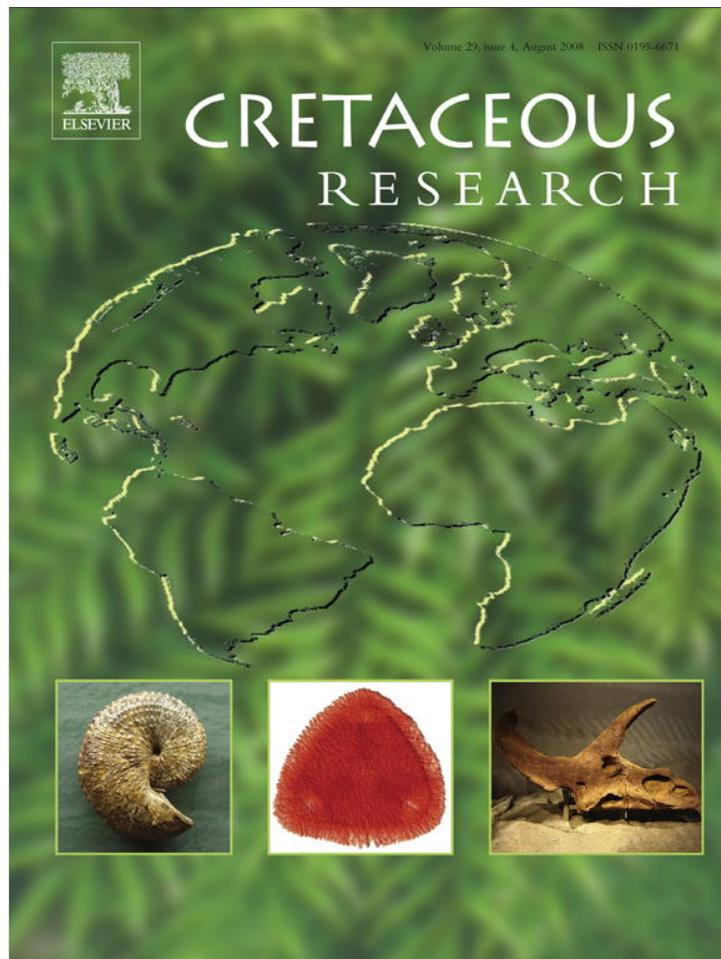


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The Late Cretaceous frog *Gobiates* from Central Asia: its evolutionary status and possible phylogenetic relationships

Zbyněk Roček^{a,b,*}

^a *Laboratory of Palaeobiology, Institute of Geology, Czech Academy of Sciences, Rozvojová 135, CZ-165 00 Prague 6, Czech Republic*

^b *Department of Zoology, Faculty of Natural Sciences, Charles University, Viničná 7, CZ-128 44 Prague 2, Czech Republic*

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Abstract

The fossil record of the Late Cretaceous anuran *Gobiates* is reviewed, and an articulated postcranial skeleton is described for the first time. A separate family status for the genera *Gobiates* Špinar et Tatarinov, 1986, *Cretasalia* Gubin, 1999, and *Gobiatoides* Roček et Nessov, 1993 is reassessed. In principle, the Gobiidae are characterized by a combination of primitive and derived characters, of which the most important for inferring phylogenetic relationships are: (1) amphicoelous (ectochordal) vertebral centra; (2) eight presacral vertebrae; (3) palatines fused to maxillae (postchoanal process of the vomer absent); and (4) pterygoid process of the maxilla absent. The Gobiidae share with the Jurassic anurans *Prosalirus*, *Notobatrachus* and *Vieraella* (and also found in other Mesozoic anurans, e.g., *Aygroua* Jones et al., 2003 and *Rhadinosteus* Henrici, 1998) the first character; however, gobiatids differ from these taxa in having a complete maxillary arch (including quadratojugal) and a lower number of presacral vertebrae. Gobiidae differ from discoglossoids and pipoids (the only other Mesozoic anurans) in the shape (opisthocelous or stegochordal, respectively, in the latter) of vertebrae, implying a different method of vertebral development. In general, the Gobiidae, in spite of their Late Cretaceous age, retain primitive features of Jurassic frogs, combined with derived features (e.g., low number of presacral vertebrae) that are quite unusual for Late Cretaceous non-pipoid anurans.

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1. Introduction

The earliest fossil record of the anuran temnospondyls is *Triadobatrachus* (Piveteau, 1936) and *Czatkobatrachus* Evans and Borsuk-Białynicka, 1998 from the early Triassic of Madagascar and Europe, respectively. Although most of features of their postcranial skeleton are still primitive (e.g., high number of praesacral vertebrae, anterior and posterior legs equal in length, ulna and radius, as well as tibia and fibula, still separate), the skull already bears typical anuran characters (e.g., the frontals and parietals are fused with each other, similar to the squamosal and praeopercular), and the ilia are elongated

posteriorly from the level of the sacral vertebra along the caudal part of the vertebral column. Judging by the condition in *Triadobatrachus* (*Czatkobatrachus* is recorded by disarticulated bones) these proanurans were not yet capable of jumping (Rage and Roček, 1989).

There is a considerable gap (about 35 Ma) in the fossil record between the mentioned earliest anuran temnospondyls and the first true frogs. The latter are evidenced only from the early Jurassic of North America, by *Prosalirus* Shubin and Jenkins, 1995. Some of its skeletal features suggest considerable hypoossification (e.g., caput humeri cartilaginous, large notochordal canal). However, this frog was no doubt already capable of jumping.

Jurassic anurans were recorded not only from North America (besides *Prosalirus*, some other anurans were also present, among them a primitive, non-burrowing rhinophrynid *Rhadinosteus* Henrici, 1998), but also from South America

* Laboratory of Palaeobiology, Institute of Geology, Czech Academy of Sciences, Rozvojová 135, CZ-165 00 Prague 6, Czech Republic.

E-mail address: rocek@gli.cas.cz

(*Vieraella* Reig, 1961 and *Notobatrachus* Reig in Stipancic and Reig, 1955), Europe (*Eodiscoglossus* Villalta, 1956), and recently also from Asia (Wang, 2007, in litt.; Yuan et al., 2004).

Cretaceous anurans are known from all continents except for Australia. However, their fossil record mostly consists of disarticulated skeletal elements, which makes their taxonomic assignment difficult. Nevertheless, articulated skeletons were also found, for instance in pipids from Israel (Nevo, 1968) and from South Africa (Trueb et al., 2005), and from Asia (e.g., Wang and Gao, 1999). For a more comprehensive review of Mesozoic anurans see Roček (2000).

The first record of Late Cretaceous anurans from Central Asia is represented by an incomplete three-dimensionally preserved skull, associated with part of the right pectoral girdle of the same individual (Borsuk-Białynicka, 1978), recovered from Khermeen Tsav in the southwest part of the Nemegt Basin in Gobi Desert, Mongolia. The outcrop here was tentatively estimated as middle Campanian in age (Gradziński et al., 1977). Because of a shallow pit-and-ridge sculpture of the maxillary and squamosal, and also absence of an anterior scapular crest, it was considered by Borsuk-Białynicka (1978) to belong to *Eopelobates*, an extinct member of the family Pelobatidae, and the specimen was described as *E. leptocolaptus*. Roček (1981) added to her description some additional anatomical details but did not reconsider the taxonomic status of this fossil.

At approximately the same time, excavations in Central Asia yielded disarticulated anuran cranial bones, some of them covered with pit-and-ridge sculpture. Those bearing sculpture were assigned (independently of Borsuk-Białynicka's material) to *Eopelobates*, as *E. sosedkoi* (Nessov, 1981a,b, 1988; Nessov and Udovitschenko, 1986).

Shortly afterwards, three other skulls were discovered at the same locality. These included articulated dermal roofing bones and the anterior three vertebrae, thus providing more complete anatomical information. On the basis of the new anatomical characters, Špinar and Tatarinov (1986) erected a new genus, *Gobiates*, and referred it, under the name *G. khermeentsavi*, to the Discoglossidae. At the same time, they recognized its close relations to *Eopelobates leptocolaptus* and, because assignment of the latter to the Pelobatidae was no longer tenable, they transferred it to the genus *Gobiates*, as *G. leptocolaptus*.

The disarticulated bones from Nessov's Central Asian localities were re-investigated by Roček and Nessov (1993) in the context of Špinar's and Tatarinov's (1986) conclusions. It turned out that, besides typical Discoglossidae, which are characterised by their opisthocelous vertebrae and the morphology of their maxillae and humeri (Roček, 1994), there is also a well defined group of small, but completely developed, adult frogs characterized by pit-and-ridge sculpture on dermal cranial roofing bones, and by amphicoelous vertebrae (sometimes with a notochordal canal). Comparisons with available articulated parts of skeletons from Khermeen Tsav revealed that these disarticulated elements belong to *Gobiates*, and that *G. sosedkoi* (Nessov, 1981) may even be conspecific with *G. khermeentsavi* (Špinar and Tatarinov, 1986). On the

other hand, variation in the morphology of the squamosal-maxillary contact and associated differences in proportions of the squamosal suggested that the samples (coming from nine sites, ranging stratigraphically from the Albian to the Campanian) may involve a larger number of species.

The combination of articulated cranial skeletons with disarticulated elements made it possible to make a reasonable reconstruction of the skull, define its taxonomically important characters, and even assess some degree of cranial variation. However, the isolated vertebrae were associated with *Gobiates* only on the basis of three articulated anterior vertebrae which were part of the holotype of *G. khermeentsavi* (Špinar and Tatarinov, 1986, fig. 3d, e). Only the third vertebra, which was partly broken off, suggested that the vertebrae were amphicoelous with a notochordal canal. The ilia and limb elements could not be associated because known articulated material lacks these elements and so precludes direct comparisons.

Information on the postcranial skeleton of *Gobiates* may now be gained from a new specimen recovered from the Djadokhta Formation (Campanian) of Udan-Sayr, Ömnögovi Aimag, Mongolia, briefly mentioned in Roček and Nessov (1993) and Roček (2000). It consists of a complete, though slightly disarticulated, vertebral column, displaced scapula and clavicle, and both the ilia and femur, thus providing a sound basis for an almost complete reconstruction of the skeleton of *Gobiates*.

The aim of this paper is to analyze all available characters of the genus *Gobiates* and related taxa, and assess their evolutionary status and phylogenetic relationships.

2. Material and methods

2.1. Institutional abbreviations

LU-N, Saint-Petersburg State University, Nessov collection; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; ZIN, Zoological Institute, Russian Academy of Sciences, Department of Herpetology, Saint-Petersburg; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

2.2. Localities and material

The material is listed after each of three known localities (Fig. 1).

1. Khermeen Tsav (Hermin Tsav in Kielan-Jaworowska et al., 2005), situated some 50 km SW from Naran Bulak in the Gobi Desert, Mongolia; Baruungoyot Formation, Santonian-Campanian. PIN 31/42/1 (*G. khermeentsavi* holotype); PIN 31/42/2 (*G. khermeentsavi* paratype 1); PIN 31/42/3 (*G. khermeentsavi* paratype 2) (see also Špinar and Tatarinov, 1986); ZPAL MgAb-III/1 (*G. leptocolaptus* holotype) (see Borsuk-Białynicka, 1978; Roček, 1981).
2. Udan-Sayr, Ömnögovi Aimag, Mongolia; Djadokhta Formation, Campanian (see also Kurzanov, 1992). PIN 3907/10 (Fig. 2).



Fig. 1. Geographic occurrence of *Gobiates* in east Asia. Figures refer to those in 2.2 *Localities and material*.

3. Dzhyrakuduk, Buchara District, Uzbekistan; Bissekty Formation, Late Turonian-Coniacian (see also Roček and Nesson, 1993; Currie et al., 1993). Material from Dzhyrakuduk was recovered from several stratigraphically different sites (abbreviations refer to those mentioned in Roček and Nesson, 1993):

CDZ-17a (lower part of Bissekty Fm.; late Turonian): LU-N 4/48 (maxilla). CBI-4v (middle part of Bissekty Fm.; Coniacian): ZIN, PHA No K77-5 (frontoparietale, '*Gobiates sosedkoi*' holotype, Nesson, 1981a, pl. XII, fig. 14 and 1988, pl. XIV, fig. 1); LU-N 5/107 (right posterior part of the skull, *Gobiates bogatschovi* holotype, Roček and Nesson, 1993, text-fig. 3A, pl. 1, fig. 2); LU-N 5/111 (squamosal, Roček and Nesson, 1993, text-fig. 5G); LU-N 5/124 (maxilla); LU-N 5/125 (squamosal); LU-N 5/129 (maxilla, Roček and Nesson, 1993, text-fig. 4D, pl. 1, fig. 1); LU-N 5/137 (squamosal, *Gobiates spinari* holotype, Roček and Nesson, 1993, text-fig. 5 F, pl. 5, fig. 7); LU-N 5/139 (squamosal); LU-N 5/140 (maxilla); LU-N 5/143 (maxilla, *Gobiates fritschii* holotype, Roček and Nesson, 1993, text-fig. 4B, pl. 1, fig. 7); LU-N 5/165 (maxilla, *Gobiates furcatus* holotype, Roček and Nesson, 1993, text-fig. 4E, pl. 1, fig. 11); LU-N 5/178 (squamosal); LU-N 5/183 (vertebra 6 or 7, Roček and Nesson, 1993, text-fig. 7E); LU-N 5/191 (sacral vertebra, Roček and Nesson, 1993, text-fig. 14A, pl. 3, fig. 9); LU-N 5/192 (vertebra, Roček and Nesson, 1993, text-fig. 8A); LU-N 5/201 (vertebra, Roček and Nesson, 1993, text-fig. 7D, pl. 3, fig. 4); LU-N 5/231 (vertebra 6 or 7, Roček and Nesson, 1993, text-fig. 7C, pl. 3, fig. 8); LU-N 5/239 (vertebra 3 or 4, Roček and Nesson, 1993, text-fig. 7B, pl. 3, fig. 3); LU-N 5/241 (vertebra, Roček and Nesson, 1993, text-fig. 8E); LU-N 5/246 (sacral vertebra, Roček and Nesson, 1993, text-fig. 14B, pl. 3, fig. 10).

CBI-14 (middle part of Bissekty Fm.; Coniacian): LU-N 6/262 (sacral vertebra, Roček and Nesson, 1993, text-fig. 14C); LU-N 6/265 (vertebra 3, Roček and Nesson, 1993, text-fig. 8D, pl. 3, fig. 7); LU-N 6/279 (vertebra 7, Roček and Nesson, 1993, text-fig. 8F, pl. 3, fig. 6); LU-N 6/324

(vertebra 7 or 8, Roček and Nesson, 1993, text-fig. 8C); LU-N 6/341 (maxilla, *Gobiates dzhyrakudukensis* holotype, Roček and Nesson, 1993, text-fig. 3B, pl. 1, fig. 3); LU-N 6/344 (maxilla, *Gobiatoides parvus* holotype, Roček and Nesson, 1993, text-fig. 6, pl. 1, fig. 10); LU-N 6/348 (vertebra 3, Roček and Nesson, 1993, text-fig. 7A, pl. 3, fig. 2); LU-N 6/357 (maxilla, Roček and Nesson, 1993, pl. 1, fig. 4); LU-N 6/363 (squamosal, *Gobiates kizylkumensis* holotype, Roček and Nesson, 1993, text-fig. 5C, pl. 5, fig. 4); LU-N 6/370 (squamosal, *Gobiates asiaticus* holotype, Roček and Nesson, 1993, text-fig. 5A, pl. 5, fig. 5); LU-N 6/405 (maxilla, *Gobiates tatarinovi* holotype, Roček and Nesson, 1993, text-fig. 4C, pl. 1, fig. 5); LU-N 6/436 (atlas, Roček and Nesson, 1993, text-fig. 19A).

CBI-17 (middle or upper part of Bissekty Fm.; Coniacian): LU-N 7/449 (vertebra, Roček and Nesson, 1993, text-fig. 8B).

2.3. Measurements

Length of skull (LC) – most anterior point of interpremaxillary suture to upper margin of the foramen magnum; width of skull (LtC) – distance between both jaw joints.

3. Systematic palaeontology

Class: Amphibia Linnaeus, 1758

Order: Anura Fischer von Waldheim, 1813

Family: Gobiatiidae Roček and Nesson, 1993

Type genus. *Gobiates* Špinar and Tatarinov, 1986, p. 114.

Revised diagnosis. Skull wider than long (LC:LtC is 0.56–0.86 in *Gobiates*, 0.88 in *Cretasalia*; Gubin, 1999). Frontal portions of frontoparietals separated by a fontanelle, parietal portions interconnected by median suture. Nasals crescent-like, only their anterior parts are in contact. Maxillae deeper anteriorly than posteriorly, with orbital margin straight or

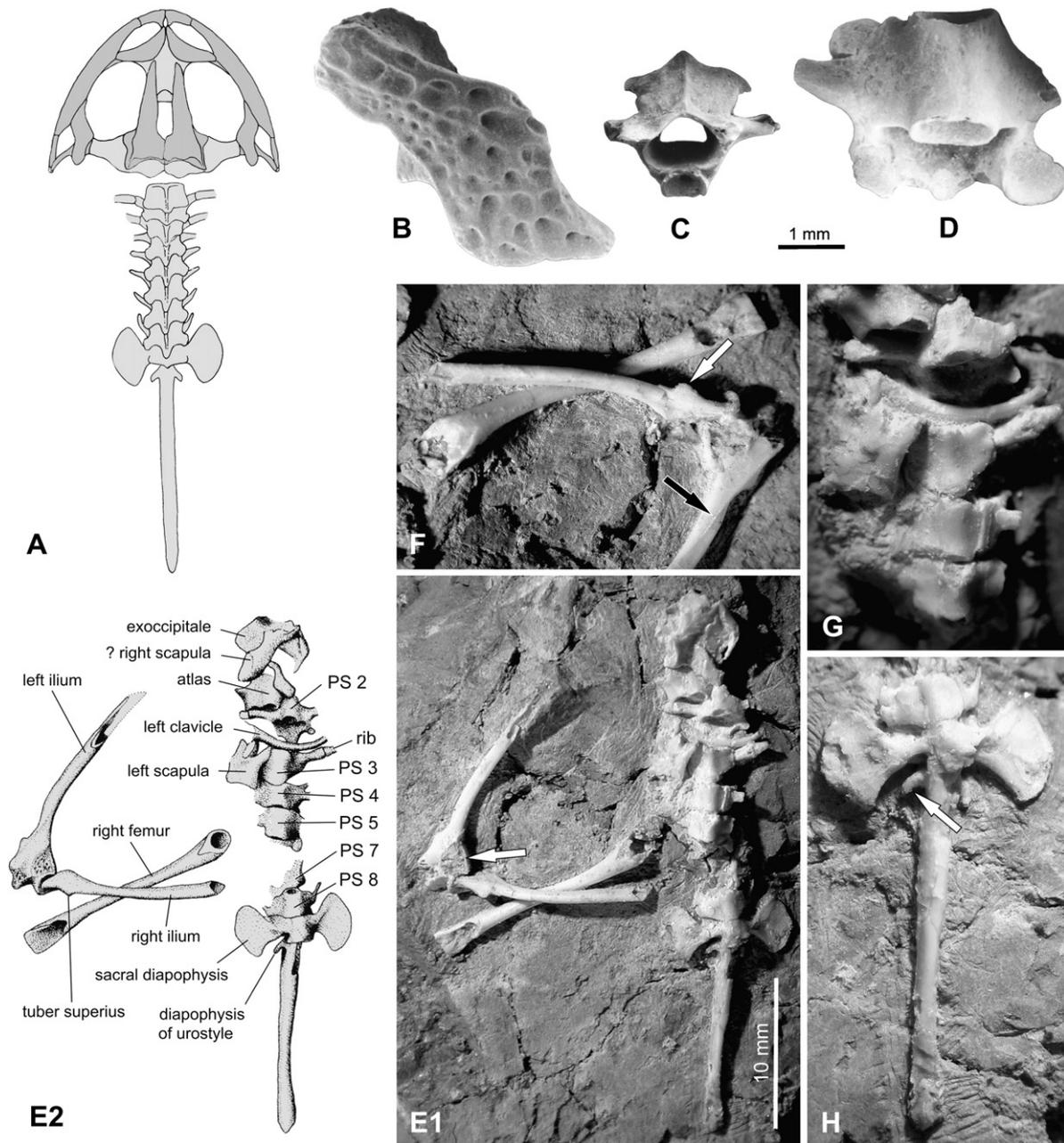


Fig. 2. *Gobiates* sp. A, Composite reconstruction of the skull and axial skeleton, dorsal view. Dermal bones are dark gray. B, Lamella alaris of the right squamosal in lateral view. LU-N 5/188. C, Presacral vertebra 3 or 4, anterior and slightly dorsal view. LU-N 5/239. D, Presacral vertebra 6 or 7, ventral view. LU-N 5/231. E1, Vertebral column, pelvic girdle and part of the hind limb, axial skeleton in ventral view, pelvis in dorsal view. PIN 3907/10. Iliac symphysis (interiliac tubercle) marked by white arrow. E2, Interpretive line-drawing of E1. F, Preserved part of pelvic region (as in E1 but rotated in 180° to show ilium in standardized position). Tuber superius marked by white arrow, oblique ridge on the inner surface marked by black arrow. G, Enlarged part of vertebral column between PS 2 and PS 5. H, Enlarged sacral vertebra with slightly disarticulated urostyle. Right diapophysis of the first caudal vertebra (transverse process of the urostyle) marked by white arrow. Figs B-D are in the same scale.

only moderately concave. Horizontal lamina on the maxillae weakly developed and with no pterygoid process. Quadratojugals present. Palatines present, although fused to palatal processes of maxillae. Extensive squamoso-maxillary contact. Vomers with no postchoanal process. Prootics and exoccipitals separated by a suture. Eight presacral vertebrae with imbricated neural arches. Vertebral centra amphicoelous, with or without notochordal canal. Ribs on vertebrae 2–4 either free

(*Gobiates*) or distinguishable from the transverse processes (*Cretasalia*). Sacro-urostyler articulation bicondylar. Urostyle with at least one pair of transverse processes. Epicondylus lateralis humeri probably absent; the latter character is based on associated disarticulated humeri (cf. Roček and Nessov, 1993; Gubin, 1999).

Contained genera. *Gobiates* Špinar and Tatarinov, 1986; *Gobiatoides* Roček and Nessov, 1993; *Cretasalia* Gubin,

1999. Note, however, that Sanchíz (1998) questioned the validity of *Gobiatoides*.

Comparisons (only with Leiopelmatidae, Discoglossidae, and non-pipoid Mesozoic taxa; see also Table 1). Gobiidae differ from the Leiopelmatidae (sensu Frost et al., 2006; *Vieraella* and *Notobatrachus* were sometimes considered members of this family which would, according e.g. to Estes and Reig (1973) and Duellman and Trueb (1986), extend the stratigraphic range of this family to the Early Jurassic) in possessing the quadratojugal, nasals anteriorly in contact with the pars facialis praemaxillae (instead of widely separated) and in weak medial contact (instead of widely separated medially), parietal portions of the frontoparietals in contact (instead of widely separated medially), extensive squamoso-maxillary contact, processus cultriformis of the parasphenoid not extending anteriorly to reach the level of the vomers, palatines present, sphenethmoid well ossified (instead of divided into a pair of lateral ossifications even in adults), lower number (8,

instead of 9) of presacral vertebrae which bear imbricated neural arches (instead of non-imbricated arches that are often not fused dorsal to the neural spine), sacral diapophyses moderately to highly dilated (instead of narrow or only slightly dilated), tuber superius ilii prominent and well-defined both anteriorly and posteriorly (absent in recent Leiopelmatidae).

Gobiatids are similar to the Leiopelmatidae in having a frontoparietal fontanelle, amphicoelous vertebrae, free ribs, a pair of posterolaterally declined diapophyses on the urostyle, and an oval iliac shaft in cross-section (i.e., the dorsal crest is absent).

Gobiidae differ from *Prosalirus* Shubin and Jenkins, 1995 (data from Jenkins and Shubin, 1998) from the Early Jurassic of North America in having sculptured dermal bones (whereas no ornamentation is present in *Prosalirus*), quadratojugal present (most probably absent in *Prosalirus*), sacral diapophyses fan-like (narrow in *Prosalirus*), caput humeri ossified (cartilaginous in *Prosalirus*), rounded dorsal margin of ilial shaft

Table 1

Diagnostic characters used in comparisons of *Gobies* with Mesozoic anuran genera preserved as more or less complete skeletons (both articulated and disarticulated), with Cainozoic Leiopelmatidae and Discoglossidae, and with taxa included in Pipoidae. Numbers refer to the characters discussed in the text (4. Evolutionary status). Note, however, that some characters can be expressed by more variants than just two extremes. Data from Báez and Basso (1996); Fey (1988); Henrici (1998); Jenkins and Shubin (1998); Jones et al. (2003); Rage and Roček (1989), and Wang (2004)

| Character categories | Characters / Taxa | Gobies | Cretasalla | Triodobatrachus | Prosalirus | Vieraella | Notobatrachus | Liobatrachus | Mesophryne | Callobatrachus | Eodiscoglossus | Wealdenbatrachus | Rhadinosteus | Aygroua | Paradiscoglossus | Enneabatrachus | Gobiidae | Leiopelmatidae | Discoglossidae | Pipoidae |
|--------------------------|--|--------|------------|-----------------|------------|-----------|---------------|--------------|------------|----------------|----------------|------------------|--------------|---------|------------------|----------------|----------|----------------|----------------|----------|
| symplesiomorphies | | 13 | 10 | 6(9) | 3 | 8(9) | 8 | 5 | 7 | 6 | 6(7) | 4(5) | 2(3) | 1 | ? | ? | | 5(6) | 9(12) | 6 |
| | skull short and wide | X | X | X | ? | X | ? | X | X | X | X | ? | ? | ? | ? | ? | X | 0-X | X | X |
| | sphenethmoid well ossified | X | X | X | X | X | 0 | ? | X | X | X | ? | ? | ? | ? | ? | X | 0 | X | X |
| | nasal-premaxillary contact | X | ? | ? | 0 | X | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0-X | 0 | 0-X | 0 |
| | nasals in contact | X | X | ? | ? | X | X | ? | ? | ? | 0 | ? | ? | ? | ? | ? | X | 0 | X | X |
| | frontoparietals paired | X | X | 0-X | ? | X | X | X | ? | ? | X | X | 0 | ? | ? | ? | X | X | 0-X | 0 |
| | parietal portions in contact | X | X | X | ? | X | X | X | ? | ? | X | X | ? | X | ? | ? | X | 0 | X | X |
| | squamoso-maxillary contact | X | X | ?X | ? | ?0 | 0 | ? | X | 0 | 0-X | 0 | ? | ? | ? | ? | X | 0 | 0-X | 0 |
| | quadratojugals present | X | X | ?X | ? | 0 | 0 | ? | X | X | ? | X | ? | ? | ? | ? | X | 0 | X | 0 |
| | palatines distinguishable | X | ? | X | ? | ? | ? | ? | ? | 0 | ? | ? | ? | ? | ? | ? | X | 0 | X | 0 |
| | mentomeckelian (hypomandibular) present | X | ? | ? | ? | X | X | ? | X | X | ? | ? | ? | ? | ? | ? | X | X | X | X |
| | amphicoelous (ectochordal) centra | X | X | X | X | ?X | X | ? | 0 | 0 | 0 | ?X | X | X | ? | ? | X | X | 0 | 0-X |
| | ribs free or ankylosed but distinguishable | X | X | X | X | X | X | X | X | X | X | X | ?X | ? | ? | ? | X | X | X | X |
| | urostyle with transverse processes | X | X | 0 | ? | X | X | X | X | X | X | X | 0 | ? | ? | ? | X | X | X | 0 |
| synapomorphies | | 3 | 3 | 0 | ? | 1 | 1 | 1 | 0 | 2 | 2 | 1 | 2 | ?-0 | ? | ? | | 1 | 2(3) | ?1 |
| | frontoparietal fontanelle | X | X | 0 | ? | X | X | X | ? | X | X | ?0 | 0 | ? | ? | ? | X | X | 0-X | 0 |
| | eight presacral vertebrae | X | X | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | X | ? | X | ? | ? | X | 0 | X | 0-X |
| | sacro-urostylar articulation bicondylar | X | X | 0 | ? | ?0 | 0 | ? | ? | X | ? | X | X | 0 | ? | ? | X | 0 | X | 0 |
| polarity unknown | | 11 | 6(8) | 4 | 2 | 5 | 4(5) | 3 | 3 | 3 | 4 | 1(3) | 1 | 0(1) | ? | ? | | 2(3) | 4(5) | 4(6) |
| | prootics and exoccipitals separated | X | X | X | ? | X | X | ? | ?0 | 0 | ? | ? | ? | ? | ? | ? | X | 0 | 0 | 0 |
| | dermal bones sculptured | X | 0-X | X | 0 | ?0 | X | X | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? | X | 0 | 0-X | 0 |
| | nasals crescent-like | X | ?X | ? | ? | X | 0 | ? | ? | ? | 0 | ? | ? | ? | ? | ? | X | 0 | 0 | ?X |
| | orbital margin of maxilla almost straight | X | X | ? | ? | ? | ?X | ?0 | ? | ? | ? | ?X | ? | ? | ? | ? | X | X | 0 | X |
| | maxillae with no pterygoid process | X | X | ? | X | X | X | ? | X | ? | X | ?X | ? | ? | ? | ? | X | X | 0 | ?X |
| | palatines fused to maxillae | X | ? | 0 | 0 | ? | 0 | ? | ?0 | ? | ? | ? | ? | ? | ? | ? | X | 0 | 0 | 0 |
| | vomers with no postchoanal process | X | ? | ? | ? | 0 | 0 | ? | ? | ? | ? | ? | ? | ? | ? | ? | X | 0 | 0 | 0 |
| | processus cultriformis of parasphenoid short | X | X | X | ? | X | 0 | ? | ? | X | ? | ? | ? | ? | ? | ? | X | 0-X | X | 0 |
| | neural arches imbricated | X | X | X | X | X | X | X | X | X | X | X | X | ? | ? | ? | X | 0 | X | X |
| | transverse processes declined anteriorly | X | X | 0 | ? | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | ? | ? | ? | X | 0 | X | X |
| | sacral diapophyses dilated | X | 0 | 0 | 0 | 0 | 0 | X | X | X | X | 0 | ? | 0-X | ? | ? | 0-X | 0 | X | X |
| ambiguous | | 4 | 1 | 2 | 1 | ? | 1(3) | ?0 | 1 | ?0 | ?0 | ?0 | 1 | ?0 | 0(2) | 0(1) | | 1 | 2 | ?0 |
| | canal for occipital artery closed dorsally | X | X | ? | ? | ? | 0-X | ? | ? | ? | ? | ? | ? | ? | ? | ? | X | ? | 0 | 0 |
| | tuber superius ilii prominent | X | ? | X | 0 | ? | ?X | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0-X | 0-X | X | 0 | X | ? |
| | iliac shaft rounded dorsally | X | ?0 | X | X | ? | X | ? | X | 0 | 0 | 0 | X | 0 | 0 | 0 | X | X | 0 | 0 |
| | epicondylus lateralis absent | X | ? | ? | 0 | ? | 0 | ? | ? | ? | ? | ? | 0 | ? | 0-X | ? | X | 0 | X | 0 |

(a narrow crest in *Prosalirus*), and tuber superius ilii prominent and well-defined (slightly raised rugose area in *Prosalirus*). Gobiatis are similar to *Prosalirus* in having a single and well-ossified sphenethmoid, amphicoelous vertebral centra sometimes pierced by notochordal canal, imbricate neural arches, and free ribs.

Gobiatis differ from *Vieraella* Reig, 1961 (data from Báez and Basso, 1996) from the Early Jurassic of Patagonia, Argentina, in having quadratojugal, nasals anteriorly in contact with the pars facialis praemaxillae (instead of widely separated) and in weak medial contact (instead of extensive medial contact in *Vieraella*), frontoparietals in median contact only to a short extent posteriorly (whereas they remain in contact along the posterior half of their length in *Vieraella*), absence of the posterolaterally extending postchoanal process of the vomer, lower number (8, instead of at least 10) of presacral vertebrae, and the transverse processes of posterior presacral vertebrae declined anteriorly (slightly posteriorly in *Vieraella*).

They are similar to *Vieraella* in possessing a relatively large frontoparietal fontanelle, lamina horizontalis maxillae lacking a pterygoid process, processus cultriformis of the parasphenoid not extending anteriorly to reach the level of the vomers, mentomeckelian bone present, prootics separated from exoccipitals, free ribs on vertebrae 2–4, pair of transverse processes on the urostyle, and possibly in having amphicoelous vertebrae with imbricated neural arches.

Gobiatis differ from *Notobatrachus* Reig in Stipancic and Reig, 1955 (based on data from Báez and Basso, 1996, and pers. observation; see also Báez and Nicoli, 2004) from the Middle to Late Jurassic of Patagonia, Argentina, in having pit-and-ridge sculpture (whereas sculpture of *Notobatrachus* is formed by irregular, longitudinal wrinkles or grooves and ridges), different shape and topography of nasals (namely their robust anterior and weak median contact: only a weak anterior process, but a comparatively long median suture occurs in *Notobatrachus*), relatively large frontoparietal fontanelle (instead of the smaller, slit-like fontanelle present in fully grown *Notobatrachus*), closed canal piercing the posterolateral part of the frontoparietal that housed occipital arteries (instead of open groove; the closed canals occur only in some more developed individuals of *Notobatrachus*), lamina horizontalis maxillae well developed (absent in *Notobatrachus*; termed “pars palatina” in Báez and Basso, 1996, p. 141), quadratojugal present (absent in *Notobatrachus*), processus cultriformis of the parasphenoid not extending anteriorly to reach the level of the vomers (reaching the posterior margin of the vomers in *Notobatrachus*), absence of the posterolaterally extending postchoanal process of the vomer, discrete palatines (absent in *Notobatrachus*), sphenethmoid well ossified (instead of divided into a pair of lateral ossifications), lower number (8, instead of 9 in *Notobatrachus*) of presacral vertebrae, sacral diapophyses moderately to highly dilated (instead of narrow), absence of rugosity on ventral side of vertebral centra, centra of presacral vertebrae almost cylindrical (not constricted at their midlength as in *Notobatrachus*), weak and anteriorly declined transverse processes on posterior presacral vertebrae

(robust and nearly perpendicular in *Notobatrachus*), direct sacro-urostyler articulation (one distinct caudal vertebra inserts between the sacrum and urostyle in *Notobatrachus*), and the lateral epicondyle absent (both epicondyles appear equally expanded distally in *Notobatrachus*).

They are similar to *Notobatrachus* in having a well-developed mentomeckelian bone, prootics separated from exoccipitals, maxilla without pterygoid process, amphicoelous vertebral centra, imbricated neural arches, and free ribs.

Gobiatis differ from the Discoglossidae in having squamoso-maxillary contact (instead of separated squamosal and maxilla), postchoanal process of vomer absent, palatine present, exoccipital and prootic separate (instead of fused), vertebral centra amphicoelous (instead of opisthocelous), and iliac shaft oval in cross-section (instead of having a dorsal crest).

Furthermore, they differ from *Callobatrachus* Wang and Gao, 1999 (Discoglossidae) from the Jurassic/Cretaceous of China (data from Wang et al., 2000; Gao and Wang, 2001; Wang, 2004) in having dermal sculpture (cranial dermal bones are smooth in *Callobatrachus*), squamosal-maxillary contact present (no contact between lamella alaris squamosi and maxilla in *Callobatrachus*), prootic and exoccipital separate (fused in *Callobatrachus*), transverse process of posterior presacral vertebrae strongly declined anteriorly (nearly perpendicular in *Callobatrachus*), and small but distinct tuber superius (absent in *Callobatrachus*).

Gobiatis are similar to the Discoglossidae in having the quadratojugal present, eight presacral vertebrae, imbricated neural arches, three pairs of free ribs on vertebrae 2–4, sacral diapophyses fan-like, bicondylar sacro-urostyler articulation (monocondylar in *Barbourula*), and a pair of posterolaterally declined diapophyses on the urostyle.

Furthermore, they are similar to the discoglossid *Callobatrachus* Wang and Gao, 1999 in having a short and wide skull (LC:LiC 0.8), frontoparietal fontanelle present, and a well ossified mentomeckelian element.

Gobiatis differ from *Eodiscoglossus* in having dermal roofing bones sculptured (smooth in both *E. santonjae* Villalta, 1956 from the Lower Cretaceous of Spain and in *E. oxoniensis* Evans et al., 1990 from the Middle Jurassic of England). Furthermore, they differ from *E. santonjae* in having nasals in contact (separated from one another in *E. santonjae*), diapophyses of the posterior presacral vertebrae thin and strongly declined anteriorly (whereas stout and only moderately declined anteriorly in *E. santonjae*), sacral vertebra concave anteriorly (biconvex in *E. santonjae*), and sacral diapophyses fan-shaped (only slightly dilated at their distal parts in *E. santonjae*). They differ from *E. oxoniensis* in having squamoso-maxillary contact (apparently no squamoso-maxillary contact in *E. oxoniensis*), iliac shaft oval (dorsal crest on iliac shaft in *E. oxoniensis*), and a distinct tuber superius (shallow and flush with the surface in *E. oxoniensis*).

Gobiatis are similar to *Eodiscoglossus* (*E. oxoniensis*) in having no pterygoid process on the horizontal lamina of the maxilla, and to *E. santonjae* in having frontoparietals with a short anterior fontanelle, squamoso-maxillary contact present, free ribs, and a pair of urostyler processes.

Gobiidae differ from *Wealdenbatrachus* Fey, 1988 in having dermal bones sculptured (frontoparietal, squamosal and maxilla are smooth in *Wealdenbatrachus*), frontoparietals with an extensive fontanelle (narrow, if any, fontanelle in *Wealdenbatrachus*), and the iliac shaft oval in cross section (dorsal crista present and dorsal tubercle prominent laterally in *Wealdenbatrachus*). They are similar to *Wealdenbatrachus* in having separated frontoparietals, quadratojugals present, possible presence of amphicoelous vertebrae with imbricated neural arches, free ribs on vertebrae 2–4, a pair of posteriorly declined diapophyses on the urostyle, and sacro-urostylar articulation bicondylar.

Gobiidae differ from *Hatzegobatrachus* Venczel and Csiki, 2003 and *Paralatonia* Venczel and Csiki, 2003 (both based only on ilia) from the latest Cretaceous (Maastrichtian) of Romania in different morphology of the tuber superius ilii (it is steep anteriorly but horizontal and confluent with the pars ascendens posteriorly, similar to *Bombina*, in *Hatzegobatrachus*, and declined laterally, similar to *Latonia*, in *Paralatonia*).

Gobiidae differ from *Mesophryne* Gao and Wang, 2001 from the Jurassic-Cretaceous of Liaoning Province, China, in having dermal sculpture on the frontoparietals, maxillae and squamosals (no sculpture occurs in *Mesobatrachus*), eight (instead of nine) presacral vertebrae, amphicoelous (instead of procoelous) vertebral centra, transverse processes on posterior presacral vertebrae declined anteriorly (oriented laterally in *Mesophryne*), and tuber superius distinct (extremely weakly developed in *Mesophryne*).

They are similar to *Mesophryne* in having short and wide skull (LC:LtC 0.7), squamosal-maxillary contact present, maxilla without pterygoid process, quadratojugal present, sphenethmoid as a single element, mentomeckelian bones present, free ribs on vertebrae 2–4, imbricated neural arches, sacral diapophyses dilated, urostyle with a pair of vestigial transverse processes, and iliac shaft with no dorsal crest.

Gobiidae differ from *Liaobatrachus* Ji and Ji, 1998 from the Jurassic-Cretaceous of Liaoning Province, China (anatomical data from Wang, 2004; Wang, 2006, pers. com. and photographs of the type specimen) in having a lower number of presacral vertebrae (8 instead of 9 in *Liaobatrachus*), diapophyses of the posterior presacral vertebrae thin and declined anteriorly (robust and perpendicular in *Liaobatrachus*), and well-defined tuber superius (whereas any such tubercle is lacking on both ilia of *Liaobatrachus* whose dorsal outlines are well preserved). Gobiidae are similar to *Liaobatrachus* in having a short and wide skull (LC:LtC 0.69, according to data from Wang, 2004), dermal bones sculptured (as evidenced by disarticulated maxillae in *Liaobatrachus*), frontoparietals separated by an anterior fontanelle (as judged by natural cast of the inner surface of these bones in *Liaobatrachus*; in contrast to Ji and Ji, 1998 (fide Wang, 2004)), imbricated neural arches, free ribs not fused to transverse processes (in contrast to Ji and Ji, 1998 (fide Wang, 2004)), sacral diapophyses fan-shaped, and urostyle with a pair of transverse processes.

Gobiidae also differ in absence of the dorsal crest from *Enneabatrachus* Evans and Milner, 1993 from the Late

Jurassic of North America, and in presence of the dorsal, well prominent tubercle and absence of elongated tuberosity on the ventrolateral surface of the iliac shaft from *Nezpercius* Blob et al., 2001 from the Late Cretaceous of North America.

Comments. Based on differences between numerous disarticulated cranial and associated postcranial elements of discoglossids and *Gobiates*-like forms from several Upper Cretaceous localities in Central Asia, Roček and Nessov (1993) proposed a separate family Gobiidae for the latter. They were later shifted to a subfamily rank of the Discoglossidae by Sanchíz (1998), as Gobiatinae, besides Alytinae, Bombinatorinae and Discoglossinae. It is obvious from the above comparisons that *Gobiates* and *Cretasalia* have close relations to *Ascaphus* and *Leiopelma* as well as to *Discoglossus* (and fossil anurans included in the Discoglossidae), and occupy an intermediate position between them. However, they differ from the latter in having different type of vertebral centra and in number of characters in which polarity cannot be determined (Table 1). According to the cladistic analysis of Wang (2004) and Wang et al. (2000), *Gobiates* (*Cretasalia* was not included) is clearly separated from discoglossids and leiopelmatids. Such relationships would seemingly support the concept of the superfamily Discoglossodea proposed by Duellman (1975), but new analyses based on morphological and non-morphological characters of recent anurans (Frost et al., 2006) suggest that the Leiopelmatidae and Discoglossidae are not as closely related as previously believed.

Genus *Gobiates* Špinar and Tatarinov, 1986

Type species. *Gobiates khermeentsavi* Špinar and Tatarinov, 1986, p. 114, figs. 1–3.

1978 *Eopelobates* Borsuk-Białynicka, p. 58, figs. 1–2, pl. 15.

1981a *Eopelobates* Nessov, p. 71.

1981 Hitherto undescribed form from the locality Khermeen Tsav, Mongolia. Roček, p. 117.

1986 *Gobiates* Špinar and Tatarinov, p. 114.

Revised diagnosis. The genus may be diagnosed by combination of following characters: (1) skull broader than long; (2) presacral vertebrae amphicoelous or even pierced by a notochordal canal (Fig. 2C, D; Špinar and Tatarinov, 1986, fig. 3D); (3) dermal roofing bones of the skull and the maxilla covered by irregular pit-and-ridge sculpture (Fig. 2B); (4) frontoparietals paired, their anterior parts separated by a long frontoparietal fontanelle; their posterior surface is pierced by the foramen for the occipital artery (Špinar and Tatarinov, 1986, fig. 3A); (5) the nasals barely in contact with the tips of the frontoparietals; (6) palatines free in juvenile individuals, coalesced to the palatine process of the maxilla in adults; (7) squamoso-maxillary contact extensive; (8) maxillary-ptyergoid contact without participation of the pterygoid process on the horizontal lamina of the maxilla; (9) parasphenoid bears a distinct keel in the midline (Špinar and Tatarinov, 1986, fig. 3C); and (10) the ilium bears a prominent and well-defined tuber superius, the iliac shaft is rounded on its dorsal margin,

and there is a shallow groove which crosses the dorsal margin of the ilium obliquely immediately anterior to the tuber (Fig. 2F).

Description. Estimated snout-vent length is ca. 50 mm.

Skull. The skull is wider than long; the ratio is 16.5 mm:29.3 mm (0.56) in PIN 31/42/1 (*G. khermeentsavi* holotype), 18.0 mm:29.0 mm (0.62) in PIN 31/42/2 (*G. khermeentsavi* paratype); estimated 18.0 mm:21.0 mm (0.86) in ZPAL MgAb-III/1 (*G. leptocolaptus* holotype). Thus it is obvious that, despite incompleteness and moderate dorsoventral compression of these specimens, the skull width ranges from very broad (nearly twice the skull length) to that in which the length is approximately equal to width. The dermal roofing bones (including maxilla and squamosal) are covered by irregular pit and ridge sculpture.

As demonstrated by PIN 31/42/1, the paired frontoparietals are only in contact with one another for the otic part of the skull; between the anterior 75% of their length is a large frontoparietal fontanelle (Špinar and Tatarinov, 1986, fig. 3A). The medial margins of the frontoparietals are composed of comparatively thick lamellae; this may represent the adult condition, contrasting with that of juveniles in which less ossification of the frontoparietals might be expected. The parietal portion of the frontoparietals is comparatively deep; its posterior surface is nearly vertical, whereas its lateral surface, adjoining the prootic, is slightly broader when compared with the facies dorsalis. Both lateral and posterior surfaces meet one another in a robust processus paraoccipitalis which bears a rounded crista slanting down from the facies dorsalis. The crista dorsally covers the foramen for the occipital artery. Along the midline, the posterior surfaces of both frontoparietals produce rounded but distinct processes separated by a median suture. The posterior surface of each frontoparietal is pierced by a foramen for the occipital artery.

The nasals are sculptured and crescent-shaped, and do not extend onto the interorbital part of the sphenethmoid. As exhibited by ZPAL MgAb-III/1, only their anterior parts were in contact (Borsuk-Białynicka, 1978, fig. 1A; Roček, 1981, fig. 45).

The maxillary arch is complete, including the quadratojugal. The frontal portion of the premaxilla is long and slender. As shown by ZPAL MgAb-II-1, these processes are in contact with each other along their entire length. The premaxillae are deep (as is the anterior part of the maxillae) but it is not clear whether they are sculptured or smooth. The maxilla is deeper anteriorly than posteriorly, with its orbital margin nearly straight (Špinar and Tatarinov, 1986, fig. 3B). Judging by ZPAL MgAb-III/1 (Borsuk-Białynicka, 1978, pl. 15, figs 2a, b; Roček, 1981, fig. 46), it had a short and broad palatine process which was probably connected, via an obliterated suture, with the palatine. This seems to be evidenced by a shallow indentation on the posterior margin of the left postnasal wall (facing the orbit) which continues across its ventral surface onto the choanal margin. Although the condition on the right postnasal wall is rather obscure, a similar indentation may be recognized. On both sides of the skull, the medial extent of each palatine can be recognized as a rounded tip protruding

from the choanal margin. Thus it may be concluded that a free palatine was most probably developed in juveniles, which later coalesced with the maxilla. The posterior part of the maxilla produced a short and rounded posterior process (Roček, 1981, fig. 47; Špinar and Tatarinov, 1986, fig. 3B) which was in contact with the quadratojugal. The latter bone is slender, devoid of sculpture, short in *G. leptocolaptus* and moderately longer in *G. khermeentsavi* (Roček, 1981, fig. 47; Špinar and Tatarinov, 1986, fig. 3B).

The squamosal consists of a smooth processus posterolateralis adjoining, in living animals, with the palatoquadrate cartilage laterally, and of the lamella alaris, the outer surface of which is sculptured (Nessov, 1988, pl. XIV, fig. 5). The anterior process of the lamella (termed processus or ramus zygomaticus) was in contact with the dorsal margin of the posterior (i.e., postorbital) part of the maxilla. The shape and proportions of the lamella alaris, as well as nature of the squamoso-maxillary contact, is a matter of considerable variation. Briefly, the lamellae may be slender or broad, nearly straight or curved, with a short or long squamoso-maxillary suture (Roček, 1981, fig. 47; Roček and Nessov, 1993, text-fig. 5). The quadrate bones are preserved in both ZPAL MgAb-III/1 and PIN 31/42/1 and are independent of the quadratojugals (Roček, 1981, figs 45, 47; Špinar and Tatarinov, 1986, fig. 3B).

As evidenced by ZPAL MgAb-III/1, the vomers have a small, elevated tooth patch directed posteriorly; medial to each patch there is a flat outgrowth reaching the midline; thus, both vomers are in contact with one another. The anterior tip of the parasphenoid reaches the level of the posterior margins of the choanae, but not between the vomers. As evidenced by PIN 31/42/1, its posterior part extends laterally as prominent lateral wings adjoining the bottom of the otic capsules. The wings are moderately constricted medially. The posterior margin of the bone bears a broad median process (Špinar and Tatarinov, 1986, fig. 3C). The medial part of the parasphenoid between both orbits produces a pronounced keel in the midline.

The pterygoid is well preserved in ZPAL MgAb-III/1. It is comparatively robust, and its orbital margin is only slightly concave (Roček, 1981, fig. 46). Although the right angulosphenial is preserved in ZPAL MgAb-III/1, its principal diagnostic characters are obscured. The mentomandibulars are present but it cannot be determined whether they were co-ossified with the dentaries.

ZPAL MgAb-III/1 provides information about principle features of the sphenethmoid. The ossified septum nasi extends beyond the level of the anterior tips of both nasals. A considerable part of its dorsal surface, rhomboid in shape, remained uncovered by dermal bones. As can be seen in ventral view, the opening of the canal for the medial branch of the ophthalmic nerve on each side was covered dorsally by a broad supraorbital lamina (Roček, 1981, figs. 45, 46). The anterior margin of the fenestra frontoparietalis is located posterior to the level of the postnasal wall.

The prootics and exoccipitals are both fragmentary and obscured by dermal bones but, as may be inferred from PIN

31/42/1 and from the morphology of the ramus paroticus of the squamosal, the lateral portion adjacent to the crista parotica is comparatively narrow in dorsal view. Both exoccipitals seem to be separated by a suture in the midline, both dorsally and ventrally; a similar suture is present between the prootics and exoccipitals (Špinar and Tatarinov, 1986, figs. 3A, C, D).

Postcranial skeleton. The vertebral column consists of eight presacral vertebrae. The centra are amphicoelous and moderately constricted at mid-length. The neural arches are imbricated. The transverse processes of the sacral vertebra are fan-like. Vertebrae 2–4 bear free ribs (Fig. 2E). The urostyle bears a pair of thin, posterolaterally declined transverse processes. The urostyle and sacral vertebra are separated and the articulation is bicondylar. The pectoral girdle is arciferal. The scapula has a deep cleft proximally (Borsuk-Białynicka, 1978, fig. 2), and the clavicle is slender and regularly arcuate (Fig. 2E). The iliac shaft is rounded in cross section, and bears a distinct tuber superius. A shallow groove extends obliquely from the outer surface onto the inner surface close to the tuber (Fig. 2F). The femur is distinctly sigmoidal.

Comparisons. *Gobiates* differs from *Cretasalia* Gubin, 1999 from the Upper Cretaceous (Campanian-Maastrichtian) of Gobi Desert, Mongolia, in having the dermal bones of the skull sculptured to a variable degree (only indistinct pits are present on the outer surface of maxilla in *Cretasalia*), frontal process of the maxilla is less prominent or absent (distinctly prominent, more than two-times greater than the depth of the bone at the level of the orbit in *Cretasalia*), processus zygomatico-maxillaris of the maxilla moderately prominent, in accordance with the type of squamoso-maxillary contact (entirely absent in *Cretasalia*), lamina horizontalis maxillae widely rounded (comparatively thin in *Cretasalia*), free ribs on vertebrae 2–4 (these are fused to the corresponding diapophyses in *Cretasalia*), and sacral diapophyses fan-like (narrow and declined posteriorly in *Cretasalia*).

Both genera are similar in having short and wide skulls, frontoparietals tapering anteriorly and separated anteriorly by a frontoparietal fontanelle, canal for the occipital artery piercing the posterolateral part of the frontoparietal and entering the orbit, nasals crescent-like and in contact with one another only anteromedially, margo orbitalis maxillae straight or only moderately concave, processus pterygoideus maxillae absent, premaxillary-maxillary suture comparatively long and vertical, quadratojugal present, squamoso-maxillary suture long, processus cultriformis parasphenoidei reaching only the level of the anterior border of the orbit and bearing a median keel on its ventral surface, prootic and exoccipital separated by a suture, vertebral centra amphicoelous, neural arches imbricated, sacro-urostylar articulation bicondylar, a pair of urostylar diapophyses present, and epicondylus lateralis humeri absent.

Gobiates differs from *Gobiatoides* Roček and Nessov, 1993 in being larger, in having a straight or only slightly concave orbital margin of the maxilla (distinctly concave in *Gobiates*), the outer surface of the maxilla sculptured (smooth in *Gobiatoides*), and the maxilla is relatively deep in its orbital section (very shallow in *Gobiatoides*).

Intrageneric taxonomic diversity. Comparisons between specimens from Mongolia which are represented by articulated skeletons, and material from central Asia which consists mainly of disarticulated bones, are restricted to features which were observable in both. Only those elements were selected for taxonomic considerations from which further cranial characteristics can be inferred. Among such elements, the squamosal and maxilla seem to be important because their morphology reveals information on the entire posterolateral part of the skull (compare, e.g., fig. 3B in Špinar and Tatarinov, 1986 and fig. 1C in Borsuk-Białynicka, 1978), even if other bones (e.g., quadratojugal, pterygoid) are not preserved. The diagnostic features are illustrated in Fig. 3 where the numbers refer to diagnostic features described in the main text.

In addition to the type species, *G. khermeentsavi*, ten further species are recognised.

Gobiates asiaticus Roček and Nessov, 1993

Holotype. ZIN, LU-N 6/370 (a partial squamosal)

Type horizon and locality. Middle part of Bissekty Formation, Coniacian, Upper Cretaceous, Dzhyrakuduk (CBI-14), central Kizylkum Desert, Uzbekistan.

Diagnosis (after Roček and Nessov, 1993, p. 17). (1) Lamella alaris squamosi slender ($a/b = 3.6–3.7$), sometimes without processus dorsalis; and (2) the lamella is declined posteriorly so that a perpendicular line constructed from the posterior end of squamoso-maxillary suture cuts the orbital margin of the lamella anteriorly.

Gobiates bogatchovi Roček and Nessov, 1993

Holotype. ZIN, LU-N 5/107 (partial jaws in articulation)

Type horizon and locality. Middle part of Bissekty Formation, Coniacian, Upper Cretaceous, Dzhyrakuduk (CBI-4b), central Kizylkum Desert, Uzbekistan.

Diagnosis (after Roček and Nessov, 1993, p. 13, amended). (1) Processus zygomaticomaxillaris maxillae prominent above the level of margo orbitalis, confluent with the posterior, tapering part of maxilla; (2) tooth row exceeds the level of the posterior end of the lamina horizontalis maxillae; (3) sculpture on maxilla consisting of shallow, indistinct but regularly distributed depressions (not figured in Fig. 3); and (4) quadratojugal fused to quadrate.

Gobiates dzhyrakudukensis Roček and Nessov, 1993

Holotype. ZIN, LU-N 6/341 (partial maxilla)

Paratype. LUN 5/140 (partial maxilla)

Type horizon and locality. Middle part of Bissekty Formation, Coniacian, Upper Cretaceous, Dzhyrakuduk (CBI-14), central Kizylkum Desert, Uzbekistan.

Diagnosis (after Roček and Nessov, 1993, p. 15, amended). (1) Processus zygomaticomaxillaris maxillae prominent above the level of margo orbitalis, its posterior margin vertical (hence the posterior part of the bone which articulates with quadratojugal is slender); (2) tooth row terminates at the level of the posterior end of the lamina horizontalis maxillae; and (3) margo orbitalis maxillae paralleled on the inner surface by a rounded ridge delimiting dorsally the groove for the palatoquadrate bar.

Gobiates fritschi Roček and Nessov, 1993

Holotype. ZIN, LU-N 5/143 (partial maxilla)

Type horizon and locality. Middle part of Bissekty Formation, Coniacian, Upper Cretaceous, Dzhyrakuduk (CBI-4b), central Kizylkum Desert, Uzbekistan.

Diagnosis (after Roček and Nessov, 1993, p. 15). (1) Tooth row of maxilla exceeds the level where lamina horizontalis turns posterodorsally; and (2) the edge for articulation with ramus maxillaris pterygoidei very distinct.

Gobiates furcatus Roček and Nessov, 1993

Holotype. ZIN, LU-N 5/165 (partial maxilla)

Type horizon and locality. Middle part of Bissekty Formation, Coniacian, Upper Cretaceous, Dzhyrakuduk (CBI-4b), central Kizylkum Desert, Uzbekistan.

Diagnosis (after Roček and Nessov, 1993, p. 17). (1) Lamina horizontalis maxillae thin and narrow; (2) its posterior end bifurcates in two ridges – upper ridge continues posterodorsally, the lower delimits the end of tooth row; (3) tooth row exceeds posteriorly level of the end of lamina horizontalis; and (4) inner surface of margo orbitalis and processus zygomaticomaxillaris wrinkled.

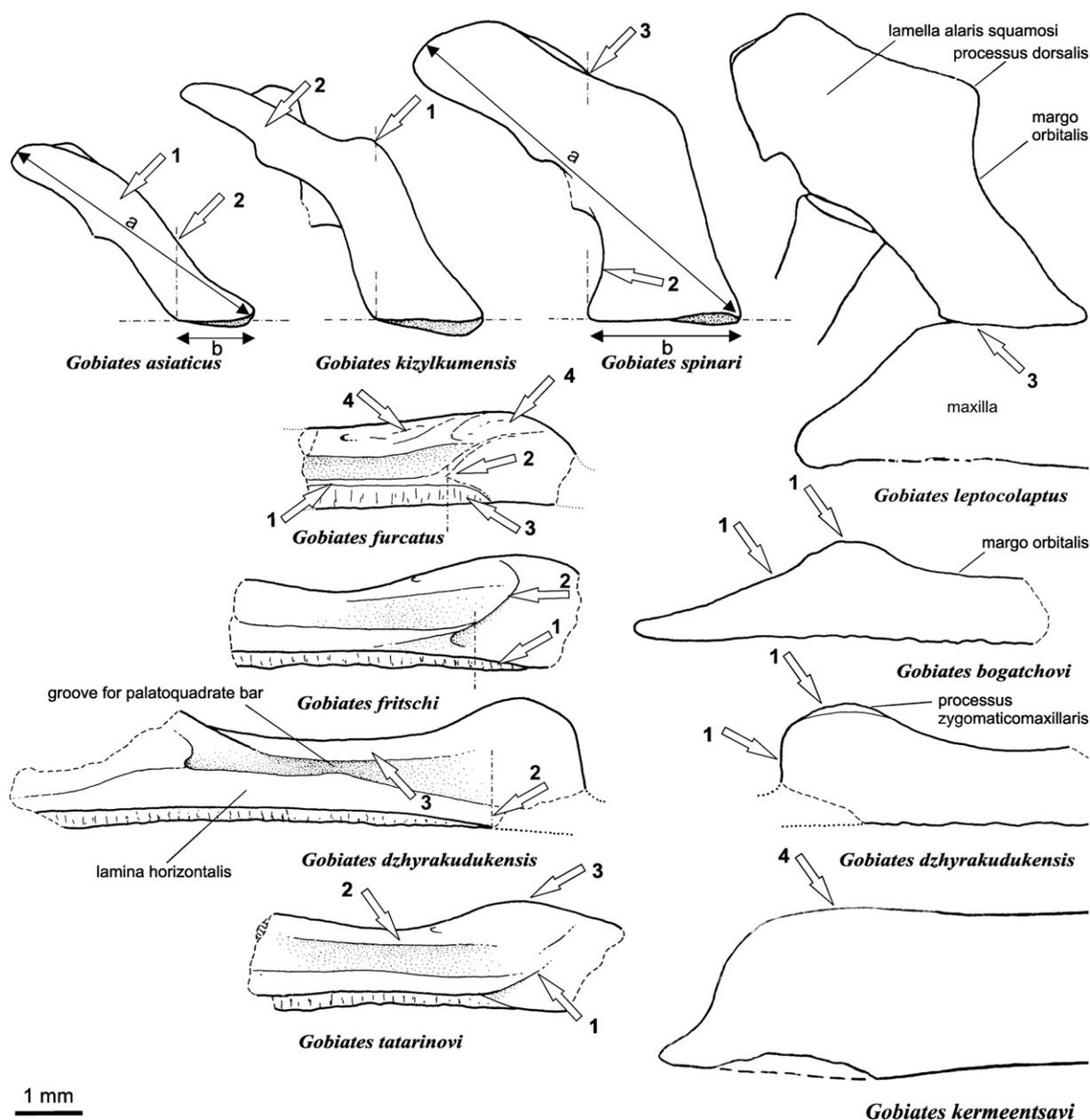


Fig. 3. Taxonomic variation of the squamosals and maxillae in *Gobiates*. The numbers refer to intrageneric diagnostic features described in the main text. To show relations between the both cranial elements, maxilla and squamosal of *Gobiates leptocolaptus* are drawn as they were originally articulated. *Gobiates khermeentsavi* and *G. furcatus* are reversed for comparison. All specimens are drawn to the same scale. Redrawn from or taken from Borsuk-Białynicka, 1978; Špinar and Tatarinov, 1986; Roček and Nessov, 1993.

Gobiates khermeentsavi Špinar and Tatarinov, 1986

Holotype. PIN 31/42/1 (nearly complete skull in articulation with some vertebrae)

Paratypes. PIN 31/42/2, PIN 31/42/3 (both partial skulls in articulation)

Type horizon and locality. Barun Goyot Formation or its equivalent, Upper Cretaceous (Santonian–Campanian after Špinar and Tatarinov, 1986, early or late Campanian after Kielan-Jaworowska et al., 2005; but see note in Gubin, 1999, p. 77 that precise stratigraphic level of *G. khermeentsavi* is unknown); Khermeen Tsav, SW of Nemegt Basin, Gobi Desert, Mongolia.

Synonymy.

1981 Hitherto undescribed form from the locality Khermeen Tsav, Mongolia. Roček, p. 117.

1993 *Gobiates 'khermeentsavi'*. Roček and Nessov, p. 11.

Diagnosis. (1) Sculpture consisting of irregular, sometimes widely spaced pits separated by ridges; (2) quadratojugal long; (3) processus zygomaticus (i.e., anterior process of the lamella alaris) slender and pointed; and (4) processus zygomaticomaxillaris maxillae absent.

Gobiates kizylkumensis Roček and Nessov, 1993

Holotype. ZIN, LU-N 6/363 (partial squamosal)

Type horizon and locality. Middle part of Bissekty Formation, Coniacian, Upper Cretaceous, Dzhyrakuduk (CBI-14), central Kizylkum Desert, Uzbekistan.

Diagnosis (after Roček and Nessov, 1993, p. 17). (1) Processus dorsalis on the lamella alaris squamosi prominent; and (2) posterior part of the lamella slender.

Gobiates leptocolaptus (Borsuk-Białynicka, 1978)

Holotype. ZPAL MgAb-II/1 (partial skull in articulation)

Type horizon and locality. Red beds of Khermeen Tsav II, which are the stratigraphic equivalent of the Barun Goyot Formation, early or late Campanian age (Gradziński and Jerzykiewicz, 1972; Gradziński et al., 1977; Averianov, 1997; Kielan-Jaworowska et al., 2003), or Campanian–Maastrichtian age (Gubin, 1999), SW of Nemegt Basin, Gobi Desert, Mongolia.

Synonymy.

1978 *Eopelobates leptocolaptus*. Borsuk-Białynicka, p. 56, figs. 1, 2.

1986 *Gobiates leptocolaptus*. Špinar and Tatarinov, p. 114.

Diagnosis. (1) Sculpture consisting of irregular extensive depressions and small shallow pits; (2) quadratojugal short; and (3) processus zygomaticomaxillaris maxillae absent.

Gobiates sosedkoi (Nessov, 1981)

Holotype. ZIN, PHA No K77-5 (partial frontoparietal)

Type horizon and locality. Middle part of Bissekty Formation, Coniacian, Upper Cretaceous, Dzhyrakuduk (CBI-4v), central Kizylkum Desert, Uzbekistan.

Synonymy

1981a *Eopelobates sosedkoi*. Nessov, p. 71.

1993 *Gobiates sosedkoi*. Roček and Nessov, p. 11.

Diagnosis. Sculpture on frontoparietals (and supposedly also on lamella alaris squamosi and on maxilla) consisting of numerous and comparatively small pits separated by broad ridges.

Remark. See discussion on possible synonymy of *G. khermeentsavi* and *G. sosedkoi* in Roček and Nessov (1993), and comment in Sanchiz (1998).

Gobiates spinari Roček and Nessov, 1993

Holotype. ZIN, LU-N 5/137 (partial maxilla)

Type horizon and locality. Middle part of Bissekty Formation, Coniacian, Upper Cretaceous, Dzhyrakuduk (CBI-4b), central Kizylkum Desert, Uzbekistan.

Diagnosis (after Roček and Nessov, 1993, p. 16, amended). (1) Squamoso-maxillary suture long ($a/b = 2.4–2.7$); (2) posterior margin of the lamella alaris squamosi approximately perpendicular to squamoso-maxillary suture; and (3) perpendicular line constructed from the posterior end of squamoso-maxillary suture cuts dorsal margin of the lamella alaris squamosi posterior to processus dorsalis.

Gobiates tatarinovi Roček and Nessov, 1993

Holotype. ZIN, LU-N 6/405 (partial maxilla)

Type horizon and locality. Middle part of Bissekty Formation, Coniacian, Upper Cretaceous, Dzhyrakuduk (CBI-14), central Kizylkum Desert, Uzbekistan.

Diagnosis (after Roček and Nessov, 1993, p. 16). (1) Edge for articulation with ramus maxillaris pterygoidei gradually lowering and ultimately disappearing; (2) margo orbitalis maxillae delimited medially by an edge; and (3) processus zygomaticomaxillaris low and widely convex.

4. Evolutionary status

The majority of the characters of the Gobiatidae may be considered primitive, and only few of them are derived. Among primitive (plesiomorphic) features are the following:

- (1) Amphicoelous (ectochordal sensu Griffiths, 1963) vertebral centra, with persisting notochordal canal. This type occurs in the proanuran amphibians *Triadobatrachus* and *Czatkobatrachus* from the early Triassic (Rage and Roček, 1989; Evans and Borsuk-Białynicka, 1998), in the earliest known anurans *Prosalirus*, *Notobatrachus*, and probably also in *Vieraella* (all from the early through Middle–Late Jurassic), in two recent genera (*Ascaphus* and *Leiopelma*), and in the early developmental stages of both extinct (as evidenced by pipoid larvae *Shomronella*; Estes et al., 1978; Roček and Van Dijk, 2006) and contemporary taxa (although only as a segmented cartilaginous perichordal tube; Mookerjee, 1931; Griffiths, 1963). Amphicoelous (ectochordal) vertebrae are also found in fossil frog

- material from the Jurassic (Henrici, 1998ab) and Cretaceous (e.g., Jones et al., 2003). The geological age of the taxa possessing this type of vertebrae and its occurrence in early development point to its primitive nature.
- (2) Skull short and wide. This is a feature shared with the younger developmental stages of temnospondyl ancestors of the anurans (e.g., Shishkin, 1973; Boy, 1974; Boy and Sues, 2000), *Triadobatrachus* (Rage and Roček, 1989), Jurassic *Vieraella* and *Notobatrachus* (Báez and Basso, 1996), and with Jurassic/Cretaceous *Liaobatrachus*, *Mesophryne* and *Callobatrachus* (all represented by articulated or only slightly disarticulated skulls; Gao and Wang, 2001). There are also some modern anurans with broad skulls (e.g., pipids), however, the shape of their skull may be associated with their life style (Emerson, 1985).
 - (3) Free ribs or ribs fused to transverse processes in adults. Available evidence suggests that all Mesozoic anurans possessed free ribs. In articulated skeletons, it is sometimes difficult to decide whether they were articulated with corresponding diapophyses or firmly fused to them. Developmental studies on recent anurans reveal that ribs are retained as separate cartilages in a considerably large number of taxa, however, in most of them they are fused to diapophyses in early development and they cannot be recognized in adults (Blanco and Sanchiz, 2000, pers. obs.)
 - (4) Palatines present, although fused to the palatal process of the maxillae. In *Triadobatrachus*, the palatines were still free (Rage and Roček, 1989). Palatines are present in almost all anurans, however, they either fused to the vomer to form a posterolaterally directed postchoanal process (e.g., in *Scaphiopus*) or to the maxilla to form the main part of a palatine process (e.g., in *Pelobates* or *Rana*; Lebedkina, 2004, see also Roček, 2003a for a review of literature).
 - (5) Quadratojugals present. The complete set of dermal bones could reasonably be considered a primitive feature of anurans because in larval temnospondyls it appears as early as in the late larval period (Boy, 1974) and remains part of the skull in all temnospondyls. In contrast is the fact that in anurans the quadratojugal is among the last bones to appear. This may be explained by paedomorphosis (i.e., shift of reproduction capability to earlier developmental stages during evolution), so adult frogs correspond to late larval stages of temnospondyls. Paedomorphosis is also associated with an arrested ossification process which may be responsible for the loss of the quadratojugal in *Notobatrachus* and *Vieraella*. It is not clear whether it was present in *Triadobatrachus* (Rage and Roček, 1989) but Báez and Basso (1996) argued that what was interpreted as the maxillary ramus of the pterygoid by Rage and Roček (1989) is in fact a quadratojugal. Therefore, the presence of quadratojugals in frogs may be considered a primitive feature and its loss as early as in some Lower Jurassic taxa may be attributed to arrested ossification of some cranial elements.
 - (6) Extensive squamoso-maxillary contact. As was the case with the quadratojugals, loss of the contact between these

- two bones in some early frogs (e.g., *Notobatrachus*; pers. obs.; see also Báez and Basso, 1996) may be a result of arrested dermal ossification of the lamella alaris squamosi.
- (7) Frontoparietals paired. Paired frontoparietals are undoubtedly a primitive feature in spite of the fact that these elements are almost completely fused in *Triadobatrachus* (Rage and Roček, 1989).
 - (8) Urostyle with at least one pair of transverse processes. Transverse processes indicate the presence of vestigial caudal vertebrae incorporated in the urostyle (Ročková and Roček, 2005). *Notobatrachus* has the first caudal vertebra still free, some Cretaceous gobiatids and/or discoglossids (Roček and Nessov, 1993), or even Neogene discoglossids (Roček, 1994), have more than one pair of diapophyses on the urostyle.

The following features of the Gobiatidae may be considered derived:

- (1) Frontoparietals separated by a fontanelle. The replacement of the incomplete suture between both frontoparietals by a fontanelle (i.e., unossified membranous layer) may be considered a result of arrested dermal ossification. An opposite situation, i.e., where both frontoparietals are fused in a single element, may be considered a result of hyperossification (evidenced in pelobatids, e.g., by ossification of such unrelated elements as the operculum; Roček, 1981).
- (2) Eight presacral vertebrae. *Vieraella* possessed ten presacral vertebrae, *Notobatrachus*, *Mesophryne*, *Callobatrachus* and *Liaobatrachus* possessed nine, and *Eodiscoglossus* possessed only eight. Eight presacral vertebrae are typical for the majority of anuran families except for permanent water dwellers (Pipidae, Palaeobatrachidae) in which further reduction occurred by means of fusion of the anterior two, or of the posterior presacrals with the sacral (e.g., Roček, 2003b; Báez and Pugener, 2003; Roček and Van Dijk, 2006). In the context of Mesozoic non-pipoid anurans in which complete articulated columns were preserved, *Gobiates*, *Cretasalia*, and *Eodiscoglossus* are derived.
- (3) Sacro-urostylar articulation bicondylar. A simple articulation morphology which corresponds to that in posterior presacrals (e.g., in *Notobatrachus* there is even one free anterior caudal vertebra, in recent Leiopelmatidae, and in *Bombina* which is considered to be an underdeveloped discoglossid), may be considered primitive. In bicondylar articulation the mobility is restricted and it can be reasonably considered derived. A complete fusion occurs in Pelobatidae and in some aquatic forms like Pipidae; it seems that in both the fusion is associated with gliding movements of the sacroiliac joint (Van Dijk, 2002; pers. obs.).

The polarity cannot be determined in the following characters:

- (1) Nasals crescent-like and in contact over a short distance. This could be a result of hypoossification (as is the case

with the frontoparietals), as well as other factors such as the anatomy of the ethmoidal endocranium. The nasals are in close contact to a great extent in *Notobatrachus*, whereas in they are in contact over a short distance in *Vieraella*, and entirely separated in the holotype of *Eodiscoglossus santonjae* (pers. obs.).

- (2) Maxillae low, with their orbital margins straight. Among Mesozoic anurans, similar maxillae were found in *Eodiscoglossus oxoniensis* and *Kizylkuma* Nessov, 1981 and, among extant taxa, in *Leiopelma*, but not in combination with the presence of a maxillo-squamosal contact.
- (3) Maxillae with no pterygoid process. As this process plays an important role in articulation of the maxilla with the pterygoid, its absence may indicate a type of contact which is different from, e.g., that of discoglossoids.
- (4) Vomers with no postchoanal process. The postchoanal process (original palatine) is developed in *Vieraella* and *Notobatrachus*, as well as in *Callobatrachus* (Wang and Gao, 1999). Instead, the palatine is coalesced to the maxilla.
- (5) Prootics and exoccipitals separated by a suture. They are separate in *Triadobatrachus*, *Notobatrachus*, *Vieraella* and in normal development of recent *Leiopelmatidae* (although they can fuse with each other in some subfossil *Leiopelma* species; Worthy, 1987), whereas they are fused in all discoglossids.
- (6) Vertebrae with imbricate neural arches (for definition of this character see Trueb, 1973). In *Triadobatrachus*, *Notobatrachus*, *Mesobatrachus*, *Callobatrachus*, *Discoglossus*, and even in *Bombina*, the neural arches are imbricate, whereas in *Vieraella*, recent *Leiopelmatidae*, and in *Alytes* (another underdeveloped discoglossid), the neural arches are nonimbricate (Duellman and Trueb, 1986).

The following two characters are of ambiguous significance:

- (1) Tuber superius of the ilium. This is used as a character for taxonomic evaluation (e.g., Jones et al., 2003) and as a character in cladistic analyses (Gao and Wang, 2001; Gao and Chen, 2004). Wang (2004) considered it “a plesiomorphic feature in primitive anurans” which seems to represent a hypothesis in which the tuber superius is a result of transformation of the posteriorly directed “postiliac process” of primitive tetrapods, such as *Ichthyostega*, into the dorsal tuber superius, accompanied by rotation of the ilium and reduction in size of the process (Ročková and Roček, 2005). This could explain the fact that the process is remarkably prominent both in Lower Triassic proanurans *Triadobatrachus* and *Czatkobatrachus* (Evans and Borsuk-Białynicka, 1998; Roček and Rage, 2000). However, it is poorly developed in *Prosalirus*, which may be attributed to abbreviated somatogenesis (similar to the interruption of the squamoso-maxillary contact and separation of both frontoparietals by a fontanelle), and only a weak tuber smoothly confluent with the dorsal surface of the ilium is developed in *Notobatrachus* (Báez and Basso, 1996). This may correspond to

a fact that the tuber is formed only during the latest period of iliac development, in correspondence with the ultimate arrangement of thigh muscles. Its size, position and morphology in adult anurans may vary significantly between species (e.g., in the Bufonidae; Sanchíz, 1998) and it is not clear whether this is due to different roles which thigh muscles (especially m. gluteus maximus, m. iliofibularis, and m. iliofemoralis, all of them inserting to the tuber superius) play in different modes of locomotion, or due to some other reasons.

- (2) Epicondylus lateralis humeri absent. This character is tentatively attributed to the Gobiidae on the basis of associated disarticulated humeri from Central Asian localities, and is shared with the Discoglossidae (Roček and Nessov, 1993). The epicondylus lateralis is a site of origin of the caput inferius of the m. flexor antibrachii lateralis superficialis, caput inferius of the m. extensor carpi radialis, caput superius of the m. abductor indicis longus, m. extensor digitorum communis longus, m. extensor carpi ulnaris, m. epicondylus cubitalis, and m. flexor antibrachii lateralis profundus. At least two of these muscles play a role in male amplexus (m. extensor carpi radialis, m. abductor indicis longus) so its absence may be related to behaviour (data from Gaupp, 1896).

5. Comments on phylogenetic relationships

The previous diagnosis of the Gobiidae (based on data on *Gobiaties*) provides a basal position of these anurans in a recent phylogenetic analysis (Wang, 2004). It branches close to Early Jurassic *Prosalirus* and *Vieraella*, and Middle-Late Jurassic *Notobatrachus*. The presence of amphicoelous (=ectochordal) vertebrae are especially important in this respect because they occur in proanurans (*Triadobatrachus*) and early (Jurassic) anurans and, among extant taxa, only in the *Leiopelmatidae*. In the latter taxon this may be attributed to arrested skeletal development. In all anurans, the early stage of the vertebral centrum is represented by a chondrified ring enclosing the notochord. The ring may later ossify still enclosing the notochord, which is the case with the *Leiopelmatidae*. In some other anurans, the notochord enclosed in the chondrified ring ossifies, together with the ring, so the solid, cylindrical centrum (generally termed “holochordal”) is formed. The ectochordal centrum was one of the reasons why *Vieraella* and *Notobatrachus* were placed by some authors (e.g., Estes and Reig, 1973; Duellman and Trueb, 1986) in the *Leiopelmatidae* (their *Ascaphidae*). Therefore, Late Cretaceous *Gobiaties* and *Cretasalia*, which were well ossified (as evidenced by their sculpture, extensive squamoso-maxillary suture, and presence of the quadratojugal), can be considered one of the last primitive representatives of the *leiopelmatid* clade, whereas *Leiopelma* and *Ascaphus* possess amphicoelous centra resulting from arrested skeletal development (absence of sculpture, squamosum widely separated from the maxilla, incomplete maxillary arch). Discoglossoids and pipoids (except for *Rhadionosteus* Henrici, 1998), as the only other Mesozoic anurans

contemporary with the Gobiatidae, may be excluded due to their opisthocelous (=stegochordal) vertebrae.

Free ribs are of lesser importance because this feature is shared with adults of all Mesozoic and of some more recent anuran taxa (Discoglossidae, Pipidae, Palaeobatrachidae), as well as with younger developmental stages of majority of others.

Apparently more important is the shape of the vomer, which in *Gobiaties* lacks the postchoanal process (Roček, 1981). The presence of the postchoanal process seems to be correlated with variation in the association of the palatine with other cranial elements. In *Gobiaties*, the palatine is clearly associated with the maxilla (disregarding the degree of its fusion to the latter) and, consequently, the postchoanal process of the vomer is absent. In *Vieraella*, *Notobatrachus*, and in all discoglossoids, the postchoanal process is present, whereas a discrete palatine is absent; hence, it can be considered a palatine fused to the vomer (i.e., vomeropalatine). In this respect, *Gobiaties* differs from all other stratigraphically relevant anurans.

Another important feature may be the reduced number of presacral vertebrae (eight) which can be considered a derived character for Mesozoic anurans. All Mesozoic discoglossoids instead retain nine presacrals.

Based on these characters it seems reasonably evident that *Gobiaties* and *Cretasalia* may be placed in their own taxon separate both from the Jurassic *Prosalirus*, *Vieraella* and *Notobatrachus*, as well as from Cretaceous discoglossoid and pipoid anurans. The combination of the following characters is important in considering their phylogenetic relationships: amphicoelous (=ectochordal) vertebral centra, palatines fused to the maxillae (correlated with absence of the postchoanal process of the vomer), absence of the pterygoid process of the maxilla, and eight presacral vertebrae. Neither of them is unique to these two genera but the combination of them is characteristic of the Gobiatidae alone.

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