lateralis are developed (though to various extent). The latter character gives an impression that this part of the humerus is dorsoventrally compressed.

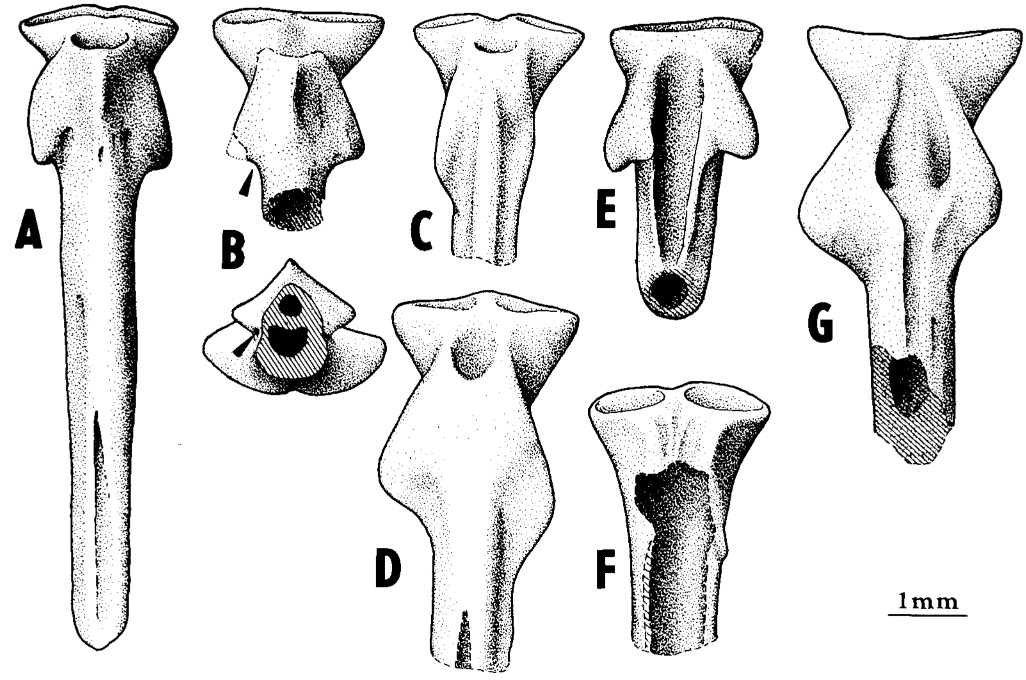
cf. Discoglossidae

Material: Centrum of the atlas, neural arches broken off, LU-N 7/457 (Text-fig. 19B; Pl. 3, fig. 1).

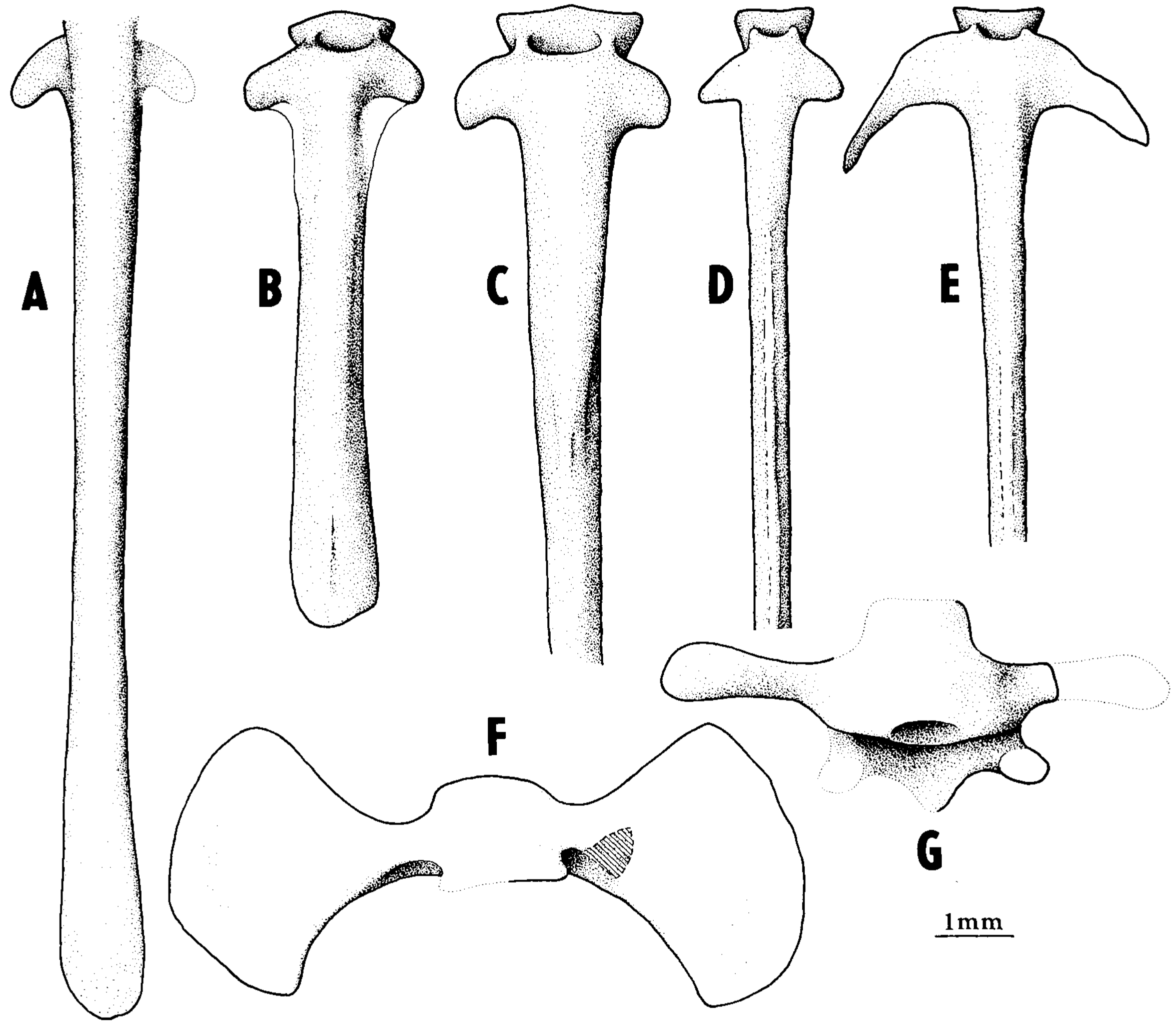
Description: Posteriorly, the centrum is concave. There are two flat facets for articulation with the occipital condyli, separated by a distinct depression that continues onto the ventral side of the centrum as a deep slot. If seen from the lateral side, both facets extend ventrally.



Text-fig. 16. Gobiatidae indet. or Discoglossidae indet. Urostyles (corresponding in size with sacral vertebrae of *Gobiates* sp. illustrated in Text-fig. 14 A, B), in dorsal aspect. A – Type I (LU-N 6/339 – see also Pl. 4, fig. 1). B – Type II (LU-N 5/189 – see also Pl. 4, fig. 2). C – Type III (LU-N 5/188 – see also Pl. 4, fig. 3; ventral aspect below). D – Type IV (LU-N 5/153 – see also Pl. 4, fig. 4). E – Type V (LU-N 2/4 – see also Pl. 4, fig. 5). F – Type V (LU-N 5/126). G–I – Type VI (LU-N 5/257, 6/268, 5/162). Arrows mark position of intervertebral canals.



Text-fig. 17. Gobiatidae indet. or Discoglossidae indet. Urostyles in dorsal view. A – LU-N 5/243. B – LU-N 5/213 (see also Pl. 4, fig. 7; below is the same specimen in posterior view, to show position of the intervertebral canal which is marked by an arrow). C – LU-N 3/46. D – LU-N 6/404. E – LU-N 5/205. F – LU-N 2/8. G – LU-N 6/395 (see also Pl. 4, fig. 8).



Text-fig. 18. A, F, G – Hitherto undescribed anuran (PIN 3907/10) from the locality Udan Sair, S. Gobi Desert, Mongolia (Upper Cretaceous, Djadokhta Formation). Urostyle (A), partly reconstructed; sacral vertebra (F); V3 (G); all in ventral view. B–E-Urostyles of some recent representatives of the Leiopelmatidae and Discoglossidae, in dorsal view. B – *Ascaphus truei* (DP FNSP 6537; Deer Creek, Montana, USA). C – *Alytes obstetricans* (DP FNSP 6457; locality unknown). D – *Bombina variegata* (DP FNSP 6441; Vyšné Ružbachy, Czechoslovakia). E – *Bombina variegata* (DP FNSP 6536; Olympos Mts., Greece).

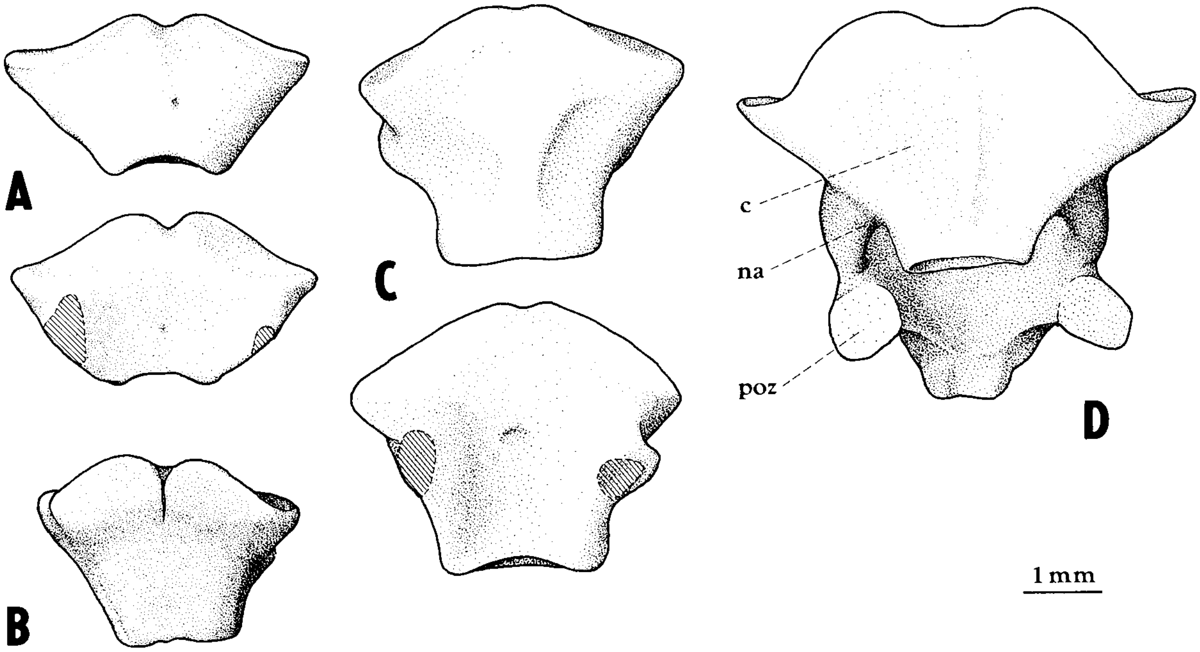
Material: Right humerus, LU-N 2/24 (Text-fig. 31B).

The specimen is described in the chap. Malformations.

Evolution of Discoglossidae

It is difficult to make comparisons with Jurassic discoglossids because these are mostly poorly preserved (the skeleton disappeared during fossilization, or is affected by recrystallization); besides, the skeletal elements are articulated and embedded in matrix.

Opisthocoely was established already in the late Turonian, as documented by the V3 of *Aralobatrachus* (LU-N 4/54). This confirms the statement by VERGNAUD-GRAZZINI (1975) that the principal discoglossid characters were developed already prior to the Late Jurassic. If it is accepted that ancestry of discoglossids should be placed among leiopelmatid-like Jurassic forms, then opisthocoely developed from amphicoely. In the early Discoglossidae (*Aralobatrachus*) the neural canal in the urostyle is open dorsally, whereas in the contemporary representatives of



Text-fig. 19. A – cf. Gobiatidae. Centrum of the atlas in ventral (above) and dorsal (below) views (LU-N 6/436). B – cf. Discoglossidae. Centrum of the atlas in ventral view (LU-N 7/457 – see also Pl. 3, fig. 1). C – Discoglossidae indet. Centrum of the atlas in ventral (above) and dorsal (below) views (LU-N 6/317). D – *Discoglossus pictus*, atlas in ventral view (DP FNSP 6514; loc. Perpignan, France).

the family (*Alytes, Discoglossus*; see BOLKAY, 1919, fig. 43; SANCHÍZ, 1984, figs. 65–68) it is partly or entirely closed. It is difficult to decide whether this suggests some evolutionary trend within the discoglossid lineage. Archaic nature of discoglossids may be seen in the fact that the neural canal of the urostyle in *Discoglossus* is partly open dorsally, similar to extinct gobiatid-like or discoglossid forms (compare Text-figs. 15C and 16A, B), and to a lesser degree also in some specimens of *Ascaphus* and *Alytes*.

Gobiatidae indet. or Discoglossidae indet.

The urostyles described below can be referred either to Gobiatidae or to Discoglossidae because in both families the articulation between the sacrum and urostyle is bicondylar. Text-fig. 16 shows the urostyles that are corresponding in size to the sacral vertebra of two forms of *Gobiates* described on pages 18–19 and illustrated in the Text-fig. 14. Similar urostyles of some Recent forms are in Text-fig. 18.

Type I – LU-N 6/339 (Text-fig. 16A; Pl. 4, fig. 1). The fossa condyloidea is distinctly bipartite; the division is reflected also on the dorsal and ventral margins of the fossa by the deep median notch in each of them. There is no roof above the neural canal; instead, the walls are directed dorsomedially but not contacting one another. This results in a formation of the neural groove. As the groove becomes shallower and walls become lower posteriorly, it disappears still within the proximal half of the bone. A pair of horizontally compressed transverse processes is developed proximally. Underneath their posterior part there is a wide intervertebral canal on each side, piercing obliquely the wall of the neural groove.

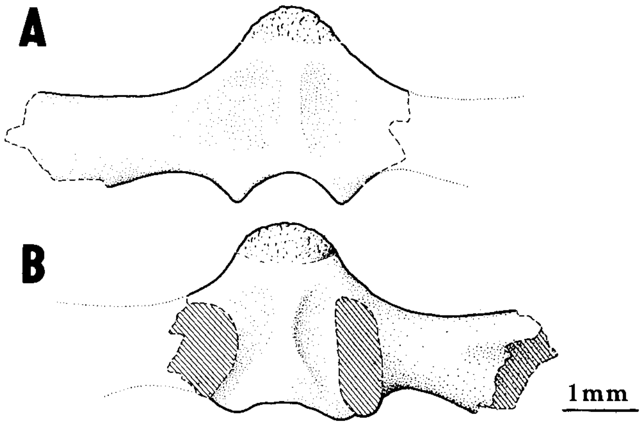
Type II – LU-N 7/189 (Text-fig. 16B; Pl. 4, fig. 2). This type is basically the same as the previous one, however, it differs in having walls of the neural groove developed along the whole length of the preserved part (more than one half of the estimated length of the bone), and in having an outer orifice of the intervertebral canal posterior (not below) of the proc. transversus. Other differences are probably due to individual variation.

Specimen LU-N 6/432 is similar to types I and II but as it is heavily damaged its closer assignment is impossible.

Type III – LU-N 5/188 (Text-fig. 16C; Pl. 4, fig. 3). This specimen is unique among other urostyles in having two pairs of transverse processes instead of one, and in having a large intervertebral canal piercing the wall of the neural canal almost transversally. The outer surface of the intervertebral canal is in a deep and well delimited depression underneath the posterior part of the proximal transverse process. The distal pair of processes is similar in shape but smaller. The neural canal is completely closed dorsally. Whereas at the level of the proximal processes its roof produces a distinct bump-like elevation from which a ridge runs down laterally toward the tip of either process, there is only a median mound at the level of the posterior pair. This mound becomes a sharp edge posteriorly.

Type IV – LU-N 5/153 (Text-fig. 16D; Pl. 4, fig. 4). This and other following urostyles are characterized by a single pair of transverse processes and by well developed neural canal. In these features they agree with the contemporary *Ascaphus, Alytes*, and young *Bombina* (see Text-fig. 18). Only exceptionally the neural canal can be open posteriorly by a narrow slot, similar to some specimens of *Ascaphus* and *Alytes*.

The fossa condyloidea is distinctly bipartite but in contrast to the previous types this is due to a median ridge that divides the fossa. The ridge is manifested in both upper and lower margins of the fossa. There is a high median bump with lateral ridges at the level of transverse processes. The bump continues both anteriorly and posteriorly as a distinct median ridge with nearly vertical walls. Laterally, there is a distinct horizontal ledge on either side, which is a continuation of a horizontal edge on the transverse processes. The orifice of the intervertebral canal below the mentioned processes is very indistinct. Tiny foramina directed posteriorly are on the upper lateral surface of the bone.



Text-fig. 20. Discoglossidae indet. Praesacral vertebra (most probably V3) in ventral (A) and dorsal (B) views (LU-N 5/222).

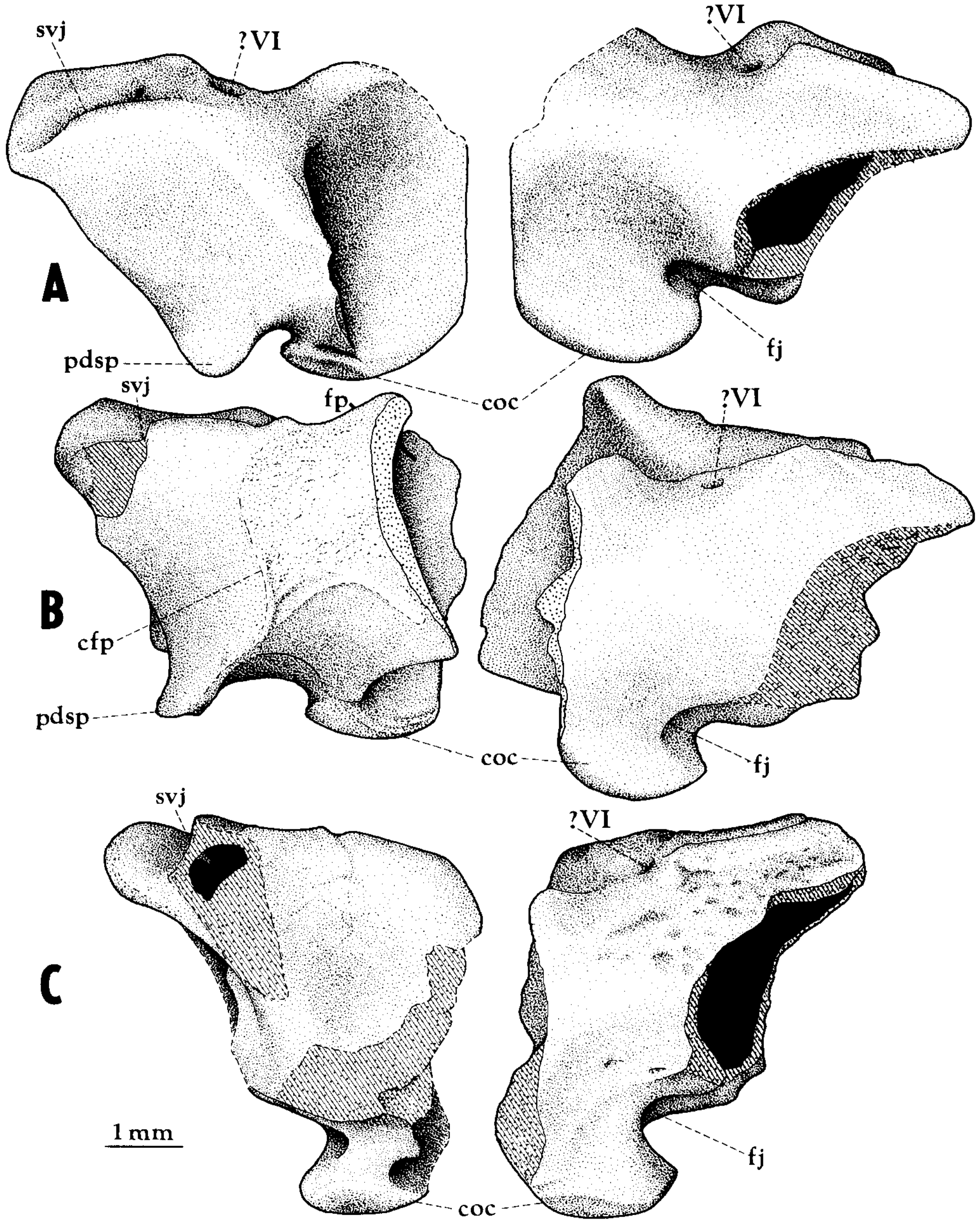
Type V – LU-N 2/4 (Text-fig. 16E; Pl. 4, fig. 5), 5/126 (Text-fig. 16F). The fossa condyloidea is distinctly bipartite; the partition may be manifested by a notch well seen from the dorsal side. The distinct and almost pointed elevation is at the level of the transverse processes (and may be thus termed the proc. spinosus). It continues posteriorly as a median ridge which may bifurcate shortly behind the level of the posterior limit of the transverse processes. The splitting of the ridge is a remnant of the communication into the neural canal. Below the posterior margin of the transverse processes there is a distinct orifice of the intervertebral canal.

Type VI – LU-N 5/162 (Text-fig. 16I), 5/257 (Text-fig. 16G), 6/268 (Text-fig. 16H). All the three specimens agree in having transverse processes triangular, with their dorsal surface almost flat. The median dorsal ridge is well developed distally rather than proximally. The outer orifice of the intervertebral canal may be rather large, and may continue posteriorly as a groove, paralleled dorsally and ventrally by ridges. The dorsal of them is continuous with the transverse processes which are distinctly compressed dorso-ventrally. Only in LU-N 5/162 the orifice of the intervertebral canal is tiny, without peripheral groove on the lateral surface of the bone. It is hard to decide whether this difference is of taxonomic value or reflects only individual variation.

Specimen LU-N6/289 is heavily damaged but according to preserved characters it may be associated with the type VI.

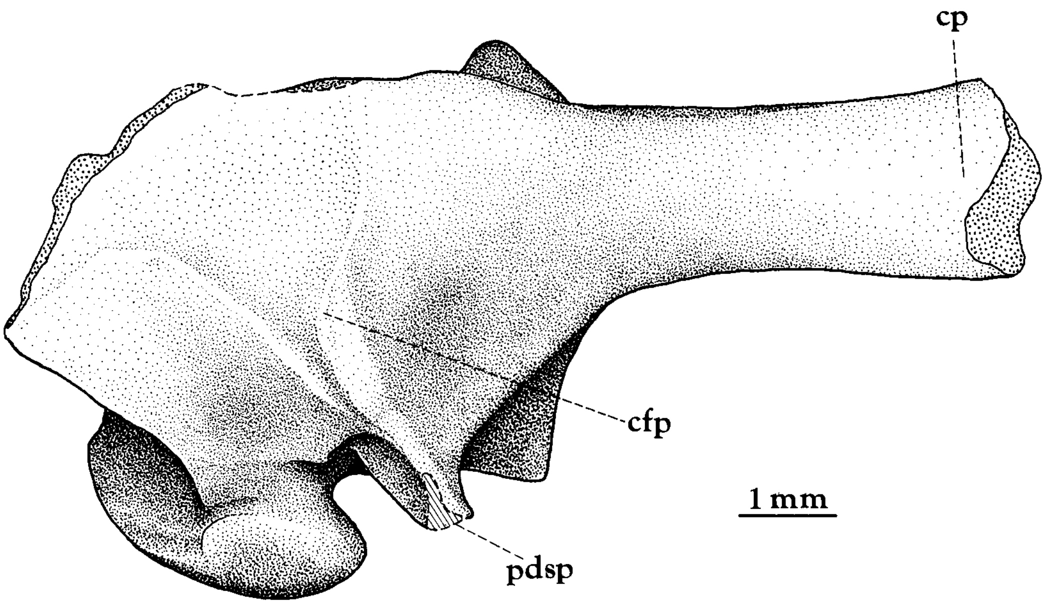
The following are larger urostyles that display certain morphological affinities with contemporary *Discoglossus* (see Text-fig. 15C). They may be divided into two basic types:

Type VII – LU-N 2/41, 2/42, 3/46 (Text-fig. 17C), 5/213 (Text-fig. 17B; Pl. 4, fig. 7), 5/243 (Text-fig. 17A), 6/399 (Pl. 4, fig. 11), 6/404 (Text-fig. 17D), and possibly LU-N 2/8 (Text-fig. 17F) and 6/320. All these urostyles have a clearly bipartite condylar fossa, widely triangular transverse processes, and a roofed neural canal. However, variation

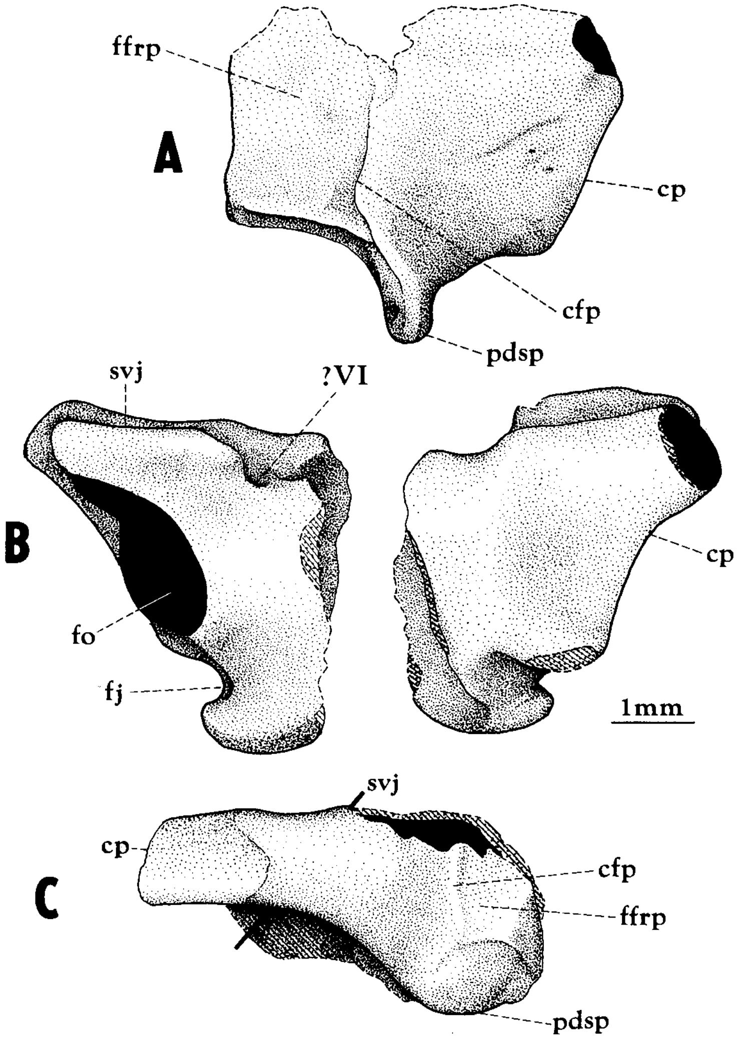


Text-fig. 21. Prooticooccipitals in dorsal (left) and ventral (right) views. A – Discoglossidae indet. (LU-N 6/325). B – Discoglossidae indet. (LU-N 6/431; reversed for comparison). C – cf. Discoglossidae (LU-N 7/459). Orifice of the canal that possibly served for the n. abducens (VI) is marked by "? VI".

Text-fig. 23. Prooticooccipitals. A – Discoglossidae indet. , right prooticooccipital in dorsal view (LU-N 5/182). B – cf. Discoglossidae, right prooticooccipital in dorsal (right) and ventral (left) view (LU-N 5/155). C – cf. *Gobiates*, left prooticooccipital in dorsal view (LU-N 5/226).



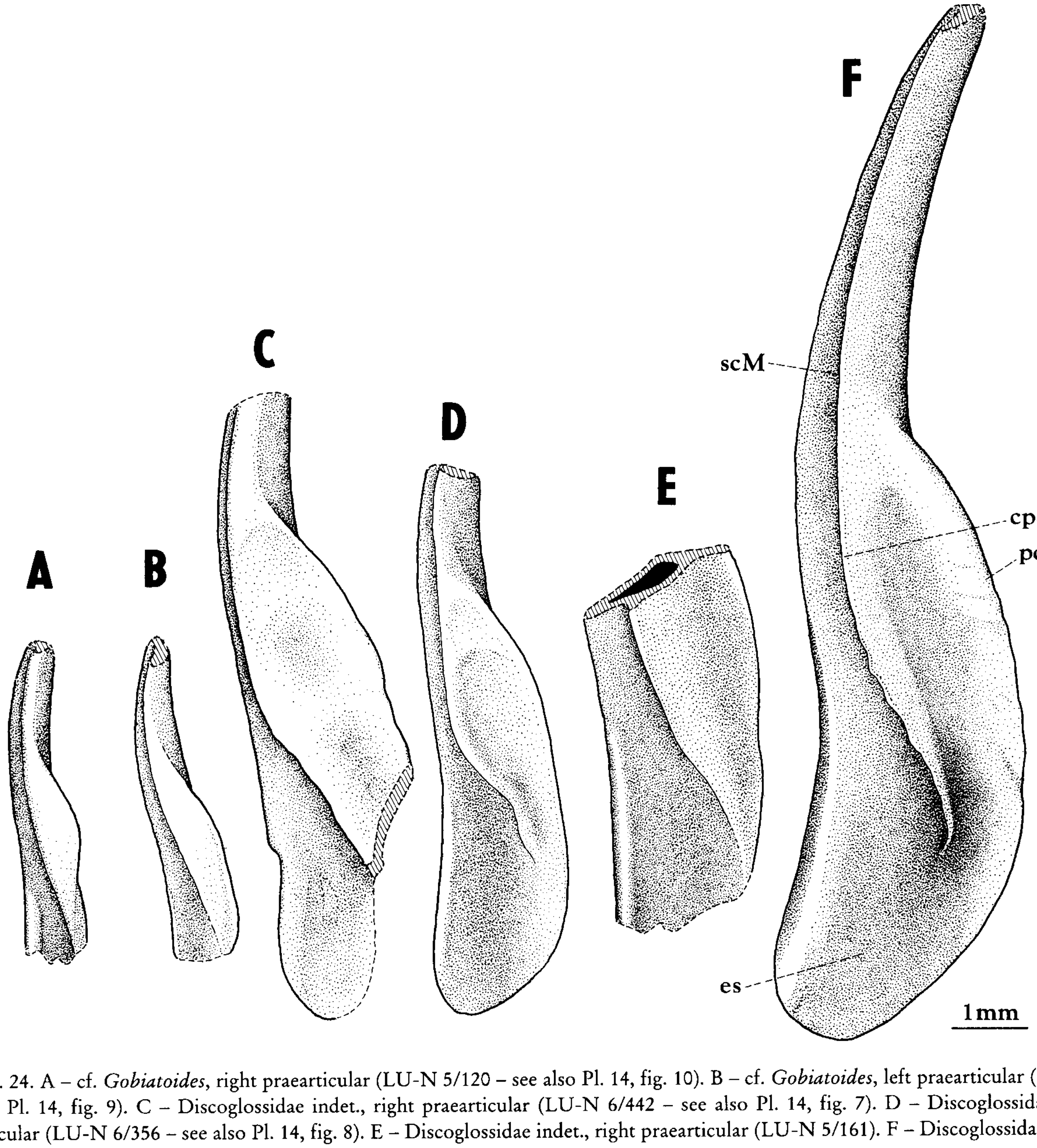
Text-fig. 22. Right prooticooccipital in dorsal view, Discoglossidae indet. (LU-N 7/445).



exists in all these characters – separation of both condylar depressions may be wide or indistinct, the fossa may be facing anteriorly or antero-dorsally, the transverse processes well or only moderately prominent, and the roof of the neural canal with longitudinal median ridge or only flat. The outer orifice of the intervertebral canal is below the posterior part of the transverse process, however, there are also accessory canals on the dorsal surface (Text-fig. 17A). Another pair of canals is more posteriorly, on the lateral side. It is difficult to say whether mentioned differences are of some taxonomic value or represent only intraspecific variation.

Type VIII – LU-N 5/205 (Text-fig. 17E; Pl. 4, fig. 9), 6/395 (Text-fig. 17G; Pl. 4, fig. 8). These urostyles are characteristic by the neural canal which is open dorsally as a fissure, and that intervertebral canals are wide. Variation in other characters is similar to that in the previous type.

Remark: Type VIII recalls types I and II (Text-fig. 16A, B) from which it differs generally by its size. Same holds for type VII which recalls type VI (Text-fig. 16G–I). However, variation of some of their characters exceeds that in contemporary species and hence the above listed types may represent real taxonomic diversity.



Text-fig. 24. A – cf. *Gobiatoides*, right praearticular (LU-N 5/120 – see also Pl. 14, fig. 10). B – cf. *Gobiatoides*, left praearticular (LU-N 4/78 – see also Pl. 14, fig. 9). C – Discoglossidae indet., right praearticular (LU-N 6/442 – see also Pl. 14, fig. 7). D – Discoglossidae indet., left praearticular (LU-N 6/356 – see also Pl. 14, fig. 8). E – Discoglossidae indet., right praearticular (LU-N 5/161). F – Discoglossidae indet., right praearticular (LU-N 8/465 – see also Pl. 14, fig. 11). A, C, E, F reversed for comparison.

Material: Left ilia, LU-N 2/7 (Text-fig. 25S), 5/100 (Text-fig. 25Q; Pl. 9, fig. 6); right ilium, LU-N 5/115 (Text-fig. 25M); left ilia, LU-N 5/170 (Text-fig. 26I), 6/278; right ilium, LU-N 6/285; left ilia, LU-N 6/301 (Text-fig. 26K), 6/315 (Text-fig. 25R), 6/328 (Text-fig. 26G; Pl. 10, fig. 7); right ilium, LU-N 5/190 (Text-fig. 26B, Pl. 9, fig. 2); left ilium, LU-N 5/198; right ilia, LU-N 5/206 (Text-fig. 25P; Pl. 8, fig. 1), 5/225 (Text-fig. 25J); left ilia, LU-N 5/240 (Text-fig. 25N; Pl. 10, fig. 6), 6/342 (Text-fig. 25K; Pl. 11, fig. 6), 6/360 (Text-fig. 25L; Pl. 11, fig. 4); right ilia, LU-N 6/383 (Text-fig. 26F; Pl. 8, fig. 8), 6/389 (Text-fig. 26H; Pl. 9, fig. 4), 6/393 (Text-fig. 26J; Pl. 9, fig. 3); left ilium, LU-N 7/453 (Text-fig. 25O; Pl. 10, fig. 8); right ilium, LU-N 8/462 (Text-fig. 25I); left ilium, LU-N 8/489.

Description: Certain number of specimens (LU-N 2/7, 5/100, 6/315, 5/225, and 6/360) may be defined by the fact that the pars ascendens is declined posteroventrally; other well defined group (e. g. LU-N 5/240, 6/383, 6/393) has the pars ascendens directed posteriorly. LU-N 8/462 is unique among other ilia by its torus superior which is continuous with the pars ascendens. LU-N 5/190 has the iliac shaft well pronounced even within the acetabular part of the ilium (same feature is expressed to a lesser extent also in LU-N 6/389). Both specimens rather recall the holotype ilium of the Late Cretaceous discoglossid *Scotiophryne pustulosa* (see ESTES 1969, fig. 1c). LU-N 6/301 and 6/389 have their pars ascendens directed posterodorsally, with no torus superior (or only poorly developed). This feature recalls the condition in *Ascaphus*. Noteworthy is also LU-N 5/170 the pars descendens of which is inclined below the acetabulum. The variation in morphology and size of the ilium does not allow a more precise determination.

Anura indet.

Material: Section of the maxillary, LU-N 2/11.

Description: The maxillary is dentate, its outer surface is smooth. The lamina horizontalis is not much prominent medially, widely rounded, and confluent with the inner surface of the bone.

Material: Section of the left maxillary, LU-N 5/255 (Text-fig. 9D); section of a dermal bone (perhaps fragment of the lamella alaris squamosi), LU-N 5/202.

Description: The outer surface of the maxillary is sculptured by numerous small pits separated by acute ridges. The lamina horizontalis is robust and rounded. The recessus vaginiformis corresponds to the shape and size of the proc. maxillaris anterior palatoquadrati. The proc. frontalis, though broken off, was obviously well developed. Noteworthy is the size of the fragment suggesting that the maxillary was larger than any of those belonging to the Gobiatidae.

The fragment of a dermal bone LU-N 5/202 may be associated with the just described fragment of the maxillary on the basis of the same type of sculpture.

Remark: The type of sculpture, as well as the size of the element recall those in *Macropelobates* from the Early/Middle Oligocene of Mongolia (NOBLE 1924, ROČEK 1982). However, the limited material and considerable time span (50 million years) between both forms prevent to associate one with another.

Material: Sphenethmoideum, LU-N 7/448 (Text-fig. 12B; Pl. 12, fig. 1), and 5/141 (Text-fig. 12C).

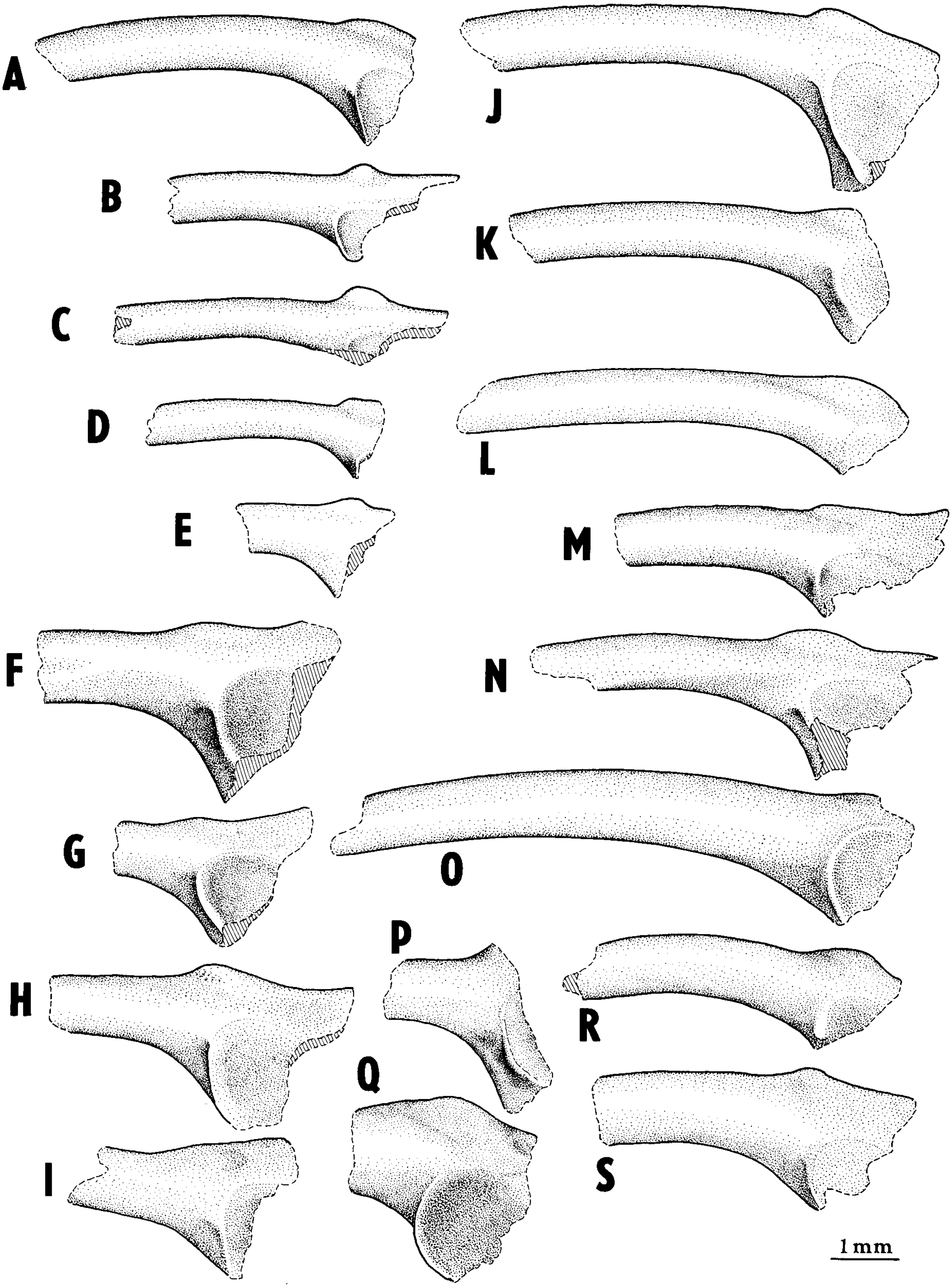
Description: The first specimen has an elevated field on its dorsal surface similar to that in LU-N 5/180 described under cf. *Gobiates*. However, it differs from the latter by unsculptured surface of this field, the shape of the margo orbitalis, and the extent of ossification of the postnasal wall. Conspicuous character of this specimen is a dorsally elevated lateral part of the solum nasi which can be seen in ventral view as a deep and well delimited depression along the lateral margin of the solum. Unfortunately, the corresponding part of the sphenethmoideum is not preserved in other specimens. LU-N 5/141 is slightly larger but too worn to be assigned either to the previous type or to cf. *Gobiates*.

Material: Left scapula. LU-N 1/1 (Pl. 13, fig. 4).

Description: This scapula is not cloven between the acromial and glenoid parts like LU-N 2/45 (see Discoglossidae indet.). Another difference is that lateral section of the anterior margin of the bone is clearly delimited medially by a process; this margin served for synchondrotic articulation with the clavicle.

Material: Middle section of the femur, LU-N 6/426 (Pl. 14, fig. 1).

Description: The crista femoris is prominent, with rather undulated edge. This, however, does not contribute to a precise taxonomic assignment.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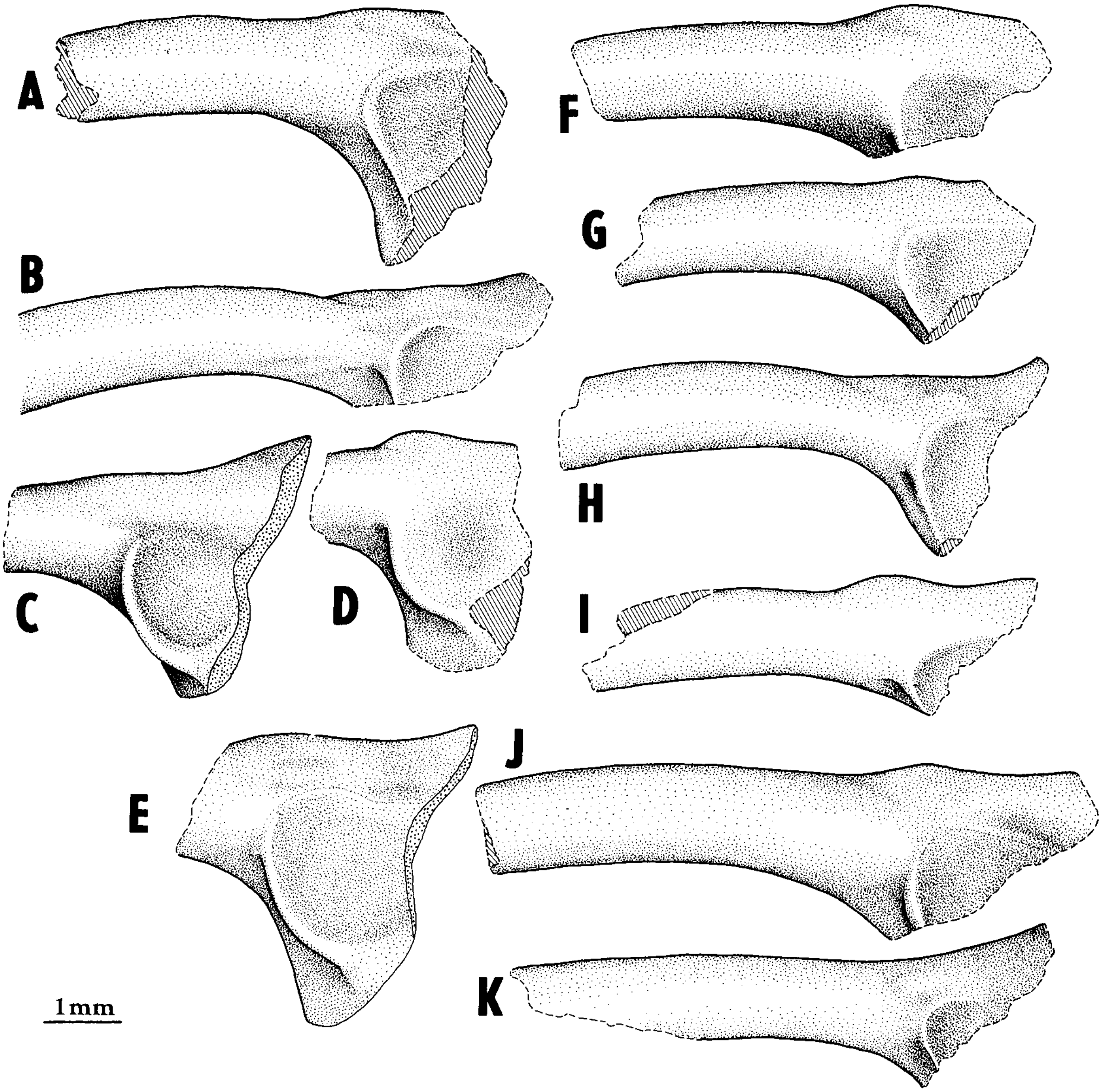
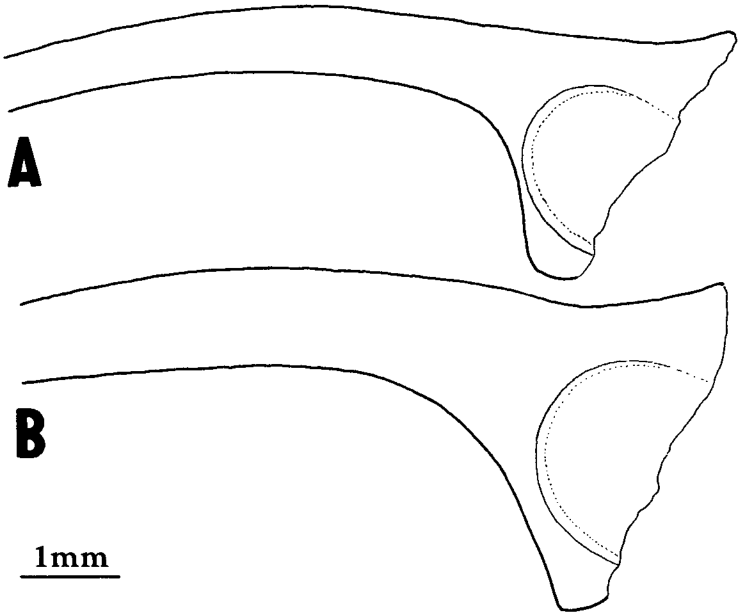


Text-fig. 26. A – Discoglossidae indet., left ilium (LU-N 6/376 – see also Pl. 11, fig. 2). B – Gobiatidae or Discoglossidae indet., right ilium (LU-N 5/190 – see also Pl. 9, fig. 2). C – Discoglossidae indet., right ilium (LU-N 6/407). D – Discoglossidae indet., right ilium (LU-N 6/403). E – Discoglossidae indet., right ilium (LU-N 8/463 – see also Pl. 8, fig. 5). F – Gobiatidae or Discoglossidae indet., right ilium (LU-N 6/383 – see also Pl. 8, fig. 8). G – Gobiatidae or Discoglossidae indet., left ilium (LU-N 6/328 – see also Pl. 10, fig. 7). H – Gobiatidae or Discoglossidae indet., right ilium (LU-N 6/389 – see also Pl. 9, fig. 4). I – Gobiatidae or Discoglossidae indet., left ilium (LU-N 5/170). J – Gobiatidae or Discoglossidae indet., right ilium (LU-N 6/393 – see also Pl. 9, fig. 3). K – Gobiatidae or Discoglossidae indet., left ilium (LU-N 6/301). All in lateral view. B – F, H, and J reversed for comparison.

Text-fig. 25. A – Gobiatidae indet., left ilium (LU-N 7/444 – see also Pl. 11, fig. 1). B – Gobiatidae indet., left ilium (LU-N 5/169 – see also Pl. 10, fig. 4). C – Gobiatidae indet., right ilium (LU-N 5/93). D – Gobiatidae indet., left ilium (LU-N 6/400 – see also Pl. 9, fig. 5). E – Gobiatidae indet., left ilium (LU-N 5/159). F – Discoglossidae indet., left ilium (LU-N 6/303 – see also Pl. 9, fig. 7). G – Discoglossidae indet., left ilium (LU-N 8/468 – see also Pl. 10, fig. 2). H – Discoglossidae indet., right ilium (LU-N 6/386 – see also Pl. 8, fig. 7). I – Gobiatidae or Discoglossidae indet., right ilium (LU-N 8/462). J – Gobiatidae or Discoglossidae indet., right ilium (LU-N 5/225). K – Gobiatidae or Discoglossidae indet., left ilium (LU-N 6/342 – see also Pl. 11, fig. 6). L – Gobiatidae or Discoglossidae indet., left ilium (LU-N 6/360 – see also Pl. 11, fig. 4). M – Gobiatidae or Discoglossidae indet., right ilium (LU-N 5/115). N – Gobiatidae or Discoglossidae indet., left ilium (LU-N 5/240 – see also Pl. 10, fig. 6). O – Gobiatidae or Discoglossidae indet., left ilium (LU-N 7/453 – see also Pl. 10, fig. 8). P – Gobiatidae or Discoglossidae indet., right ilium (LU-N 5/206 – see also Pl. 8, fig. 1). Q – Gobiatidae or Discoglossidae indet., left ilium (LU-N 5/100 – see also Pl. 9, fig. 6); R – Gobiatidae or Discoglossidae indet., left ilium (LU-N 6/315). S – Gobiatidae or Discoglossidae indet., left ilium (LU-N 2/7). All in lateral view. C, H, I, J, M, P reversed for comparison.



Text-fig. 27. Shape of the left ilia. A – *Ascaphus truei* male, DP FNSP 6537, Deer Creek, Montana. B – *Leiopelma hamiltoni*, DP FNSP uncatalogued, locality unknown.

Material: Radioulnae, LU-N 2/28, 4/76 (Pl. 12, fig. 8), 5/94, 5/121, 5/146, 5/149 (Text-fig. 30C; Pl. 13, fig. 1), 5/152 (Text-fig. 30D; Pl. 12, fig. 6), 5/184, 5/214, 5/234, 5/236 (Text-fig. 30B), 6/266, 6/309 (Text-fig. 30E; Pl. 7, fig. 7), 6/318, 6/323 (Text-fig. 30A), 6/368, 8/471, 8/478.

Description: The material comprises mostly proximal sections of the bones that considerably vary in size (see Text-fig. 30) but other diagnostic features are not significant.

Material: Ischia, LU-N 5/166 (Pl. 2, fig. 5). The element bears no diagnostic characters.

Material: Femurs (mostly their distal sections), LU-N 2/35, 2/39, 4/52, 4/80, 4/85, 5/132, 5/138, 5/154, 5/157, 5/187, 5/217, 5/230, 5/232 (Pl. 11, fig. 7), 5/253, 6/269, 6/312, 6/316, 6/326, 6/329 (Pl. 14, fig. 6), 6/331, 6/349, 6/364, 6/413, 6/438, 8/482.

Description: LU-N 6/269 and 6/364 are distinctly "S" shaped and correspond by their size to those determined as Gobiatidae indet. LU-N 2/35 is similar in its size, but is spiral shaped. Specimen LU-N 6/312 lacks completely the crista femoris but instead, it is laterally compressed within its proximal section. LU-N 6/413 has a faint rugosity instead of the crista femoris. LU-N 5/232 is described in the chap. Malformations.

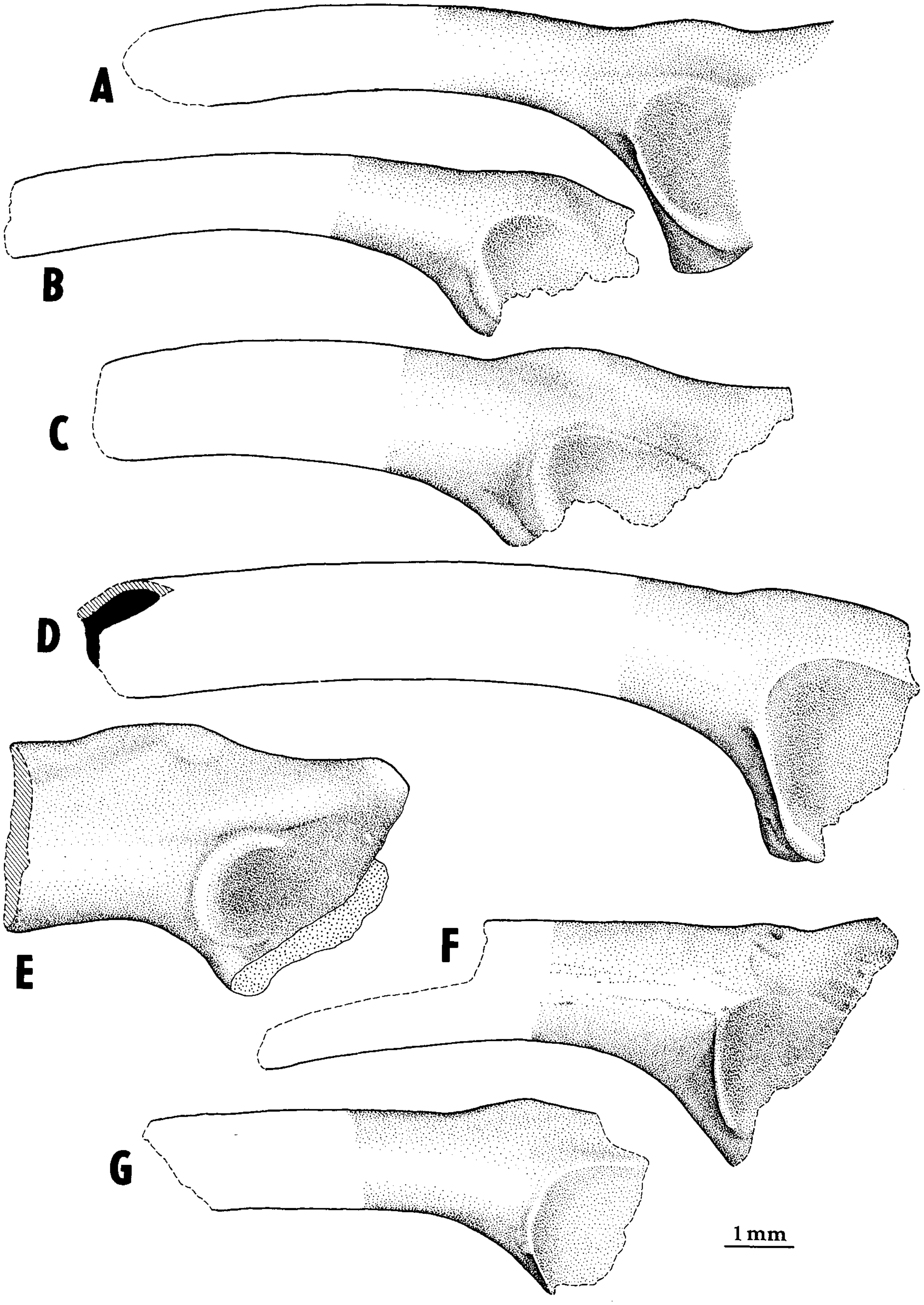
Material: Tibiofibulae, LU-N 1/3, 2/5, 2/6, 2/13, 2/16, 2/17, 2/20, 2/22, 2/23, 2/27, 2/36, 2/37, 4/47, 4/50, 4/53, 4/59, 4/60, 4/61, 4/63, 4/66, 4/72, 4/79, 4/83, 4/87, 4/91, 5/92, 5/99, 5/101, 5/103, 5/104, 5/112, 5/114, 5/116, 5/131, 5/134, 5/144, 5/148, 5/163, 5/175, 5/181, 5/195, 5/196, 5/208, 5/216, 5/233, 6/261, 6/292, 6/297a, 6/298, 6/300, 6/321, 6/327, 6/330, 6/334, 6/345, 6/346, 6/351, 6/361, 6/370a, 6/373, 6/379, 6/387, 6/391, 6/397, 6/408, 6/414, 6/425, 6/430, 7/446, 7/460, 7/461, 9/496.

Description: The tibiofibulae are uniform, varying only in size and presence or absence of the sulcus for the arteria nutritia.

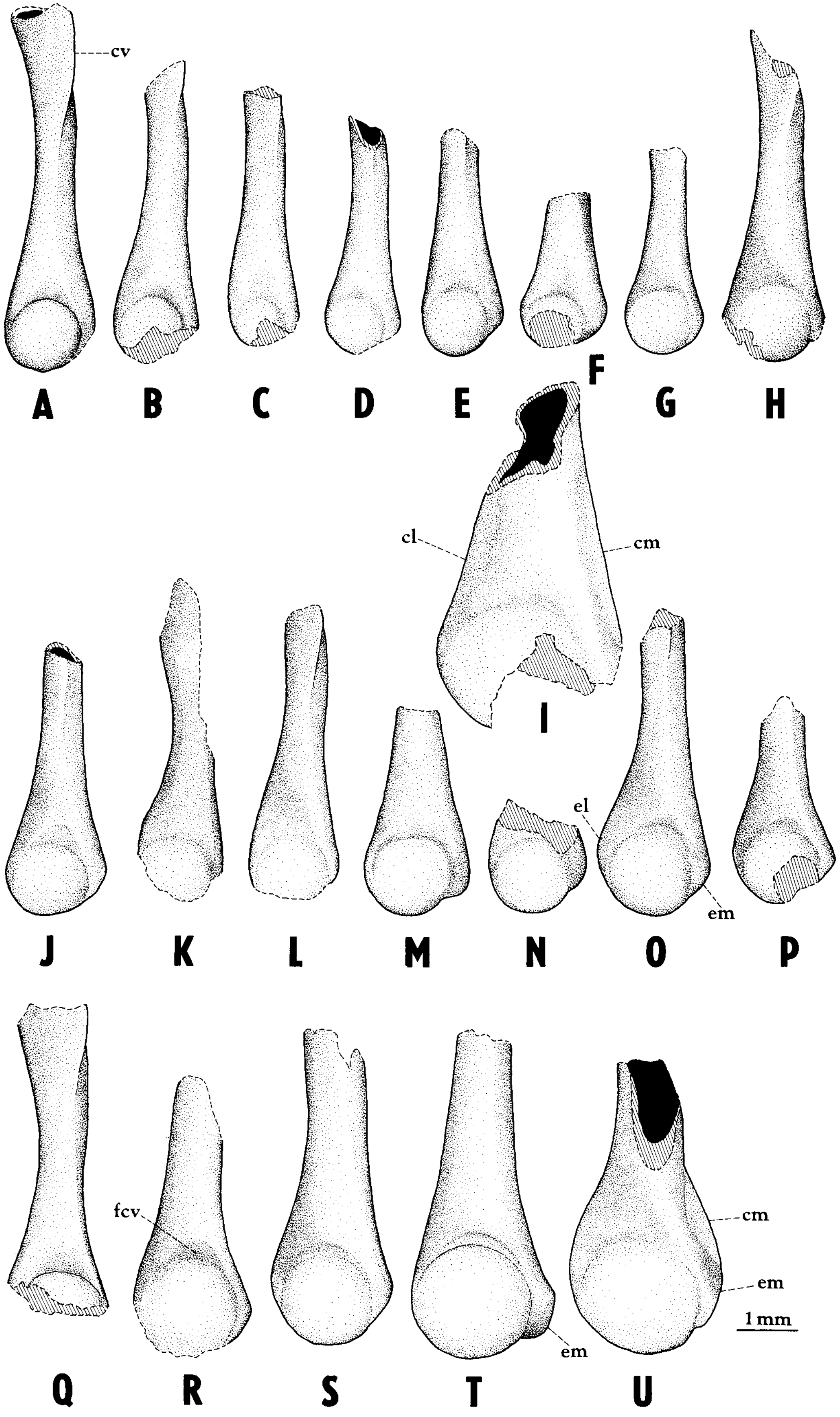
Remark: Sculptured dermal bones LU-N 5/259, 6/264 (Pl. 13, figs. 2 and 3) differ in their sculpture from all other anuran dermal bones in the material. This makes their assignment to the Anura doubtful.

Malformations

The humerus LU-N 2/43 (Text-fig. 31A) is remarkable by the fact that its caput is not developed. Instead, there is only a deep cavity rimmed by a mound. Noteworthy are also thin diaphysis and weakly developed medial and lateral cristae. This might be suggestion that the leg was not movable. Absence of the fossa cubitalis and size of the bone suggest that it might be assigned to *Kizylkuma*. Similar malformation may be found in the gobiatid humeri LU-



Text-fig. 28. A–D Discoglossidae indet. A – Left ilium (LU-N 6/421). B – Left ilium (LU-N 6/291 – see also Pl. 9, fig. 9). C – Left ilium (LU-N 6/406 – see also Pl. 9, fig. 8). D – Left ilium (LU-N 7/456). E – Anura indet., right ilium (LU-N 2/15 – see also Pl. 8, fig. 2). F–G Discoglossidae indet. F – Right ilium (LU-N 6/378). G – Left ilium (LU-N 8/493 – see also Pl. 10, fig. 3). All in lateral view. E and F reversed for comparison.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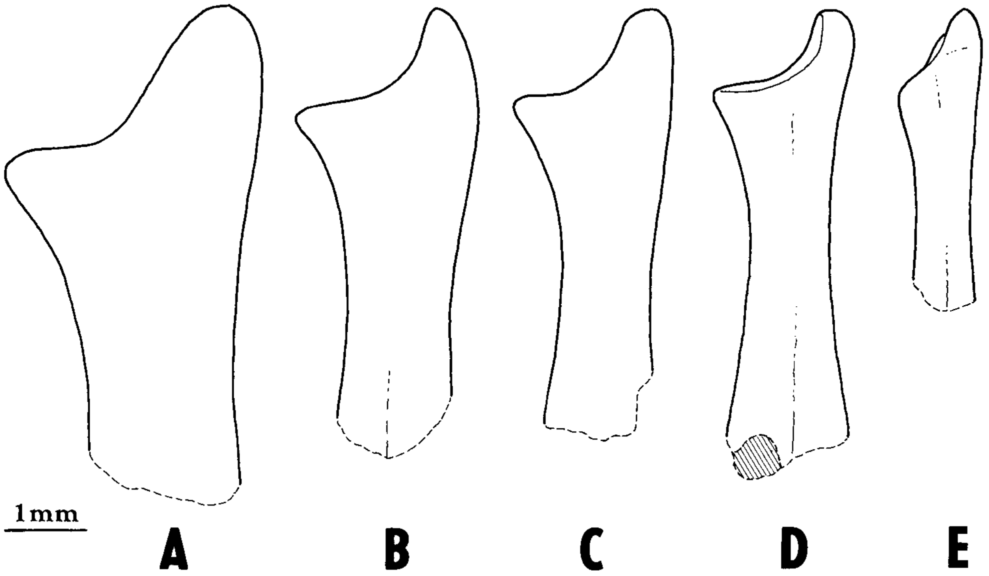
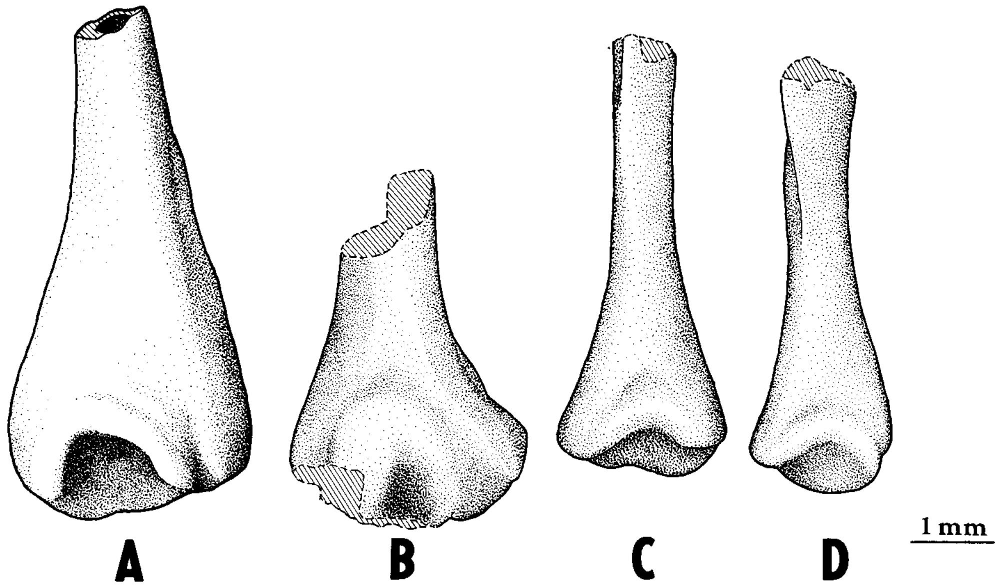


Text-fig. 30. Anura indet., proximal parts of radioulnae. A – LU-N 6/323; B – 5/236; C – 5/149 (see also Pl. 13, fig. 1); D – LU-N 5/152 (see also Pl. 12, fig. 6); E – LU-N 6/309 (see also Pl. 12, fig. 7). A and B reversed for comparison.



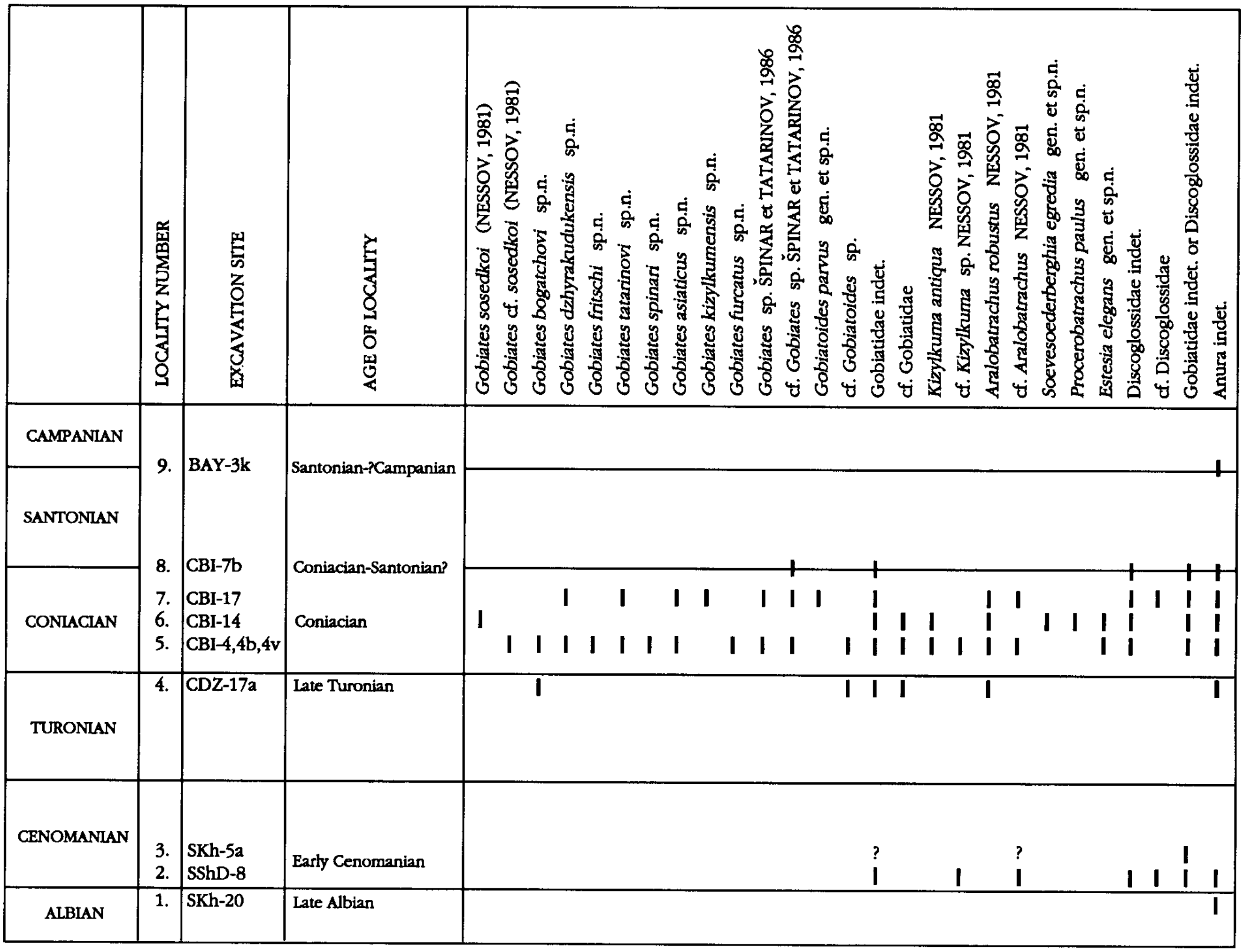
Text-fig. 31. Malformations of the humerus. A – cf. *Kizylkuma* NESSOV, 1981, distal part of the right humerus (LU-N 2/43); B – cf. Discoglossidae, right humerus (LU-N 2/24); C – Gobiatidae indet., left humerus (LU-N 4/90); D – Gobiatidae indet., left humerus (LU-N 5/113). The caput humeri is poorly developed.

◄

Text-fig. 29. A–H, J–T humeri of the Gobiatidae. A – LU-N 6/377 (see also Pl. 6, fig. 2); B – LU-N 5/102; C – 6/358; D – LU-N 5/168; E – LU-N 5/133 (see also Pl. 6, fig. 7); F – LU-N 5/151; G – LU-N 5/142; H – LU-N 6/338 (see also Pl. 6, fig. 5); J – LU-N 6/372; K – LU-N 5/174; L – LU-N 6/410; M – LU-N 5/164; N – LU-N 5/160; O – LU-N 5/212 (see also Pl. 7, fig. 2); P – LU-N 5/119; Q – LU-N 6/396, R – LU-N 6/307; S – LU-N 6/336 (see also Pl. 7, fig. 1); T – LU-N 5/244 (see also Pl. 7, fig. 3). Discoglossidae indet. I – LU-N 5/135; U – LU-N 5/118. All are right humeri except for B, G, H, L, M, O, P and R which are reversed for comparison.

N 4/90, 5/113 (Text-fig. 31C, D; Pl. 11, fig. 9), 5/108, and 6/362. Their diaphyses are, however, well developed, incl. the crista ventralis. The humerus LU-N 2/24 (Text-fig. 31B) has its caput humeri almost complete, but with a sign of similar underdevelopment on its distal surface. It should be noted that these specimens were otherwise fully ossified and grown up, so incomplete epiphysial ossification due to younger developmental stages must be excluded. This is confirmed by another gobiatid specimen LU-N 5/167 (Pl. 11, fig. 8) which is similar in its malformation to the previous ones but, moreover, has a peculiar fully ossified outgrowth in the fossa cubitalis ventralis.

The malformation of the femur in the specimen LU-N 5/232, an indeterminable anuran (Pl. 11, fig. 7), obviously prevented any joint movements as well. The femur LU-N 6/329 (Pl. 14, fig. 6) has a partially healed break.



Text-fig. 32. Stratigraphical occurrence of described anurans from central Asia.

Discussion

Among Cretaceous anurans of central Asia, *Aralobatrachus* and indeterminate anuran LU-N 5/202 are the biggest ones. However, compared with contemporary frogs they were only medium sized because the length of the humerus in *Aralobatrachus* corresponds e. g. to that of *Discoglossus sardus* (Text-fig. 10). The majority of other forms were much smaller.

Gobiatidae display some characters that are undoubtedly primitive, namely the continuous notochord in some adults, amphicoelous centra, free ribs, and probably also urostyles with one (or even two) transverse processes. Some of these characters are preserved also in contemporary Leiopelmatidae and might thus indicate some relations between these two groups. Theoretically it would be possible to derive them from forms related to *Vieraella* and *Notobatrachus*, considered to be primitive leiopelmatids (Estes & Reig 1973). Discoglossidae are more advanced but similarly to Gobiatidae they also share some common characters with leiopelmatids. Close relationship between discoglossids and leiopelmatids may be evidenced e.g. by a striking similarity of the cranial anatomy of *Bombina* with the Leiopelmatidae (Slabbert & Maree 1945: 95); it should be emphasized that *Bombina* displays paedomorphic features (Smirnov 1989). The primitive and archaic status of leiopelmatids and discoglossids is generally accepted since Noble (1924) removed Leiopelmatidae as a separate group (see also e.g. Hecht 1960), and this is also reflected in all recent classifications (e.g. Lynch 1973, Savage 1973, Duellman 1975, Duellman & Trueb 1985). Structurally, gobiatids are intermediate between the Leiopelmatidae and Discoglossidae but this fact must not necessarily reflect real evolutionary history of these groups. In fact, if the conclusion by Vergnaud-Grazzini (1975) that principal discoglossid characteristics were established prior to the Late Jurassic is correct (presence of opisthocoelous forms simultaneously with amphicoelous ones in the Late Turonian of central Asia seems to confirm this statement), then gobiatids cannot be taken as discoglossid ancestors but rather an independent lineage. Ancestry of both Gobiatidae and Discoglossidae may be placed among the Jurassic Leiopelmatidae. All the three groups could have developed later independently, the former two reaching Laurasian continents before their separation from the former Gondwana. The time span for this migration was long enough – about 40 million years.

Acknowledgements

Our sincere thanks belong to Professors Z.V. Špinar and L.P. Tatarinov who kindly permitted comparisons of our material both with *Gobiates 'khermeentsavi'* and with an articulated anuran postcranial skeleton from the Upper Cretaceous of Gobi Desert (PIN 3907/10) that has not yet been published. Dr. Borja Sanchíz, Madrid, offered useful suggestions and criticism. Dr. Jiří Zídek, Socorro, USA kindly provided us with helpful comments and improved the text linguistically. Thanks are due also to A. Abramov, D.V. Bugaenko, G.O. Cherepanov, L. P. Fiodorova, L. B. Golovneva, A. O. Ivanov, M. N. Kazhyshkin, N.P. Kolomiytsev, T.B. Krassovskaya, R.A. Mertiniene, L.A. Nalbadjan and M. A. Sablin for collecting the material. Some technical works were financially supported by Stensiő Paleozoological Fund, Stockholm.

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Explanation of the plates

Plate 1

Fig. 1. *Gobiates* cf. *G. sosedkoi*. Right maxillary in lateral (a) and medial (b) views (LU-N 5/129; see also Text-fig. 4 D).
Fig. 2. *Gobiates bogatchovi* sp. n., holotype. Complex of the right maxillary, quadratojugal, quadrate, and lower jaw in lateral (a) and ventral (b) views (LU-N 5/107; see also Text-fig. 3 A).
Fig. 3. *Gobiates dzhyrakudukensis* sp. n., holotype. Right maxillary in lateral view (LU-N 6/341; see also Text-figs. 3 B, 4 A).
Fig. 4 *Gobiates dzhyrakudukensis* sp. n. Left maxillary in lateral view (LU-N 6/357).
Fig. 5. *Gobiates tatarinovi* sp. n., holotype. Right maxillary in lateral (a) and medial (b) views. (LU-N 6/405; see also Text-fig. 4 C).
Fig. 6. *Gobiates tatarinovi* sp. n. Right maxillary in lateral (a) and medial (b) views (LU-N 5/124).
Fig. 7. *Gobiates fritschi* sp. n., holotype. Right maxillary in lateral view (LU-N 5/143; see also Text-fig.4 B).
Fig. 8. *Gobiates dzhyrakudukensis* sp. n. Anterior part of the left maxillary in medial view (LU-N 5/140; see also Text-fig. 4 A).
Fig. 9. cf. *Aralobatrachus* NESSOV, 1981. Right praemaxillary in inner view (LU-N 5/158).
Fig. 10. *Gobiatoides parvus* gen. et sp. n., holotype. Right maxillary in medial view (LU-N 6/344; see also Text-fig. 6).
Fig. 11. *Gobiates furcatus* sp. n., holotype. Left maxillary in medial view (LU-N 5/165; see also Text-fig. 4 E). Bar equals 1 mm.

Plate 2

Fig. 1. *Kizylkuma antiqua* NESSOV, 1981. Right maxillary in medial view (LU-N 5/127).
Fig. 2. *Estesina elegans* gen. et sp. n., holotype. Right maxillary in lateral (a) and medial (b) views (LU-N 5/172; see also Text-fig. 9 H, I).
Fig. 3. *Saevesoederberghia egredia* gen. et sp. n. Right maxillary in medial view (LU-N 6/371).
Fig. 4. *Estesina elegans* gen. et. sp. n. Right maxillary in medial view (LU-N 5/98).
Fig. 5 Anura indet. Ischia in posterior view (LU-N 5/166).
Fig. 6 Anura indet. Tarsus (tibiale and fibulare) (LU-N 6/439).
Fig. 7 Gobiatidae indet. Section of femur in anterior view (LU-N 5/122).
Fig. 8 Gobiatidae indet. Proximal section of the femur in lateral view (LU-N 6/354). Bar equals 1 mm.

Plate 3

Vertebrae of Gobiatidae and Discoglossidae.
Fig. 1. cf. Discoglossidae. Centrum of the atlas in dorsal view (LU-N 7/457; see also Text-fig. 19 B).
Fig. 2. *Gobiates* sp. Praesacral vertebra 3 in posterior view (LU-N 6/348; see also Text-fig. 7 A).
Fig. 3. *Gobiates* sp. Praesacral vertebra 3 or 4 in anterior and slightly dorsal view (LU-N 5/239; see also Text-fig. 7 B).
Fig. 4. Gobiatidae indet. Praesacral vertebra in anterior view (LU-N 5/201; see also Text-fig.7 D).
Fig. 5. *Aralobatrachus robustus*. Third praesacral vertebra in dorsal (a) and ventral (b) views (LU-N 4/54; see also Text-fig. 15 A).
Fig. 6. Gobiatidae indet. Praesacral vertebra (most probably V7) in ventral view (LU-N 6/279; see also Text-fig. 8 F).
Fig. 7. Gobiatidae indet. Praesacral vertebra 3 in anterior view (LU-N 6/265; see also Text-fig. 8 D).
Fig. 8. Gobiatidae indet. Praesacral vertebra 6 or 7 in ventral view (LU-N 5/231; see also Text-fig.7 C).
Fig. 9. *Gobiates* sp. Sacral vertebra in posterior view (LU-N 5/191; see also Text-fig. 14 A).
Fig. 10. *Gobiates* sp. Sacral vertebra in posterior view (LU-N 5/246; see also Text-fig. 14 B). Bar equals 1 mm.

Plate 4

Urostyles of Gobiatidae and Discoglossidae indet. (except for 6).
Fig. 1. LU-N 6/339 (see also Text-fig. 16 A).
Fig. 2. LU-N 5/189 (see also Text-fig. 16 B).
Fig. 3. LU-N 5/188 (see also Text-fig. 16 C).
Fig. 4. LU-N 5/153 (see also Text-fig. 16 D).
Fig. 5. LU-N 2/4 (see also Text-fig. 16 E).
Fig. 6. *Aralobatrachus robustus* (LU-N 6/299; see also Text-fig. 15 B).
Fig. 7. LU-N 5/213 (see also Text-fig. 17 B).
Fig. 8. LU-N 6/395 (see also Text-fig. 17 G).
Fig. 9. LU-N 5/205 (see also Text-fig. 17 E).
Fig. 10. LU-N 5/243 (see also Text-fig. 17 A).
Fig. 11. LU-N 6/399. All except for 10 in dorsal view. Bar equals 1 mm.

Plate 5

Squamosals of Gobiatidae.

Fig. 1. *Gobiates asiaticus* sp. n. Right lamella alaris in lateral (a) and medial (b) views (LU-N 5/125; see also Text-fig. 5 B).

Fig. 2. *Gobiates* cf. *G. sosedkoi* NESSOV, 1981. Right lamella alaris in lateral (a) and medial (b) views (LU-N 5/111; see also Text-fig. 5 G).

Fig. 3. *Gobiates spinari* sp. n. Right lamella alaris in lateral (a) and medial (b) views (LU-N 5/139; see also Text-fig. 5 D).

Fig. 4. *Gobiates kizylkumensis* sp. n., holotype. Right lamella alaris in lateral view (LU-N 6/363; see also Text-fig. 5 C).

Fig. 5. *Gobiates asiaticus* sp. n., holotype. Right lamella alaris in medial view (LU-N 6/370; see also Text-fig. 5 A).

Fig. 6. *Gobiates spinari* sp. n. Left lamella alaris in medial (a) and lateral (b) views (LU-N 5/178; see also Text-fig. 5 E).

Fig. 7. *Gobiates spinari* sp. n., holotype. Left lamella alaris in dorsal (a) and lateral (b) views (LU-N 5/137; see also Text-fig. 5 F). Bar equals 1 mm.

Plate 6

Fig. 1. *Aralobatrachus robustus*. Distal section of the right humerus (LU-N 6/419).

Fig. 2. Gobiatidae indet. Right humerus in lateral view (LU-N 6/377; see also Text-fig. 29 A).

Fig. 3. *Aralobatrachus robustus*. Distal section of the left humerus (LU-N 6/343; see also Text-fig. 10 B).

Fig. 4. Gobiatidae indet. Distal section of the right humerus (LU-N 5/142).

Fig. 5. Gobiatidae indet., distal section of the left humerus (LU-N 6/338; see also Text-fig. 29 H).

Fig. 6. *Aralobatrachus robustus*. Distal section of the right humerus (LU-N 6/296).

Fig. 7. Gobiatidae indet. Distal section of the right humerus (LU-N 5/133; see also Text-fig.29 E). Bar equals 1 mm.

Plate 7

Fig. 1. Gobiatidae indet. Distal section of the left humerus (LU-N 6/336; see also Text-fig. 29 S).

Fig. 2. Gobiatidae indet. Distal section of the left humerus (LU-N 5/212; see also Text-fig. 29 O).

Fig. 3. Gobiatidae indet. Distal section of the left humerus (LU-N 5/244; see also Text-fig. 29 T).

Fig. 4. Gobiatidae indet. Distal section of the left humerus (LU-N 6/423).

Fig. 5. Gobiatidae indet. Proximal section of the femur in lateral view (LU-N 6/352).

Fig. 6. cf. *Kizylkuma*. Distal section of the left humerus (LU-N 6/319).

Fig. 7. cf. *Kizylkuma*. Distal section of the left humerus (LU-N 5/247).

Fig. 8. cf. *Kizylkuma*. Distal section of the left humerus (LU-N 5/95).

Fig. 9. Gobiatidae indet. Proximal section of the femur in lateral view (LU-N 5/123). Bar equals 1 mm.

Plate 8

Fig. 1. Gobiatidae indet. or Discoglossidae indet., right ilium in lateral view (LU-N 5/206; see also Text-fig. 25 P).

Fig. 2. cf. *Aralobatrachus*. Right ilium in lateral view (LU-N 2/15; see also Text-fig. 28 E).

Fig. 3. cf. *Kizylkuma*. Right ilium in lateral view (LU-N 5/150).

Fig. 4. *Aralobatrachus robustus* (LU-N 5/130; see also Text-fig. 13 B).

Fig. 5. Discoglossidae indet. Right ilium in lateral view (LU-N 8/463; see also Text-fig. 26 E).

Fig. 6. *Aralobatrachus robustus*. Right ilium in lateral view (LU-N 7/452).

Fig. 7. Discoglossidae indet. Right ilium in lateral view (LU-N 6/386; see also Text-fig. 25 H).

Fig. 8. Gobiatidae indet. or Discoglossidae indet. Right ilium in lateral view (LU-N 6/383; see also Text-fig. 26 F). Bar equals 1 mm.

Plate 9

Fig. 1. Discoglossidae indet. Right ilium in lateral view (LU-N 6/340).

Fig. 2. Gobiatidae indet. or Discoglossidae indet. Right ilium in lateral view (LU-N 5/190; see also Text-fig. 26 B).

Fig. 3. Gobiatidae indet. or Discoglossidae indet. Right ilium in lateral view (LU-N 6/393; see also Text-fig. 26 J).

Fig. 4. Gobiatidae or Discoglossidae indet. Right ilium in lateral view (LU-N 6/389; see also Text-fig. 26 H).

Fig. 5. Gobiatidae indet. Left ilium in medial view (LU-N 6/400; see also Text-fig. 25 D).

Fig. 6. Gobiatidae indet. or Discoglossidae indet. Left ilium in lateral view (LU-N 5/100; see also Text-fig. 25 Q).

Fig. 7. Discoglossidae indet. Left ilium in lateral view (LU-N 6/203; see also Text-fig. 25 F).

Fig. 8. Discoglossidae indet. Left ilium in lateral view (LU-N 6/406; see also Text-fig. 28 C).

Fig. 9. Discoglossidae indet. Left ilium in lateral view (LU-N 6/291; see also Text-fig. 28 B). Bar equals 1 mm.

Plate 10

Fig. 1. *Aralobatrachus* sp. Left ilium in lateral view (LU-N 7/447).
Fig. 2. Discoglossidae indet. Left ilium in lateral view (LU-N 8/468; see also Text-fig. 25 G).
Fig. 3. Discoglossidae indet. Left ilium in lateral view (LU-N 8/493; see also Text-fig. 28 G).
Fig. 4. Gobiatidae indet. Left ilium in lateral view (LU-N 5/169; see also Text-fig. 25 B).
Fig. 5. Discoglossidae indet. Left ilium in lateral view (LU-N 7/450).
Fig. 6. Gobiatidae or Discoglossidae indet. Left ilium in lateral view (LU-N 5/240; see also Text-fig. 25 N).
Fig. 7. Gobiatidae indet. or Discoglossidae indet. Left ilium in lateral view (LU-N 6/328; see also Text-fig. 26 G).
Fig. 8. Gobiatidae indet. or Discoglossidae indet. Left ilium in lateral view (LU-N 7/453; see also Text-fig. 25 O). Bar equals 1 mm.

Plate 11

Fig. 1. Gobiatidae indet. Left ilium in lateral view (LU-N 7/444; see also Text-fig. 25 A).
Fig. 2. Discoglossidae indet. Left ilium in lateral view (LU-N 6/376; see also Text-fig. 26 A).
Fig. 3. *Alytes obstetricans* rec. Right ilium in lateral view (DP FNSP 6457).
Fig. 4. Gobiatidae or Discoglossidae indet. Left ilium in lateral view (LU-N 6/360; see also Text-fig. 25 L).
Fig. 5. Gobiatidae indet. or Discoglossidae indet. Left ilium in lateral view (LU-N 6/342; see also Text-fig. 25 K).
Fig. 6. cf. *Gobiates*, left prooticooccipital in dorsal view (LU-N 6/385).
Fig. 7. Anura indet. Section of the femur in lateral view, see chapter Malformations (LU-N 5/232).
Fig. 8. Gobiatidae indet. Left humerus in lateral and anterior view (LU-N 5/167).
Fig. 9. Gobiatidae indet. Left humerus (LU-N 5/113; see also Text-fig. 1 D). Bar equals 1 mm.

Plate 12

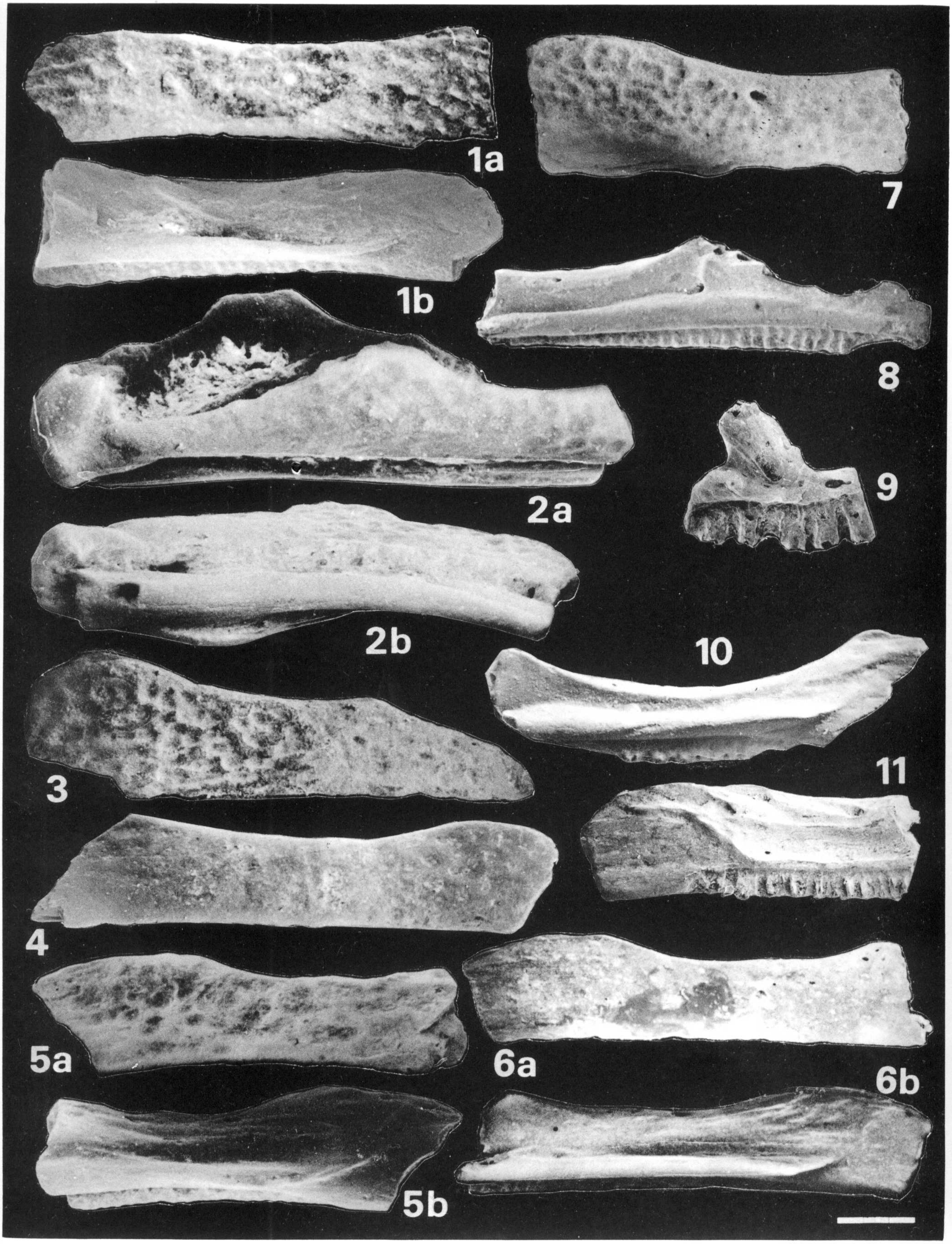
Fig. 1. Anura indet. Sphenethmoideum in dorsal view (LU-N 7/448; see also Text-fig. 12 B).
Fig. 2. cf. *Gobiates*. Sphenethmoideum in anterior (a) and posterior (b) views (LU-N 5/180; see also Text-fig.12 A).
Fig. 3. cf. Discoglossidae. Left prooticooccipital in posterior view (LU-N 6/283).
Fig. 4. Discoglossidae indet. Left prooticooccipital in posterior view (LU-N 6/325; see also Text-fig. 21 A).
Fig. 5. Discoglossidae indet. Right prooticooccipital in posterior view (LU-N 6/431; see also Text-fig. 21 B).
Fig. 6. Anura indet. Radioulna (LU-N 5/152; see also Text-fig. 30 D; a – anterior, b – lateral view).
Fig. 7. Anura indet. Radioulna (LU-N 6/309; see also Text-fig. 30 E).
Fig. 8. Anura indet. Radioulna (LU-N 4/76; a – anterior, b – lateral view). Bar equals 1 mm.

Plate 13

Fig. 1. Anura indet. Radioulna (LU-N 5/149; see also Text-fig. 30 C).
Fig. 2. Sculptured dermal bone (? anuran nasal) (LU-N 6/264).
Fig. 3. Sculptured dermal bone (? Anura) (LU-N 5/259).
Fig. 4. Anura indet. Left scapula in outer (a) and inner (b) views (LU-N 1/1).
Fig. 5. Discoglossidae indet. Right scapula in inner (a) and outer (b) views (LU-N 2/45).
Fig. 6. cf. Gobiatidae. Right coracoid in dorsal (a) and ventral (b) views (LU-N 4/69).
Fig. 7. cf. Gobiatidae. Coracoid (LU-N 6/350). Bar equals 1 mm.

Plate 14

Fig. 1–5. Proximal sections of the femurs in ventral or nearly ventral view, to show degree of development of the crista femoris.
Fig. 1. Anura indet. (LU-N 6/426).
Fig. 2. Gobiatidae indet. (LU-N 4/67).
Fig. 3. cf. Gobiatidae (LU-N 5/194).
Fig. 4. Gobiatidae indet. (LU-N 8/464).
Fig. 5. Anura indet. (LU-N 6/413).
Fig. 6. Anura indet. Distal part of the femur, partially healed break (LU-N 6/329, not to scale with other material).
Fig. 7. Discoglossidae indet. Right praearticular in dorsal view (LU-N 6/442; see also Text-fig.24 C).
Fig. 8. Discoglossidae indet. Left praearticular in dorsal view (LU-N 6/356; see also Text-fig. 24 D).
Fig. 9. cf. *Gobiatoides*. Left praearticular in dorsal (a) and lateral views (b) (LU-N 4/78; see also Text-fig.24 B).
Fig. 10. cf. *Gobiatoides*. Right praearticular in dorsal view (LU-N 5/120; see also Text-fig. 24 A).
Fig. 11. Discoglossidae indet. Middle part of the right praearticular in medial view (LU-N 8/465; see also Text-fig. 24 F). Bars equal 1 mm.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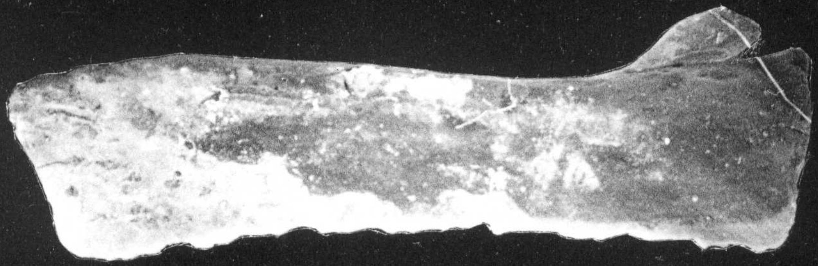

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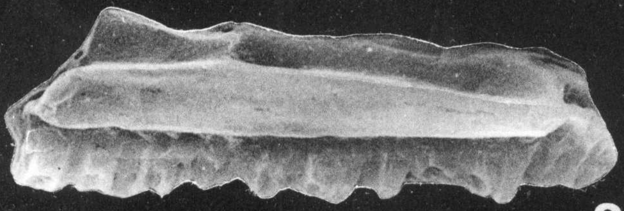

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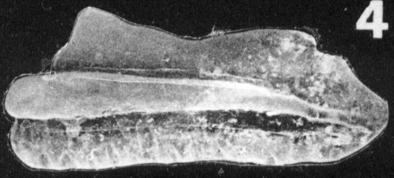

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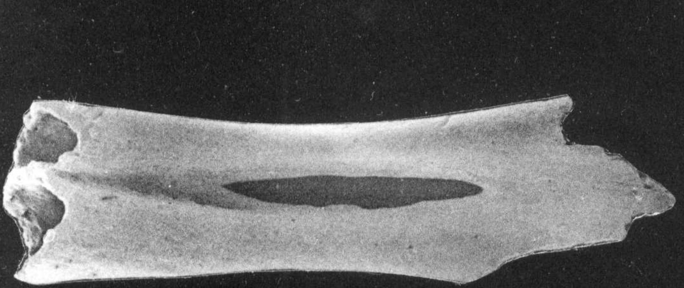

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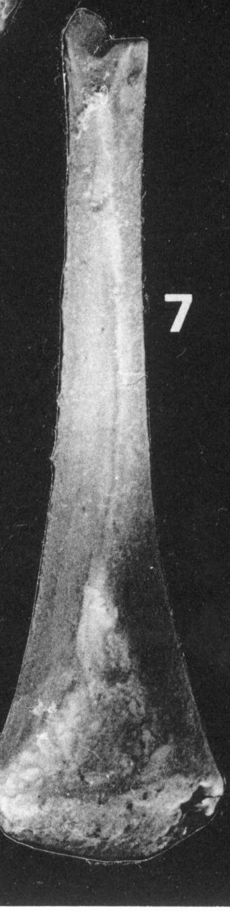

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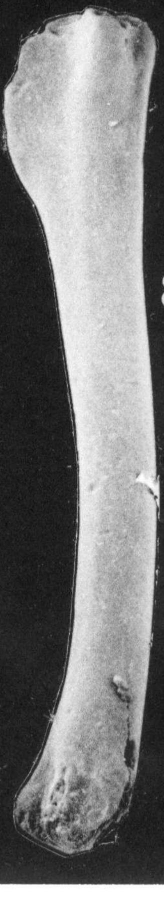

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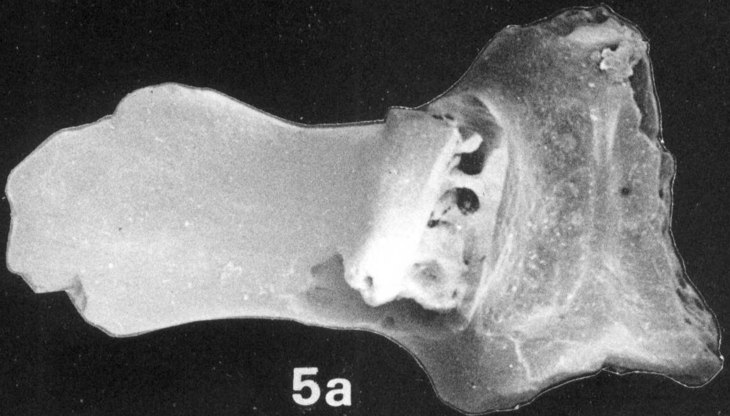
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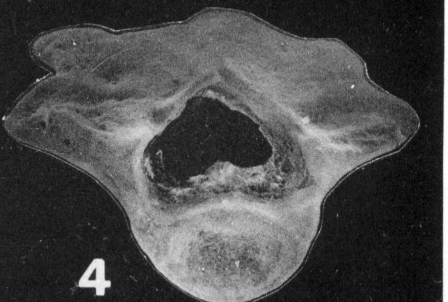
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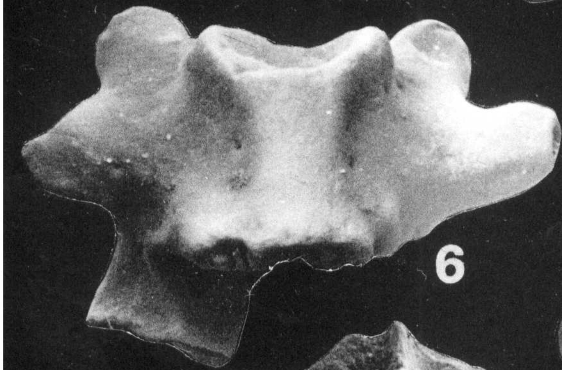
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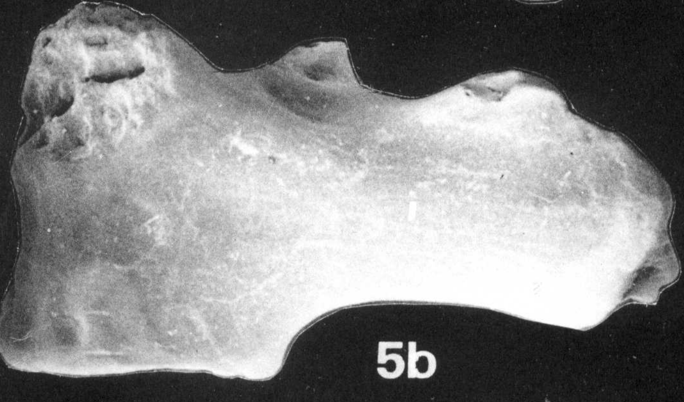
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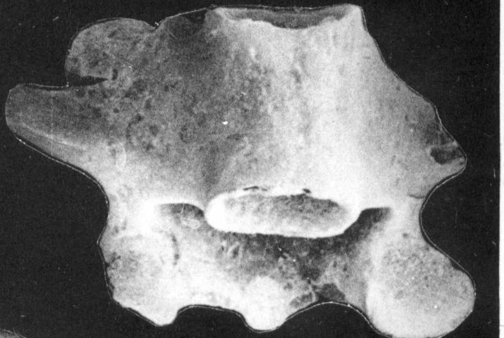
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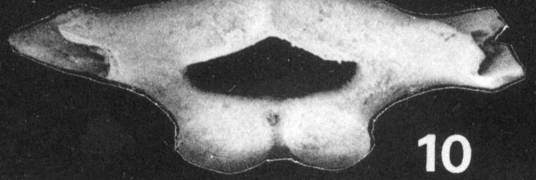
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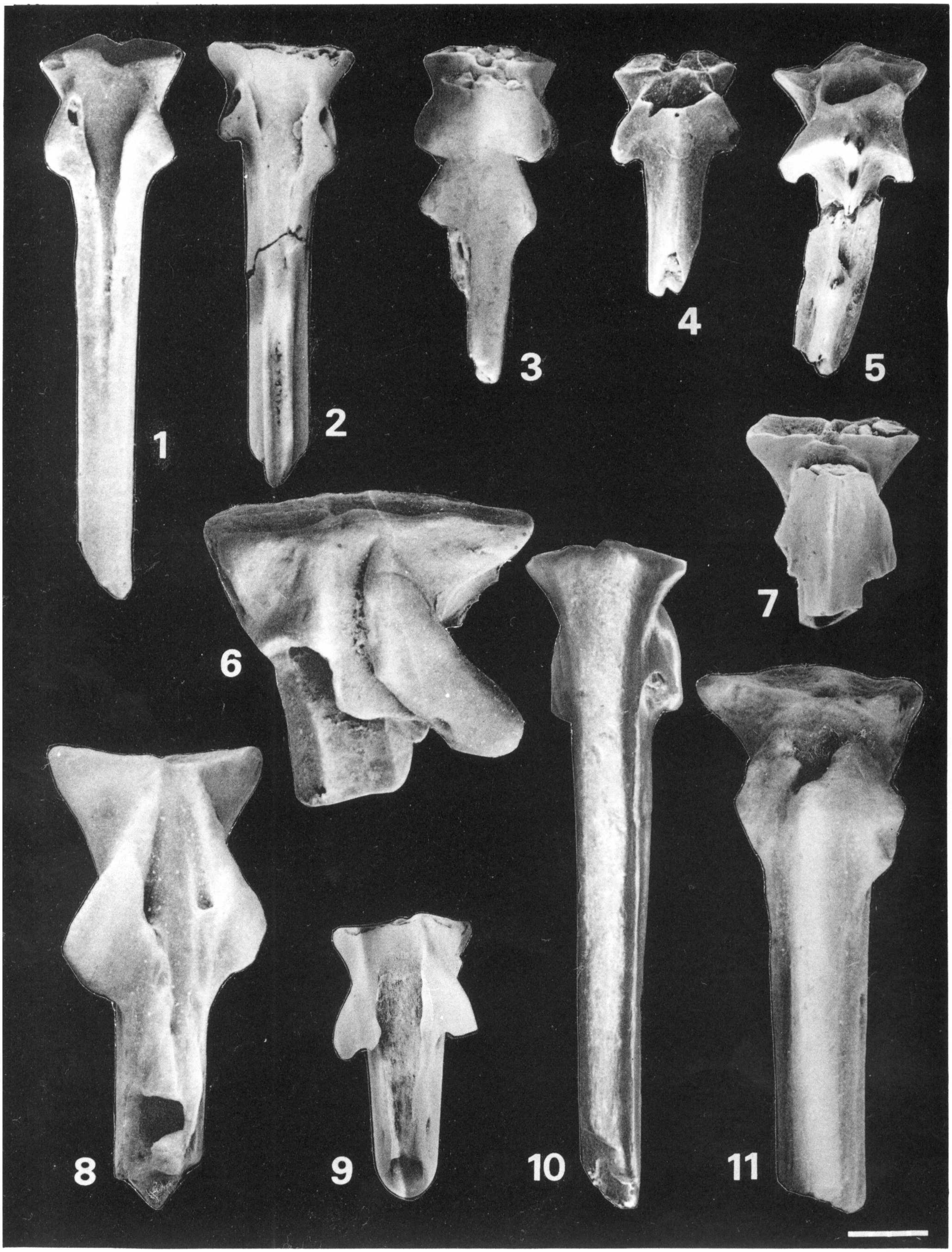
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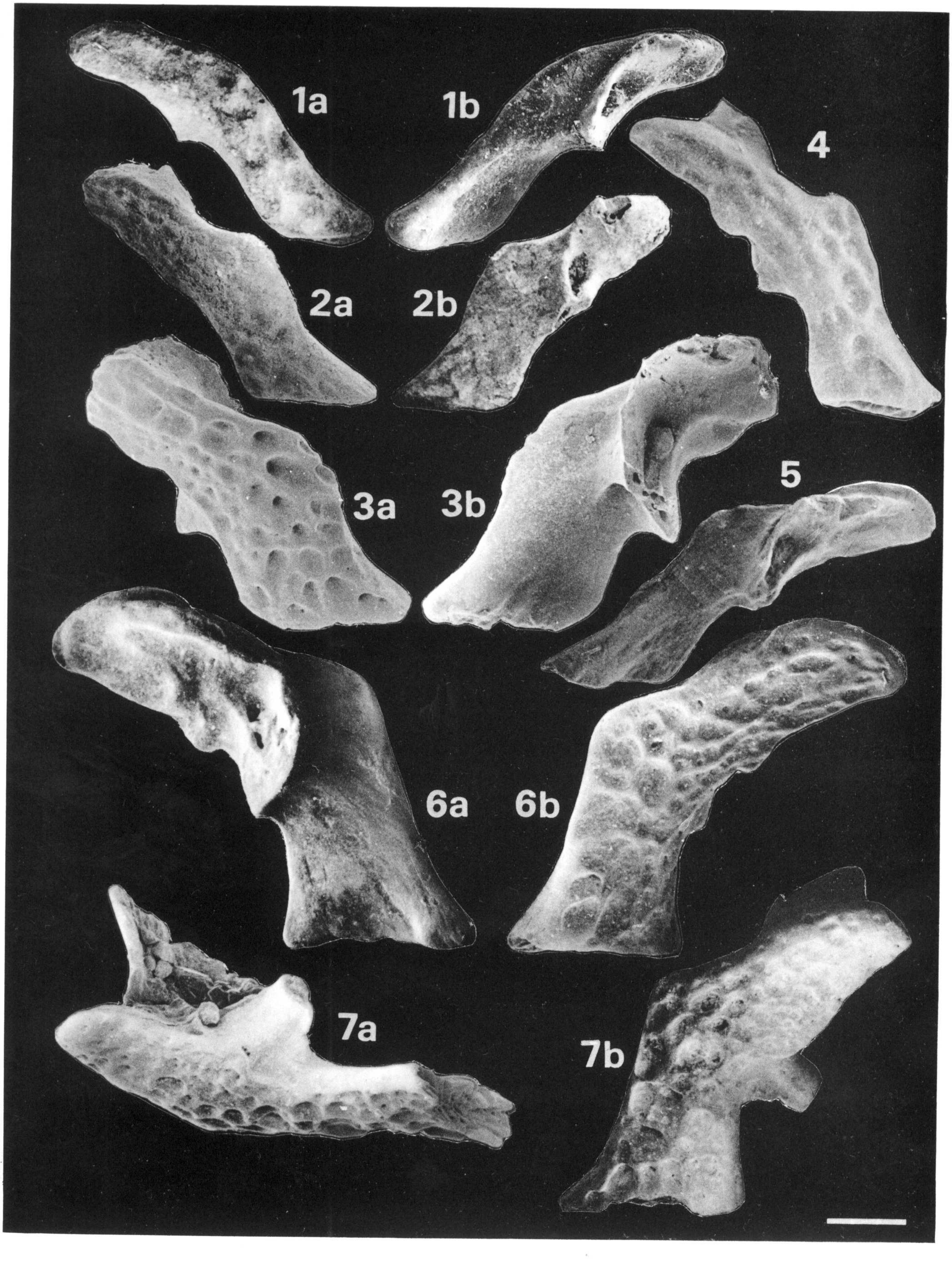
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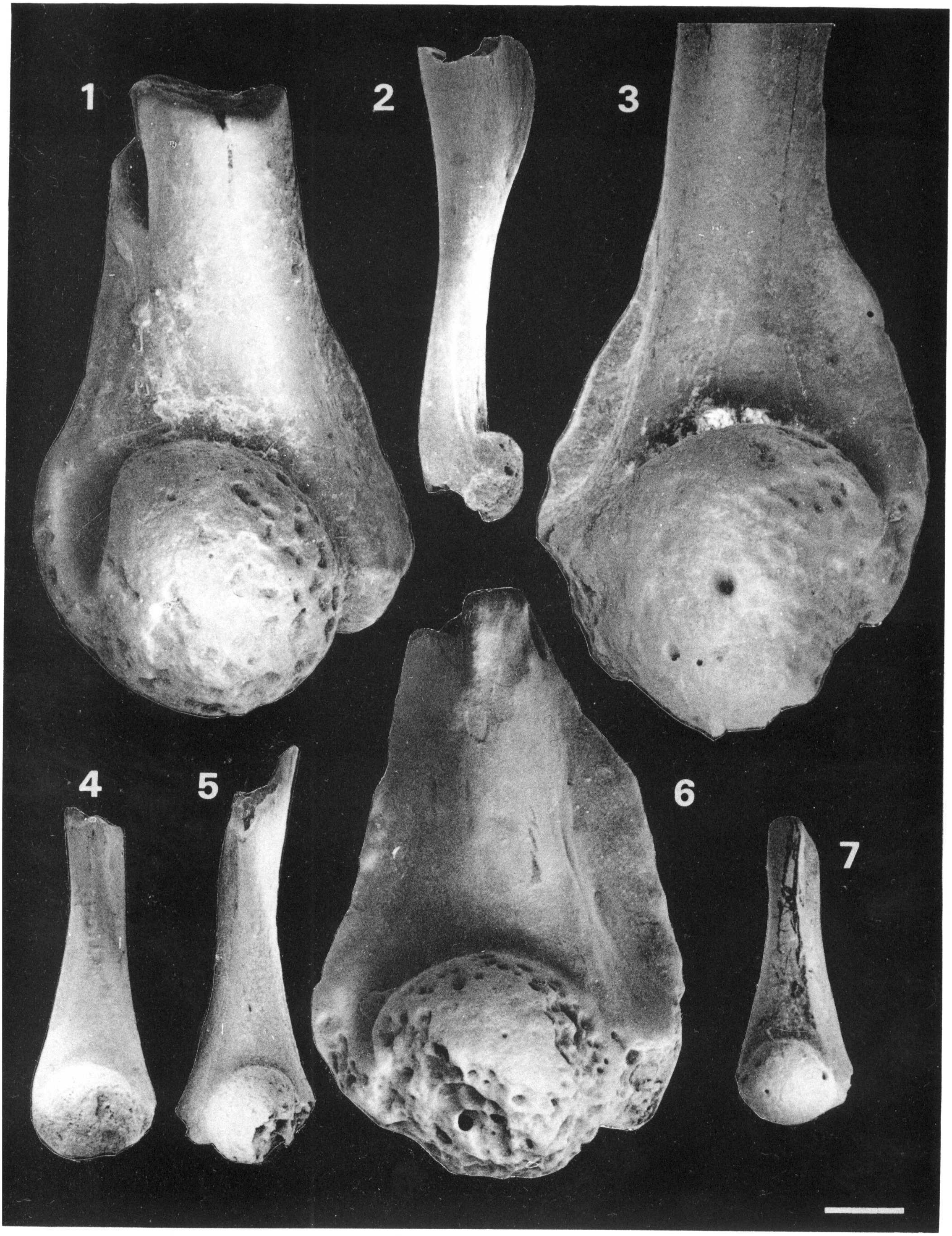
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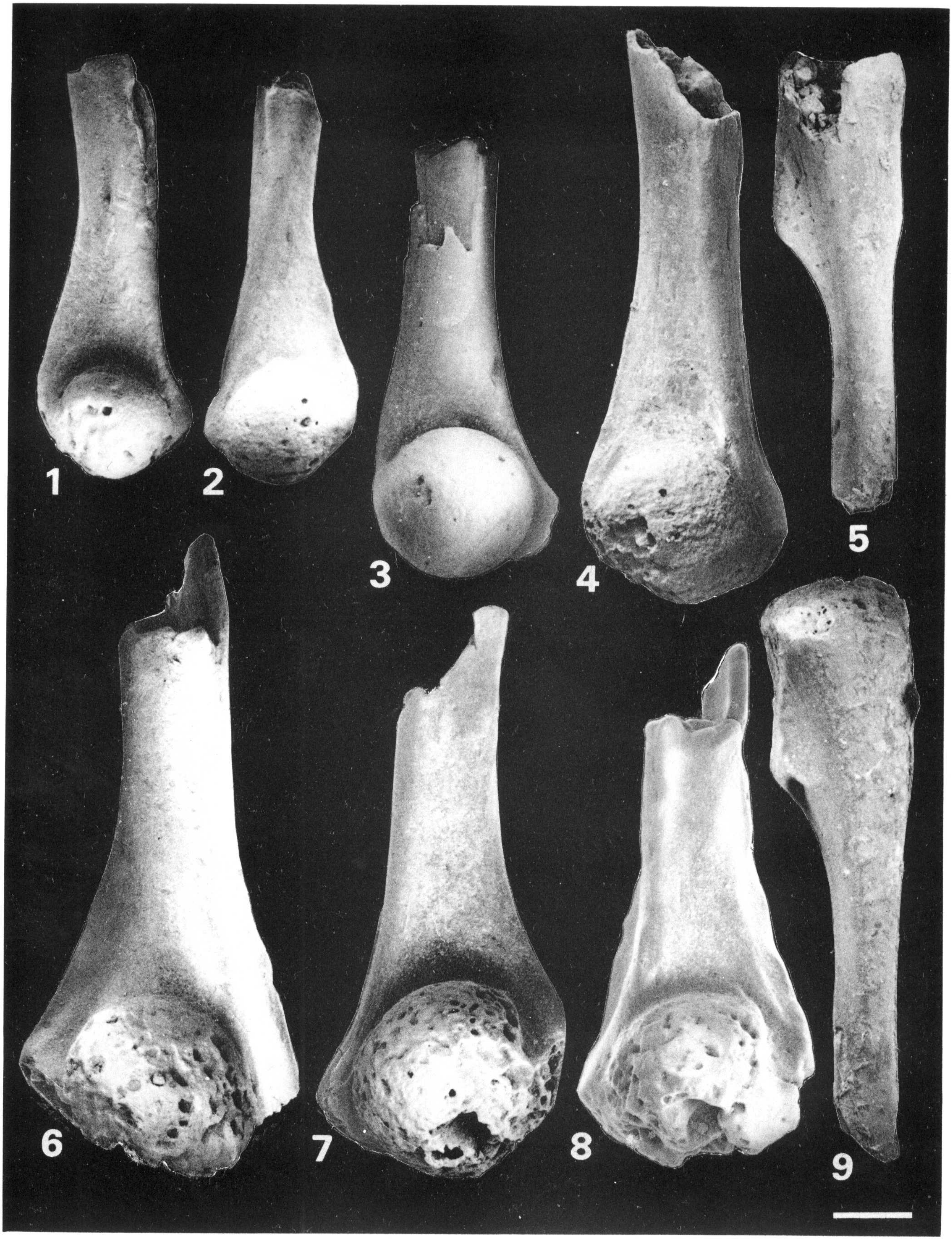
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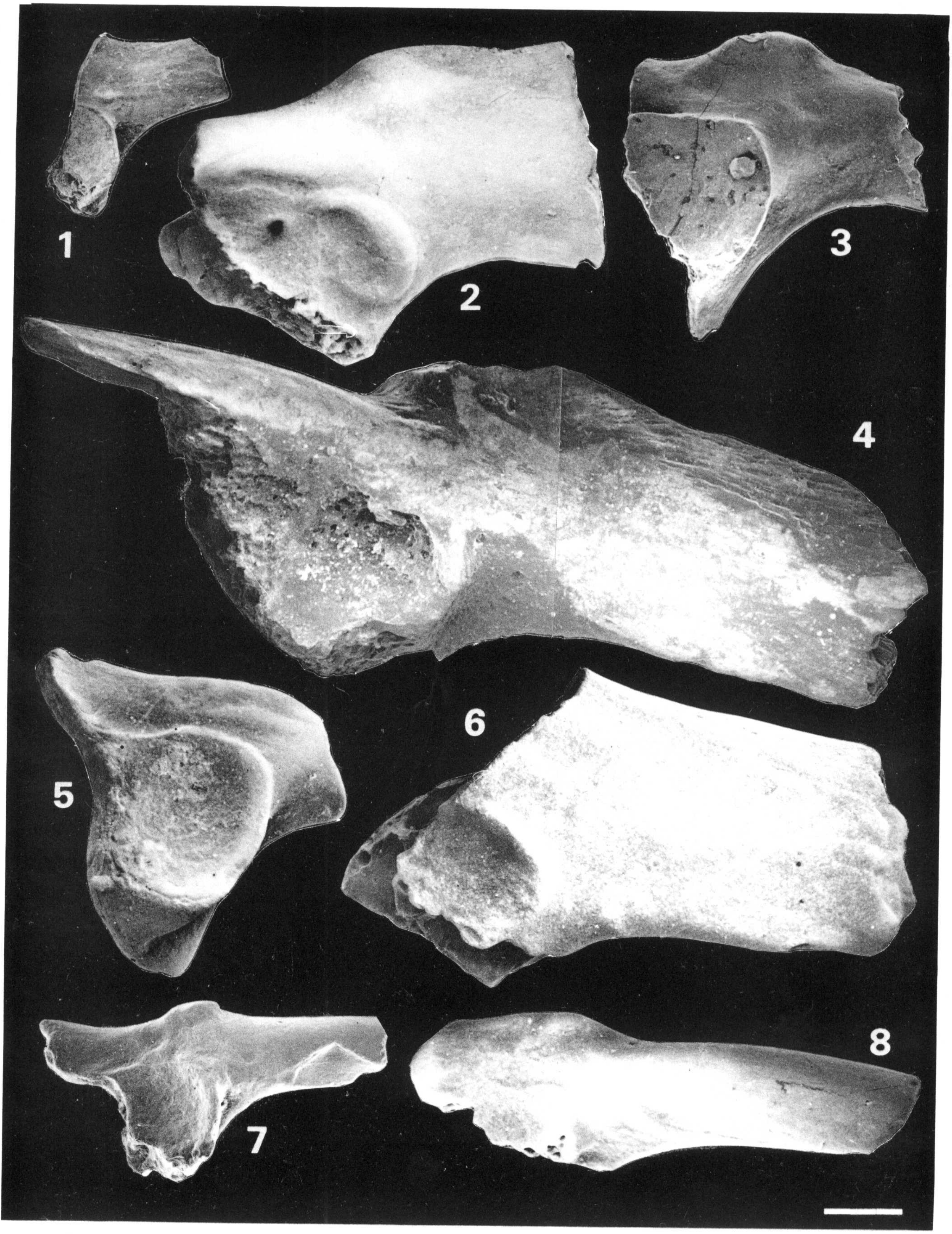

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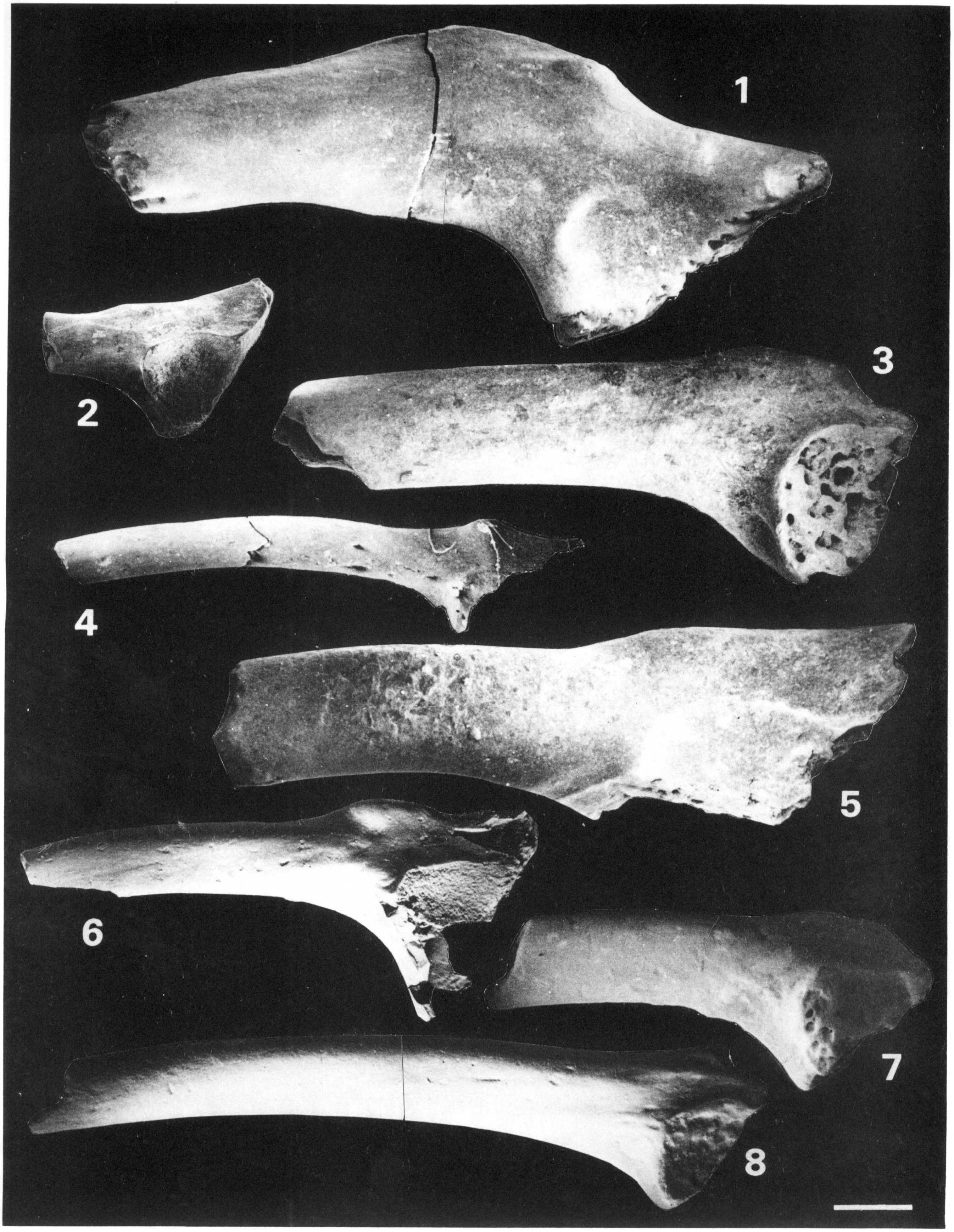
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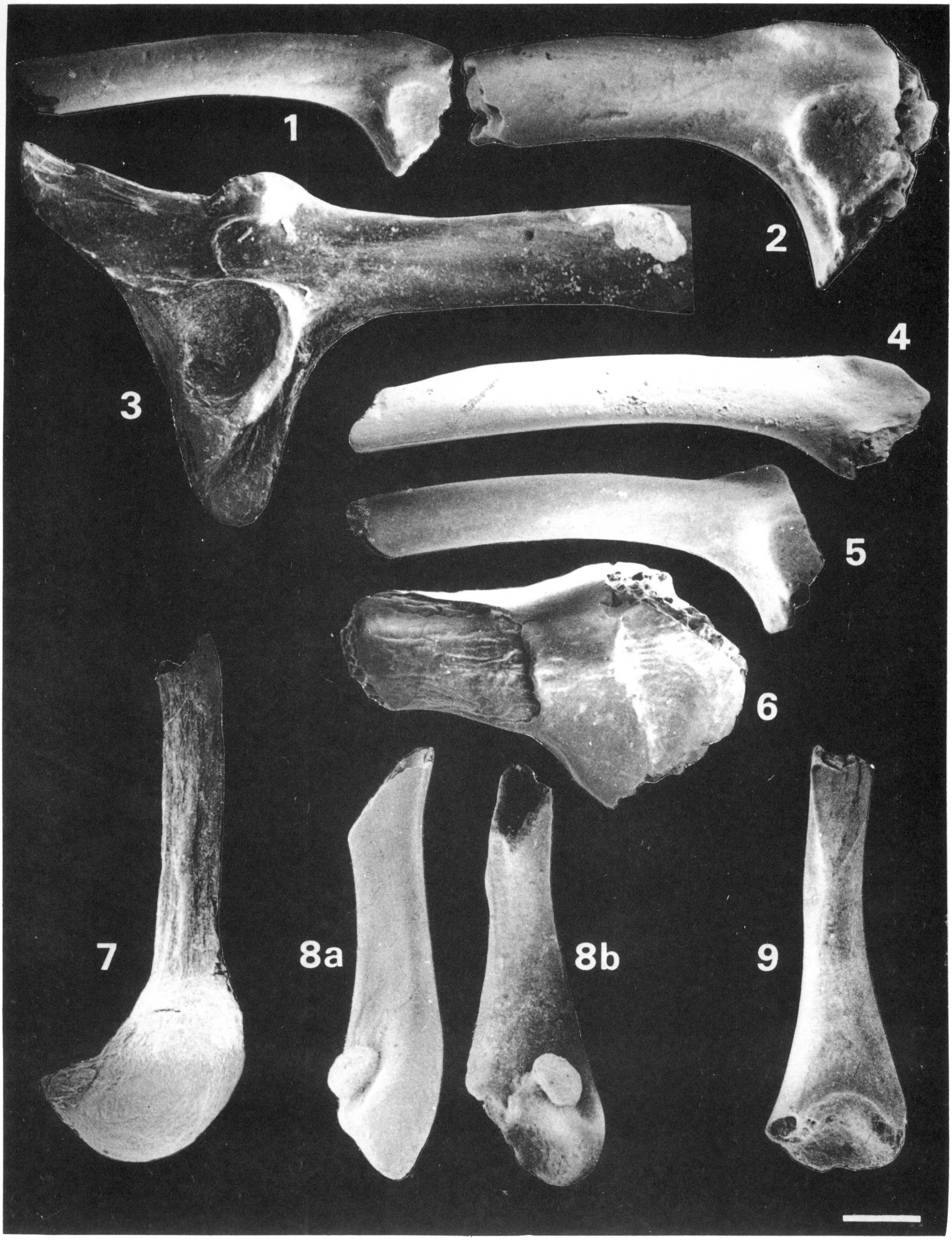
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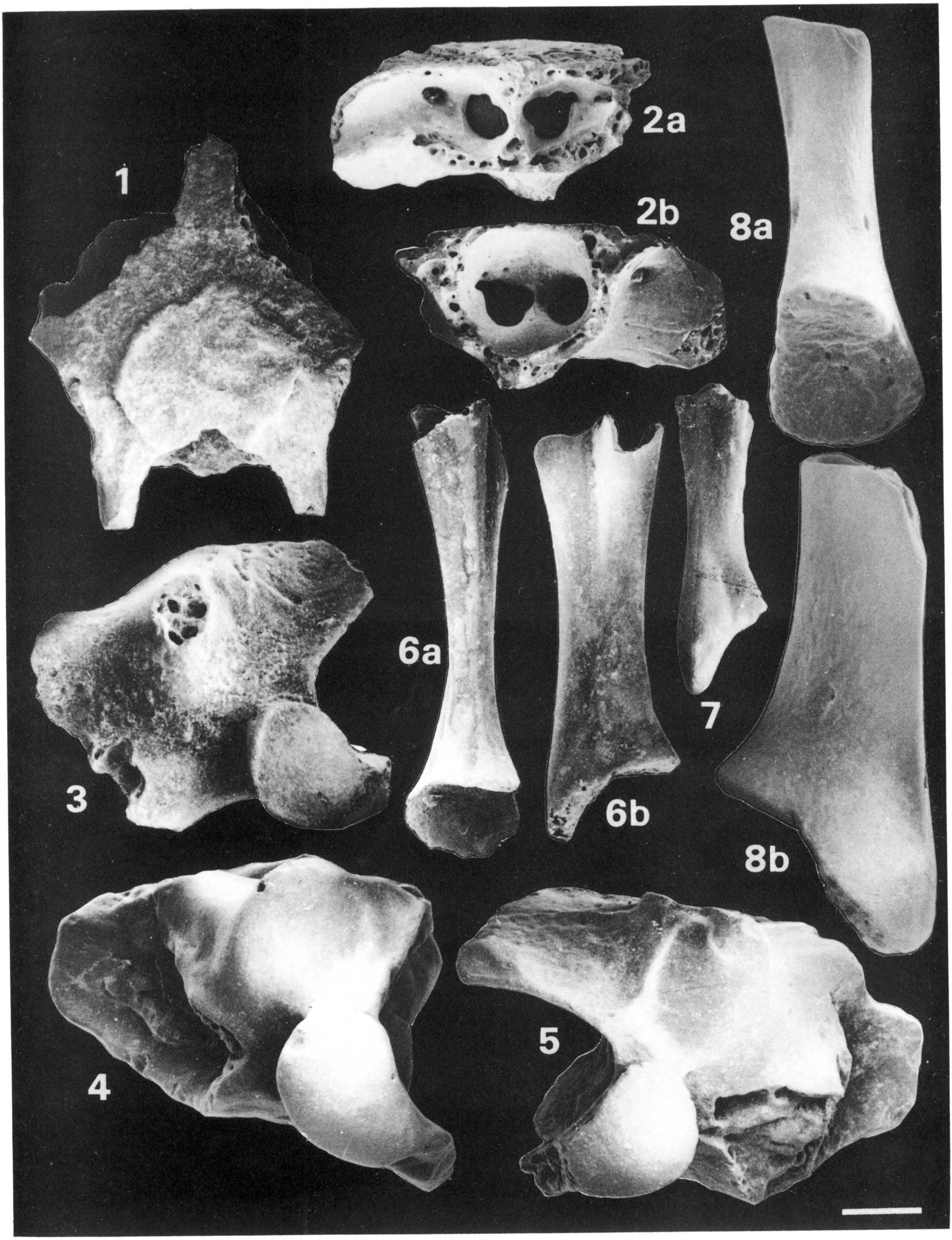
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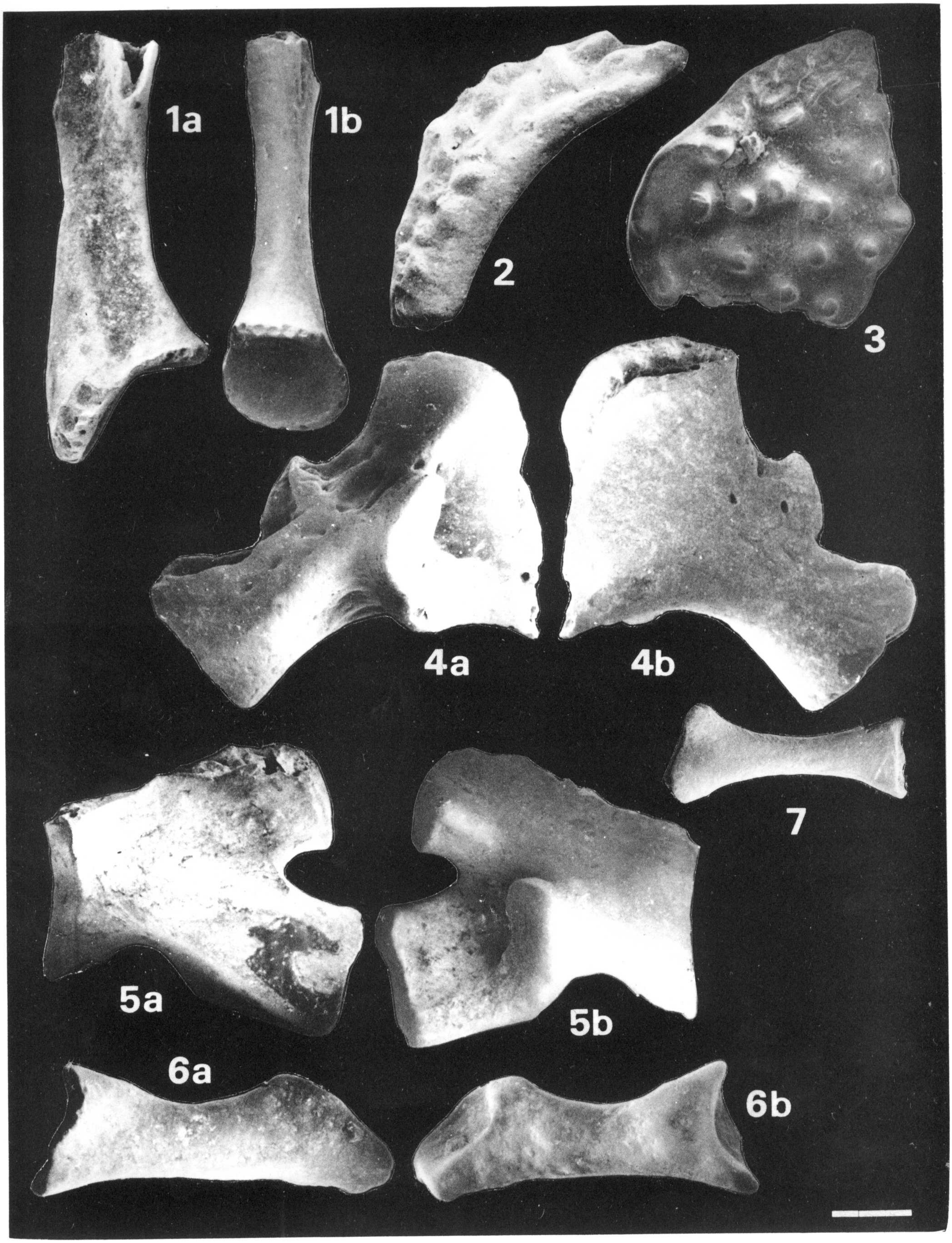

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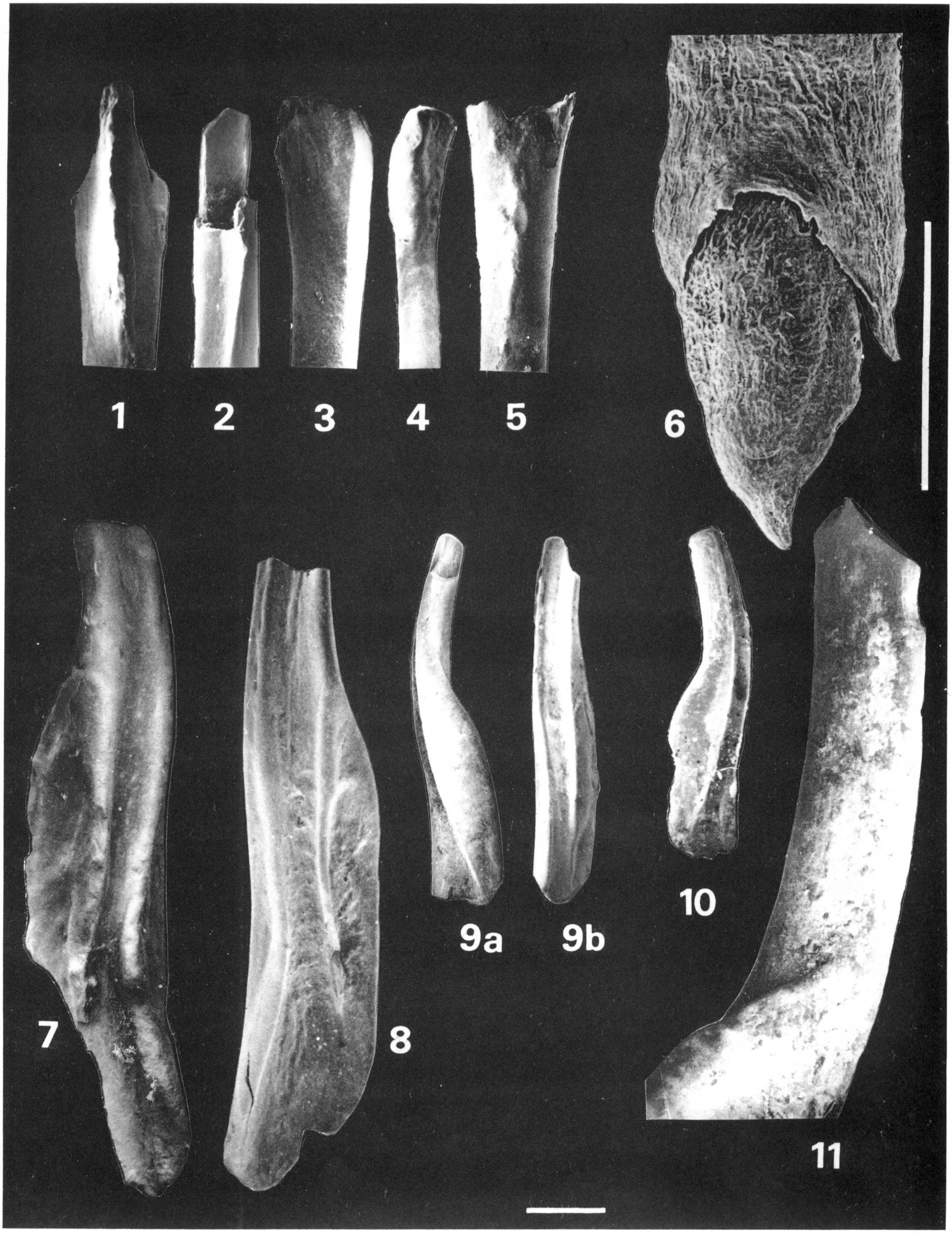

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