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Mesozoic Anurans

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I. INTRODUCTION

THE evolutionary process that culminated in the appearance of anurans began as early as the late Paleozoic. The earliest known fossil record of true anurans is from the Early Jurassic (Table 1). The only fossils that may be taken as intermediate stages in this process are *Triadobatrachus* and *Czatkobatrachus*. If these unique fossils had not been found, one could speak about the "sudden" appearance of anurans. However, it is obvious that the early evolution of the anuran skeleton was not rapid. It certainly required tens of millions of years before the *Triadobatrachus* stage was attained and there were about 40 million years between *Triadobatrachus* and the earliest known true anuran.

Constitution of the Anura was a relatively slow process, but once their basic structural scheme was attained in the Early Jurassic (or perhaps earlier) their morphological evolution practically stopped. Due to this, one of the earliest known anurans, *Vieraella*, was tentatively associated (Estes and Reig 1973) with contemporary representatives (Leiopelmatidae). For nearly 200 million years the basic structural scheme of frogs has been maintained without any significant change, which suggests that an equilibrium between function and structure and the mode of life was attained. This long-term optimum cannot be considered an extreme ecological specialization because it made possible their survival without apparent reduction through the mass extinction at the end of the Mesozoic. Although constrained structurally, anuran evolution has been manifested in a wide range of modes of breeding, e.g., *Rheobatrachus*, the gastric-brooding frog (Tyler 1983).

II. EARLY JURASSIC FROGS

The earliest known fossil anuran is *Prosalirus bitis* (Shubin and Jenkins 1995; Jenkins and Shubin 1998) from the Lower Jurassic (Pliensbachian), Kayenta Formation in Arizona (Fig. 1). The material includes several partly articulated and three dimensionally preserved skeletons. These frogs are associated with the earliest caecilians, which still retain limbs (see Chapter 17). Information regarding the institutions in which these and other anuran specimens are housed can be found in Sanchíz (1998).
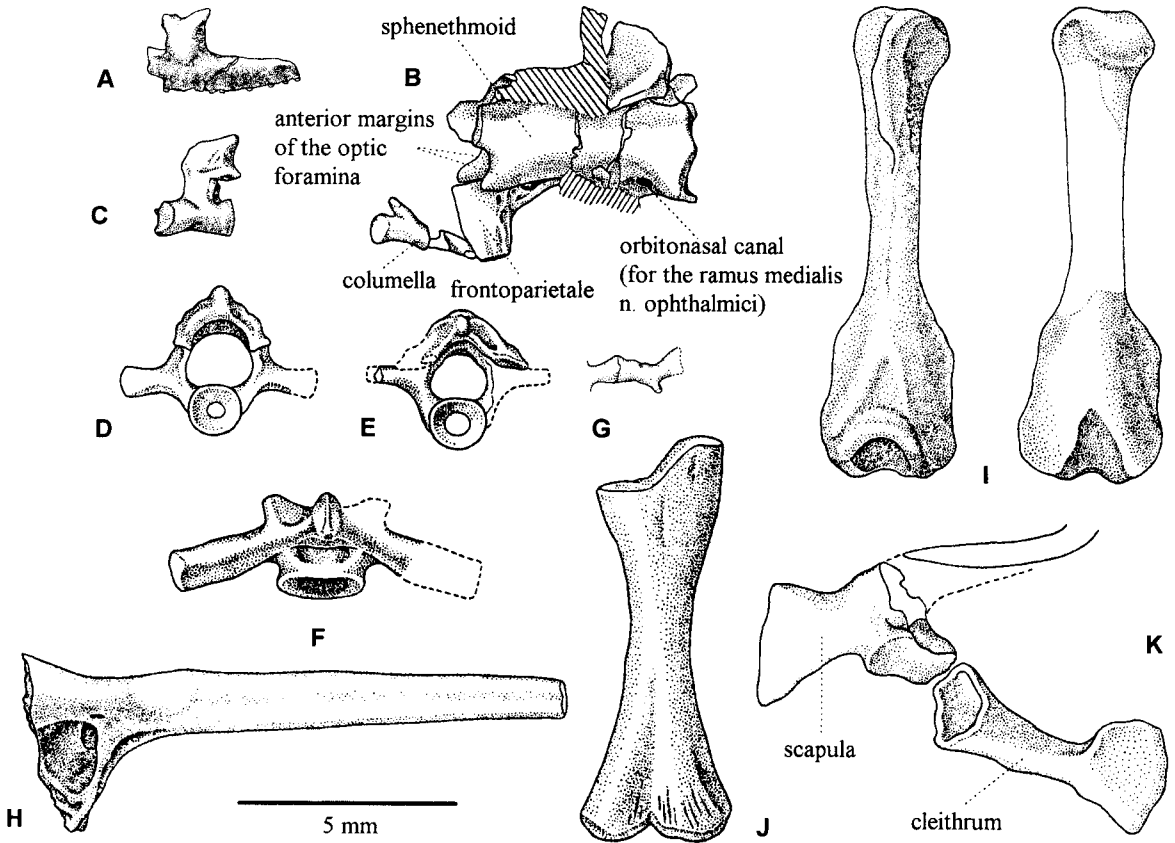
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Table 1. Stratigraphic occurrence of Mesozoic anurans. Lines are portrayed more narrowly when they represent vague stratigraphic data.

AFRICA
- "Zaire anurans"
- *Pachybatrachus taqueti*
- "In Beceten pipid I", Niger
- "Wadi Milk anurans", Sudan
- "Malawi anurans"
- "Cameroon anurans"

ASIA
- "Naskal ?hylid", India
- "Naskal discoglossid", India
- "Pisdura anuran", India
- "Gitti Khadan ?pelobatid", India
- *Gobiates kermeentsavi*
- *Gobiates leptocolaptus*
- *Estesina elegans*
- *Procerobatrachus paulus*
- *Soevesoederberghia egredia*
- *Aralobatrachus robustus*
- *Ki?ylkuma antiqua*
- *Gobiatoides parvus*
- *Gobiates sosedkoi*
- *Gobiates furcatus*
- *Gobiates ki?ylkumensis*
- *Gobiates asiaticus*
- *Gobiates spinari*
- *Gobiates itaravowi*
- *Gobiates fritschi*
- *Gobiates d?ijyrakudukensis*
- *Gobiates bogatchovi*
- *Itemirella cretacea*
- *Cordicephalus longicostatus*
- *Cordicephalus gracilis*
- *Thoraciliacus rostriceps*
- *Shomronella jordanica*

EUROPE
- "Nioi Veli anurans", Spain
- "Fontllonga anurans", Spain
- "Carlet anurans", Spain
- "Laño palaeobatrachid", Spain
- "Laño discoglossid", Spain
- "Villeveyrac palaeobatrachid", France
- "Las Hoyas anurans"
- *Eodiscoglossus* sp. (Galve, Teruel)
- *Wealdenbatrachus jucarense*
- *Montsechobatrachus gaudryi*
- *Neusibatrachus wilferti*
- *Eodiscoglossus santonjae*
- "Purbeck anurans"
- "Guimarota anurans"
- *Eodiscoglossus oxoniensis*

SOUTH AMERICA
- "Pajcha Pata unident. anuran", Bolivia
- cf. *Xenopus* sp.
- "Los Alamitos leptodactylids", Patagonia
- "Los Alamitos pipids", Patagonia
- *Baurubatrachus pricei*
- *Saltenia ibanezi*
- "Rio Limay ?pipid", Patagonia
- "Chapada do Araripe anuran", NE Brazil
- *Notobatrachus degiustoi*
- *Vieraella herbsti*

NORTH AMERICA
- *Theatonius lancensis*
- *Eopelobates* sp.
- *Palaeobatrachus occidentalis*
- *Paradiscoglossus americanus*
- *Scaphiopus pustulosa*
- "Montana ?pelobatid"
- "Montana discoglossid III"
- "Montana discoglossid II"
- "Montana discoglossid I"
- "Utah anurans"
- "Comanchean unident. anuran", Texas
- "Comanchean ?pelobatid", Texas
- "Comanchean discoglossid", Texas
- *Rhadinosteus parvus*
- *Comobatrachus aenigmatis*
- *Eobatrachus agilis*
- "Quarry Nine ?pelobatid"
- *Enneabatrachus hechti*
- *Prosalirus bitis*

Time scale (columns, left to right):

CRETACEOUS — Senonian: Maastrichtian, Campanian, Santonian, Coniacian; Turonian, Cenomanian, Albian, Aptian, Barremian; Neocomian: Hauterivian, Valanginian, Berriasian.

JURASSIC — Late: Portlandian, Kimmeridgian, Oxfordian; Middle: Callovian, Bathonian, Bajocian; Early: Aalenian, Toarcian, Pliensbachian, Sinemurian, Hettangian.

Fig. 1. *Prosalirus bitis* Shubin and Jenkins 1995, the earliest known anuran. Early Jurassic (Pliensbachian), Arizona, U.S.A.; Anura *incertae sedis*. **A.** Left premaxilla, outer view. **B.** Frontoparietal, sphenethmoid, and stapes of specimen V 8725, preserved in the Museum of Northern Arizona. Cross-hatched lines indicate comminuted bone. **C.** Atlas in left lateral view. **D, E.** Anterior and posterior presacral vertebrae in posterior view. **F.** Sacral vertebra in dorsal view. **G.** Shape of rib. **H.** Right ilium in lateral view. **I.** Left humerus in anterior (left) and posterior (right) views. **J.** Left radioulna in anterolateral view. **K.** Reconstruction of the right shoulder girdle in lateral view. From Jenkins and Shubin (1998).

A composite reconstruction of *Prosalirus bitis* indicates a medium-sized frog, with a snout-vent length (SVL) of about 50 mm. The premaxilla is about 27% of the length of the associated maxilla and bears 21 tooth positions. The maxilla bears approximately 40 tooth positions, and attenuates posteriorly where it is thin and edentulous. Since there is no articular facet for the quadratojugal, Jenkins and Shubin (1998) believed the quadratojugal to be absent. The teeth are pedicellate. The parasphenoid consists of a lanceolate cultriform process and well developed posterolateral alae. The frontoparietal is smooth on its dorsal surface (as is the case for other known dermal cranial components), and bears a posterolateral flange that would have overlapped the otic capsule. A ventral deflection of the orbital margin forms a narrow, vertical flange. The sphenethmoid is large and extends posteriorly to include the anterior margin of the optic foramen; it extends anteriorly as an ossified septum nasi.

The prearticular is moderately sinusoidal in shape. The columella is broad and oval in outline proximally, whereas its distal end tapers slightly; near the footplate the shaft continues as a proximally directed process that is characteristic of Palaeozoic temnospondyls.

The atlas lacks transverse processes and bears neural arches, the pedicles of which are narrow anteroposteriorly. The anterior end of the centrum is broadly expanded with two elliptical cotyles, slightly separated by a small notochordal fossa. Dorsal to the fossa is

a small, nubbin-like process representing an anterior extension of the floor of the neural canal. The funnel-shaped notochordal fossa at the posterior end of the atlantal centrum is deeper and wider than that at the anterior end; the fossae do not communicate to form a continuous notochordal canal. The succeeding presacral vertebrae retain a broad notochordal canal; however, their number cannot be determined. The articular facets of the prezygopophyses and postzygapophyses are oriented nearly horizontally. On most vertebrae the neural spines are represented only as low crests but the neural arches extend posteriorly, especially in the midline, and thus were probably imbricate. The thickened posterior margin of each arch bears a pair of fossae; the fossae are separated at the midline by a short, posteriorly directed process. Anterior presacrals have a wide neural canal but a relatively constricted notochordal canal; their neural arches (bearing a rugosity on their dorsal surface adjacent to the posterior margin) are short anteroposteriorly. Vertebrae from the middle section of the vertebral column retain a comparatively wide neural canal and constricted notochordal canal; however, their transverse processes have a bulbous expansion at their distal end where they articulated with free ribs. The posterior vertebrae have a narrow neural canal, relatively wide notochordal canal, but slender transverse processes.

The sacral vertebra has a relatively short centrum with a posterior notochordal fossa. The bases of the neural arches form the roof of the neural canal only over the anterior part of the centrum. The prezygapophyses are robust, as is the neural spine, but postzygapophyses are lacking. The transverse processes (triangular in cross-section, with flat ventral surface and slightly convex anterodorsal and posterodorsal surfaces) are directed posterolaterally. The sacral-urostyle articulation was cartilaginous, with no evidence of a condylar structure. The urostyle is short and conical.

Four (possibly five) pairs of ribs are preserved, one of which was ankylosed; the others are joined by mobile joints. The ribs are shortened and unicapitate; they extend proximally to form a broad contact with the transverse processes but are flattened distally. Two ribs articulating with the vertebrae bear anteriorly projecting uncinate processes. One rib possesses both anterior and posterior uncinate processes.

The clavicle is bowed laterally but is straight medially; it bears a longitudinal sulcus that indicates an extensive articulation with the anterior border of the scapula. The scapula was completed by a suprascapular cartilage; its glenoid facet is shallowly concave, facing posteriorly and slightly ventrally. The coracoid bears an elongate articular facet corresponding to the glenoid facet of the scapula. The medial end of the coracoid is expanded as a blade-like process, whereas the middle part of the bone is constricted. The humerus bears a large deltopectoral crest on its ventral surface. The caput humeri was not ossified; instead, a deep, circular fossa with slightly elevated margins is preserved. The radioulna exhibits a shallow longitudinal sulcus along the whole of its length, delineating the zone of radial and ulnar fusion.

The ilia are straight and articulated ventral to the sacral diapophysis; the shaft appears to bear a narrow crest on its dorsal margin, in contrast to the more rounded ventral margin. The tuber superius is represented by a slightly raised, rugose area anterodorsal to the acetabulum. The femur exhibits a sigmoid curvature; the tibiofibula is fused as in modern anurans. The proximal tarsus is elongate, with the tibiale and fibulare unfused.

Comparison with various fossil and extant anurans revealed no clear relationships and this is why the new family Prosaliridae was established to accommodate this earliest fossil anuran. However, because information provided by the material is not sufficient for formal establishment of a new family, Sanchíz (1998) preferred to place *Prosalirus* among Anura *incertae sedis*.

Judging by the proportions of the hind limbs, structure of the pelvic girdle (mobile sacro-urostylic and sacro-ilial joints), and fused radioulna and tibiofibula, *Prosalirus* apparently was capable of jumping. The only primitive features preserved in its skeletal anatomy seem to be the nature of the coracoid-scapular articulation, straight iliac shaft,

wide notochordal canal, extensive sphenethmoid, and free ribs. However, some of these characters are also retained in contemporary anurans.

Another early Jurassic anuran is *Vieraella herbsti* (Figs 2, 3). It is based on a single specimen, part of which was discovered by R. Herbst and J. C. Viera and described by Reig (1961). The counterpart of this specimen was discovered much later by R. Casamiquela, S. Archangelsky and R. Herbst, and was described in detail by Casamiquela (1965). It was recovered from the plant-bearing Roca Blanca Formation in the Santa Cruz Province in southern Patagonia, Argentina. The age of the deposit was established by Herbst (1961) as Liassic; it is now considered late Liassic to early Dogger (Toarcian-Aalenian) according to Stipanicic and Bonetti (1970). The holotype and the counterpart are preserved as imprints in matrix and remains of the animal are badly crushed. Descriptions were published by Reig (1961), Hecht (1963), Casamiquela (1965), Estes and Reig (1973), and Báez and Basso (1996).

Vieraella was a small frog; its snout-vent length is about 30 mm. The skull seems to be wider than long. The frontoparietals are paired, with posterolateral processes and a smooth dorsal surface; anteriorly they are separated by a fontanelle. Nasals (identified as "prevomers" by Casamiquela 1965) are extensive, contacting each other in a long median suture. The maxillae bear about 18 teeth (however, this obviously does not indicate the total number of tooth positions, which would be at least twice as high). Quadratojugals were recognized by Estes and Reig (1973) but doubted by Báez and Basso (1996). Only fragments of the squamosals were preserved. The vomers are paired and sickle-shaped, with a medial (perhaps tooth-bearing) extension. Báez and Basso mentioned a long posterolateral process, which they tentatively interpreted as the palatine coalesced to the vomer. The pterygoids are triradiate; the parasphenoid has extensive lateral alae. The sphenethmoid is crushed but apparently without lateral exposure.

The prearticular bears a coronoid process. There may be a well-developed mentomeckelian bone attached to the dentary. The otic capsules are relatively blunt and of limited lateral extent; a distinct fissure separates the prootic and exoccipital, indicating that these bones were in synchondrotic connection. The posteromedial processes of the hyoid are ossified and rather large. The vertebral column most probably consists of ten presacrals with supposedly amphicoelous centra; the eleventh vertebra is the sacral. Vertebrae three and four, and probably also two, bore free ribs provided with posterolateral spines (= uncinate processes). The atlas lacks transverse processes; those on vertebrae five through nine are relatively long, and do not decrease in size posteriorly. Some have distal expansions, perhaps indicating the presence of fused ribs. The neural arches are not imbricated anteriorly, the sacral diapophyses are only moderately dilated, and the urostyle has lateral diapophyses.

The pectoral girdle is probably arciferal. The clavicles apparently are curved, the scapula probably is as long or longer than the clavicle, the suprascapula is cartilaginous, the cleithrum is not forked, and the coracoid is short with a slightly dilated medial end. The humerus possesses epicondyles that are scarcely distinguishable from the caput humeri; the latter is unossified. The radius and ulna are fused, with the olecranon process well developed. At least seven carpals are ossified: centrale 2-3 are apparently fused; a prepollex is present. The manus is tetradactyl, the phalangeal formula 2?-2-3-3. The pelvic girdle is not preserved. The tibia and fibula are fused.

This individual represents the second earliest known anuran. It seems not to be fully mature, as evidenced by the lack of ossified epiphyses and the unossified sphenethmoidal portion of the postnasal wall. From this point of view, the inter-frontoparietal fontanelle and perhaps also the free ribs may be considered juvenile features. Estes and Reig (1973) discussed the phylogenetic position of *Vieraella* and concluded that it can be considered a structural ancestor for both Leiopelmatidae and Discoglossidae. Because of many characters shared with *Leiopelma*, they referred it to the former family. Sanchíz (1998) placed it among the Anura *incertae sedis*.
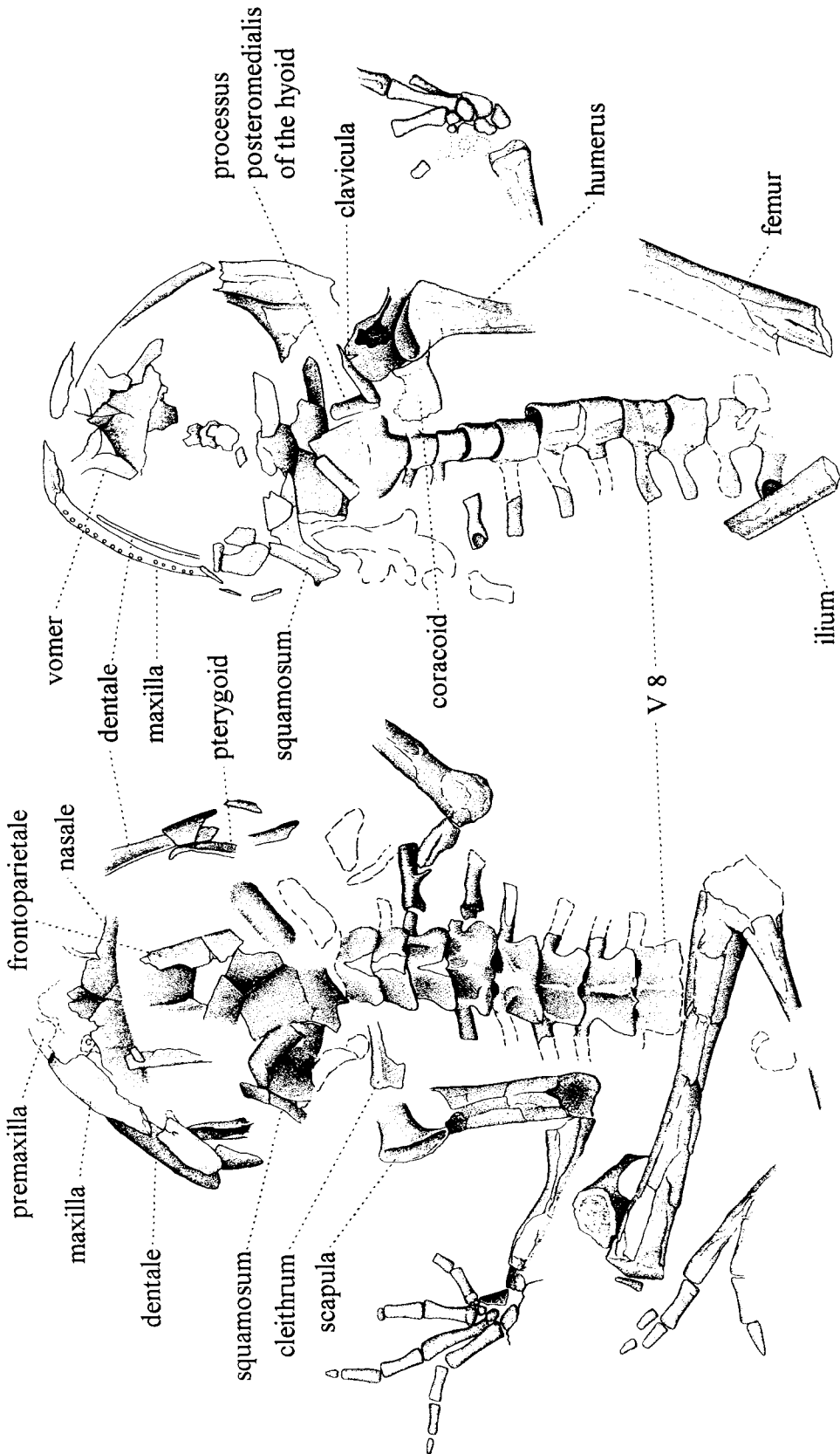
processus
posteromedialis
of the hyoid

clavicula

humerus

femur

vomer

dentale

maxilla

pterygoid

squamosum

coracoid

V 8

ilium

frontoparietale

nasale

premaxilla

maxilla

dentale

squamosum

cleithrum

scapula

5 mm

Fig. 2. Vieraella herbsti Reig 1961. Early Jurassic, Argentina; Anura *incertae sedis*. Holotype in dorsal (left) and ventral (right) views. From Báez and Basso (1996).
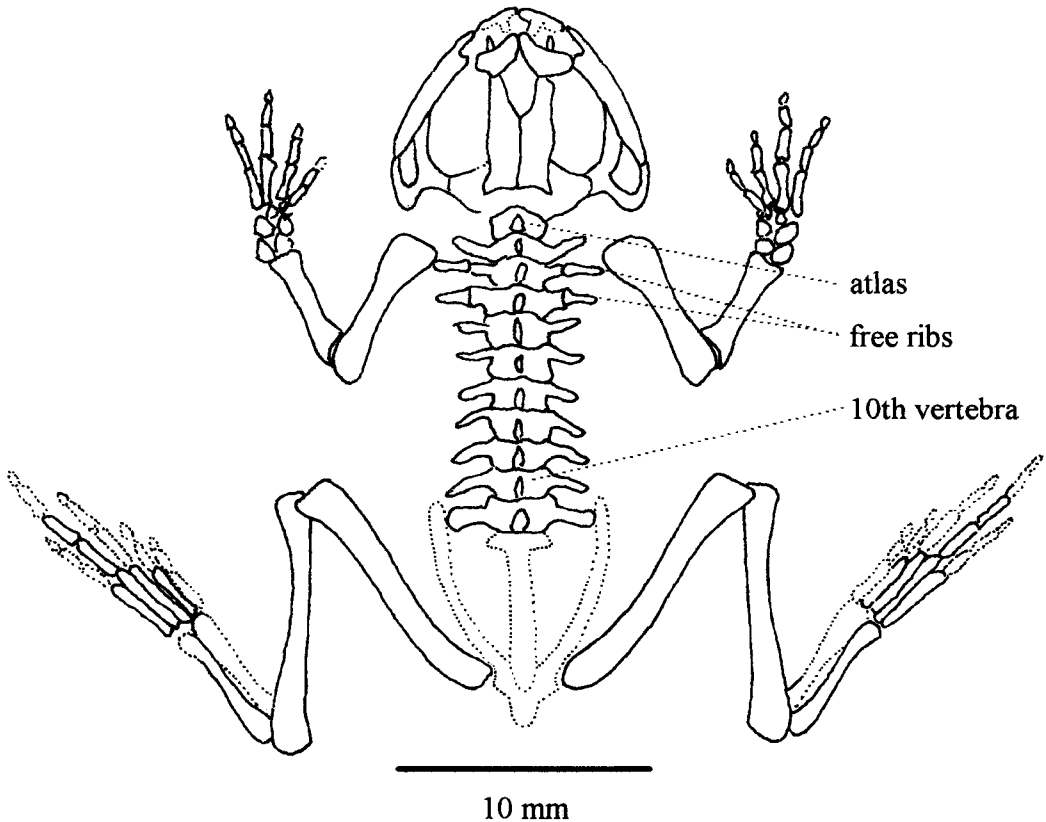
atlas

free ribs

10th vertebra

10 mm

Fig. 3. Vieraella herbsti Reig 1961. Early Jurassic, Argentina; Anura *incertae sedis*. Restoration of skeleton in dorsal view. From Estes and Reig (1973), modified after data in Báez and Basso (1996).

Some doubtful remains of frogs from the Lower Jurassic Kota Formation in India were reported by Yadagiri (1986) as well as an indeterminate pelobatid, but according to Prasad and Rage (1995) the poorly preserved iliac shaft is not diagnostic at the family level and the dentary does not belong to the anurans.

III. MIDDLE JURASSIC FROGS

Undoubtedly of Middle Jurassic age is *Eodiscoglossus oxoniensis* (Evans, Milner and Musset 1990). It was a medium-sized frog reaching up to 80 mm in snout-vent length. The taxon is based on disarticulated premaxillae, maxillae, prearticulars, broken atlas centra, isolated neural arches, sacral vertebra, urostyle, scapulae, ilia, ischia, humeri, radioulnae and tibiofibulae. It was first reported by Freeman (1979) from the Kirtlington Mammal Bed of Upper Bathonian age, at Kirtlington in Oxfordshire, England (also see Evans and Milner 1991). Evans *et al.* (1990) referred it to *Eodiscoglossus* Villalta 1956 on the basis of the following features: processus pterygoideus maxillae poorly developed, elongate flattened atlantal cotyles, trunk and sacral centra amphicoelous with notochordal canal (Evans 1992; Estes and Sanchíz 1982a), and neural arches lacking upturned flared posterior margins. The principal diagnostic characters distinguishing *E. oxoniensis* from *E. santonjae* (see below) appear in the iliac shaft and premaxilla. Recently, additional material of *Eodiscoglossus* was discovered in two other localities of Bathonian age in Dorset — Watton Cliff and Swyre (Evans 1992; Evans and Milner 1994).

Eodiscoglossus is undoubtedly a member of the Discoglossidae, closely resembling *Discoglossus* in that the ilium has a dorsal crest and a tuber superius; there are 15–18 premaxillary and about 50 maxillary teeth, the coronoid process is smooth and convex with no notches, the vertebral centra opisthocoelous, the anterior vertebrae bear free ribs,

the urostyle has small anterior transverse processes, and the iliac synchondrosis is absent (Evans *et al.* 1990). In summary, *Eodiscoglossus oxoniensis* represents the earliest known discoglossid and displays close morphological resemblance with some Recent representatives. It thus provides evidence of the conservative nature of this group.

IV. UPPER JURASSIC FROGS

Among Late Jurassic (Kimmeridgian) anurans belongs *Eobatrachus agilis* Marsh 1887 and *Comobatrachus aenigmatis* Hecht and Estes 1960, both from the Morrison Formation (latest Oxfordian to middle Tithonian) (Turner 1993) of Como Bluff, Wyoming, U.S.A. The material was originally described by Marsh and later revised by Moodie (1912, 1914), Hecht and Estes (1960), and Estes and Reig (1973). Both taxa were represented by humeri and a few other skeletal elements. The humerus of *Eobatrachus* resembles most closely that of pipids, especially in the shape of the fossa cubitalis ventralis (Hecht and Estes 1960; Hecht 1963; Nevo 1968; Estes and Reig 1973) but it cannot be referred to the Pipidae. *Comobatrachus* was distinguished from *Eobatrachus* by Hecht and Estes (1960). Estes and Sanchíz (1982b) noted that the *Comobatrachus* humerus resembled those of discoglossids. This is consistent with the conclusion of Reig (1957) who suggested that the atlas and urostyle (illustrated but not discussed by Moodie [1914] from the material originally assigned to *Eobatrachus*) might belong to a representative of the Discoglossidae. However, Evans and Milner (1993) recently suggested that the differences between the type specimens of *Eobatrachus* and *Comobatrachus* (both are humeri) may be ontogenetic; neither of these humeri can be placed securely in any recognized family and are thus indeterminate. Sanchíz (1998) designated both of them as *nomina vana*.

In addition to these taxa, Evans and Milner (1993) described two ilia from the upper part of the Morrison Formation (Quarry Nine, Como Bluff, Wyoming). One of them represents a discoglossid described as *Enneabatrachus hechti*, with a narrow iliac shaft and the dorsal crest little developed, the tuber superius prominent, the pars ascendens and pars descendens distinct but moderately developed, and the acetabular rim expanded. This specimen definitely confirms the presence of discoglossids in the Morrison Formation. Henrici (1998a) has since recognized an incomplete skeleton of *Enneabatrachus hechti* in the material from the Morrison Formation in Utah. The second ilium from Quarry Nine, Como Bluff, Wyoming, was determined by Evans and Milner (1993) as Pelobatidae *incertae sedis*, presumably the earliest record of this family. However, according to Rage (pers. comm.), the elongate pars ascendens of this ilium points instead to the Discoglossidae, and the very small tuber superius also does not agree with assignment to the Pelobatidae.

Further frog material was collected from the Morrison Formation between 1968 and 1979 but has not yet been described (Prothero and Estes 1980; Prothero 1981). Other frogs, from the Brushy Basin Member (Tithonian) of the Morrison Formation of Dinosaur National Monument, both articulated and disarticulated, were preliminarily announced by Chure and Engelmann (1989) and Chure *et al.* (1989), and more completely described by Henrici (in press, 1998).

Of great interest is a primitive, non-burrowing rhinophrynid *Rhadinosteus parvus* Henrici 1998a (Fig. 4) which is based on several partial and loosely articulated skeletons deposited in the Dinosaur National Monument. All individuals are small, with an estimated snout-vent length of about 20 mm. The incompletely ossified vertebrae, urostyles, and epiphyses of some limb bones suggest that these individuals had recently undergone metamorphosis.

The frontoparietal is unpaired and smooth on its surface. The premaxilla and maxilla are provided with bicuspid, pedicellate teeth; the anterior end of the maxilla is deep. The mentomeckelian bones have not been identified. The parasphenoid lacks lateral alae. The vertebral column consists of eight presacrals and the sacral vertebra. Their ectochordal (i.e., hollow, cylindrical) centra are incompletely ossified in all but one example; the neural arches are slightly imbricated. The anterior vertebrae have long, cylindrical
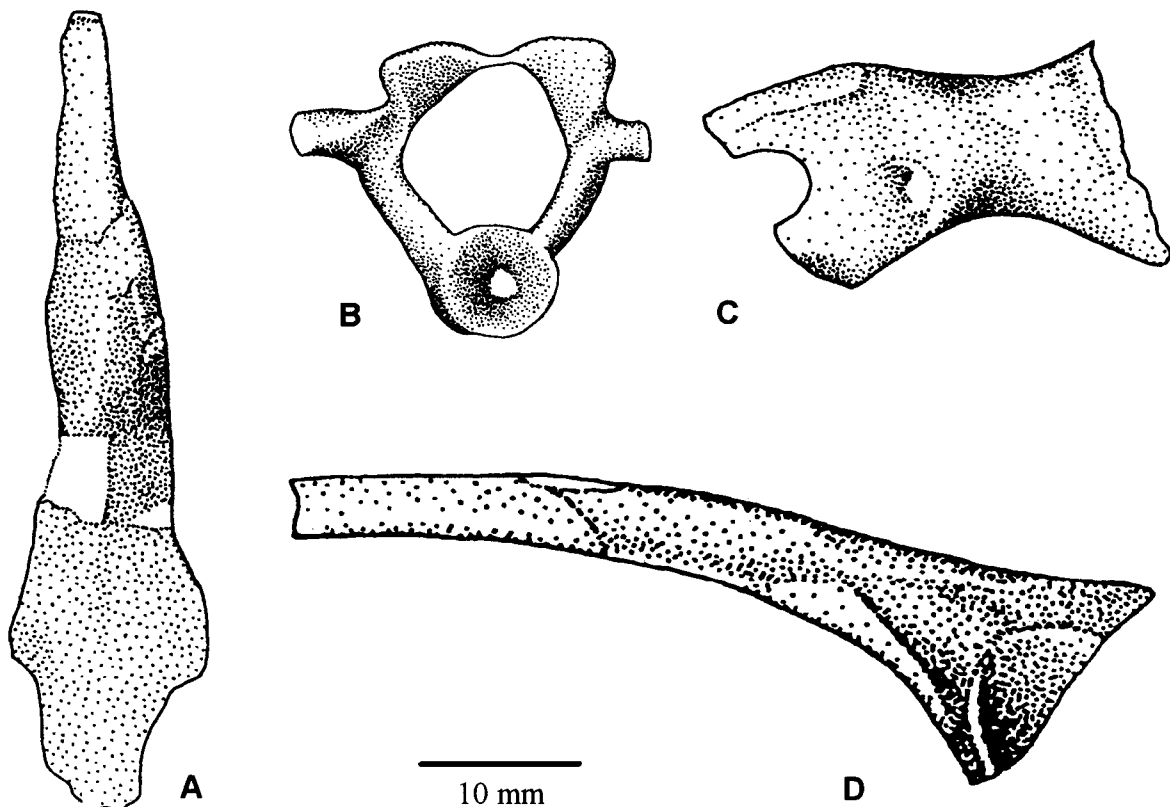
Fig. 4. Rhadinosteus parvus Henrici 1998a. Late Jurassic (Tithonian), Utah, U.S.A.; Rhinophrynidae. **A.** Parasphenoid. **B.** Fifth vertebra in posterior view. **C.** Right scapula in lateral view. **D.** Left ilium in lateral view. From Henrici (1998a).

transverse processes. There is some, although not definitive, evidence of free ribs. The sacro-urostylar connection is bicondylar; the length of the urostyle is equal to at least the length of five presacral vertebrae.

The cleithrum is forked at its medial end where it bears an elongate, anteroposteriorly oriented anterior process and a small, triangular posterior process. The scapula is relatively long and overlain anteriorly by the clavicle. The caput humeri is ovoid, with its long axis oriented mediolaterally. The medial epicondyle is slightly larger than the lateral one. The iliac shaft lacks a dorsal crest. The bones of the hind limb are slender, the femur is sigmoidal, and the tibiofibula exceeds the length of the femur. The tibiale and fibulare are not fused at their ends.

Assignment of *Rhadinosteus parvus* to the Pipoidea is based on the azygous (unpaired) frontoparietal and parasphenoid lacking lateral alae. It is the oldest pipoid currently known and is the only one that possesses bicuspid, pedicellate teeth. The presence of ectochordal vertebrae suggests affinities with the Rhinophrynidae.

Notobatrachus degiustoi Reig 1955 (Figs 5, 6) is based on well preserved impressions of both complete and incomplete skeletons from two fossiliferous layers in three different localities of the La Matilde Formation (Bahia Laura Group, Callovian-Oxfordian, Middle to Late Jurassic), northeastern Santa Cruz Province (near Puerto Desado), Patagonia, Argentina. *Notobatrachus* was preliminarily described by Stipanicic and Reig (1955), and later thoroughly described and/or discussed by Reig (1957), Hecht and Ruibal (1958), Casamiquela (1961, 1965), Eaton (1959), Hecht (1963), Griffiths (1963), Estes and Reig (1973), and Báez and Basso (1996). An extensive diagnosis may be found in Sanchíz (1998). *Notobatrachus* is of special importance because it is the earliest completely known anuran, represented by numerous specimens.
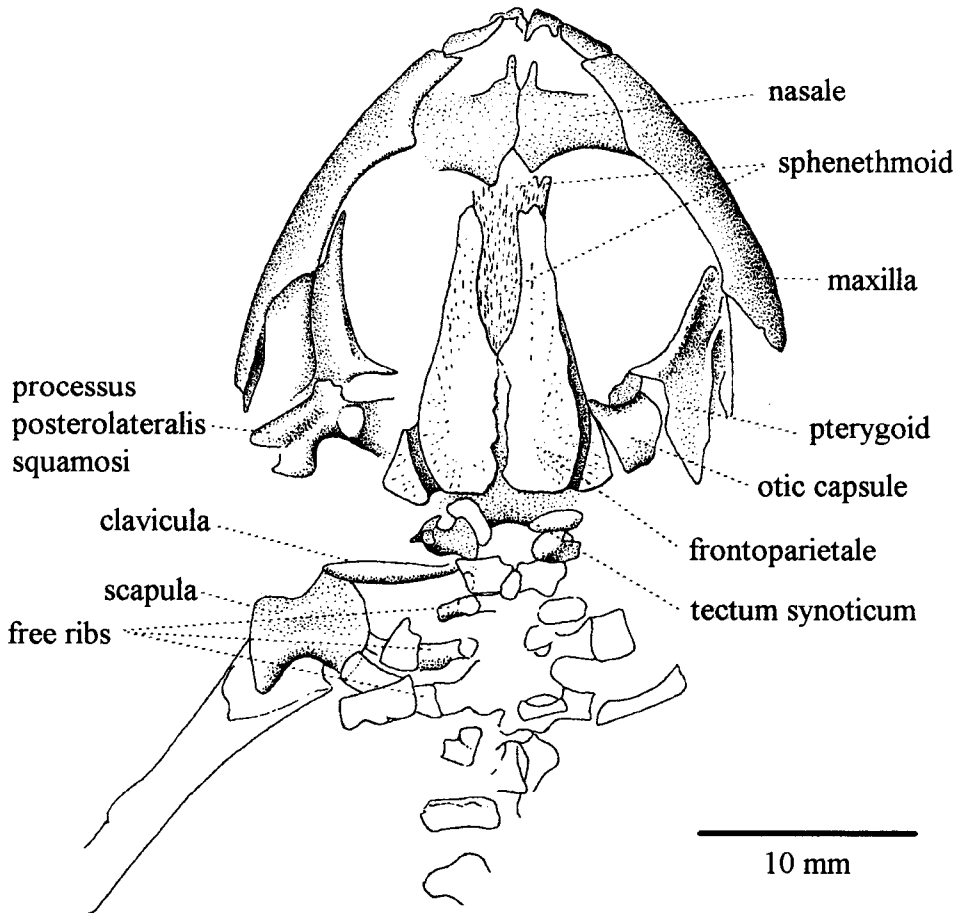
Fig. 5. Notobatrachus degiustoi Reig 1955. Skull and anterior part of the postcranial skeleton in dorsal view. Note the deep grooves for the a. occipitalis on the dorsal surface of the frontoparietals. Drawn after a latex cast provided by Richard Estes.

Notobatrachus reached a relatively large size (a specimen from the Instituto-Fundación Miguel Lillo in Tucuman No. PVL 2196 has a snout-vent length of 145 mm and a head length of 50 mm). The skull appears to be moderately wider than long. The nasals are broad, contacting one another in a long median suture; each has a slender anterior process meeting the premaxilla. Laterally they are in broad contact with the maxillae. In juvenile individuals, retaining incompletely ossified neural arches, the frontoparietals are paired and separated anteriorly by a fontanelle, through which a solid and anteroposteriorly striated dorsal roof of the sphenethmoid is exposed. The median suture reaches to the posterior margin of the bones. The dorsal surface of the frontoparietal is covered with very weakly expressed irregular, pitlike and ridgelike ornamentation. In fully grown individuals, the fontanelle may be reduced to a slit-like opening. The arteria occipitalis ran in a groove on the dorsal surface of the bone (covered by ornamentation in some specimens, so that the artery is enclosed in a canal). This groove separates a small triangular posterolateral part of the frontoparietal and continues anteriorly along the medial portion of the orbital margin. The premaxillae have about 15 teeth; the maxillae, each with a long posterior process, bear about 50 teeth. The lamina horizontalis maxillae was not developed; instead, a narrow and dorsomedially directed shelf, together with the anterior ramus of the pterygoid, formed a groove for the pterygoid process of the palatoquadrate. Due to absence of the horizontal lamina, the processus pterygoideus maxillae was also missing. Consequently, the contact with the anterior ramus of the pterygoid must have taken place along the whole length of the subocular section of the
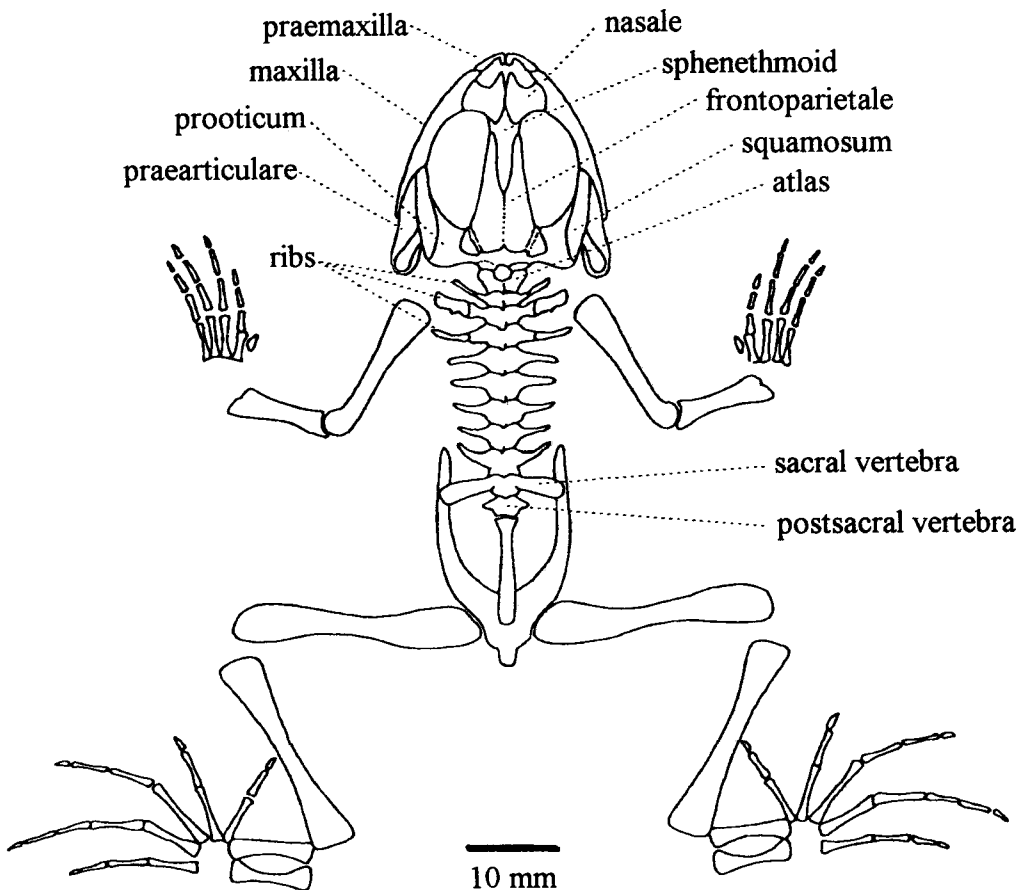
Fig. 6. Notobatrachus degiustoi Reig 1955. Late Jurassic, Patagonia, Argentina; Leiopelmatidae. Restoration of the skeleton of a medium-sized individual in dorsal view. Based on casts of the holotype and specimen P.V.L. 2196.

maxilla. A quadratojugal has not been found in any of the specimens. The squamosal has a comparatively narrow horizontal lamella alaris, which probably made contact with the maxilla (but see Estes and Reig 1973). The vomers are toothed, having 4–6 pedicellate teeth aligned in a row. The medial anterior part of the parasphenoid, formed by its processus cultriformis, extended between the vomers, whereas its lateral margins expanded in broad lobes. The posterolateral alae are broad and meet the ramus medialis pterygoidei anteriorly. They border the unossified part of the otic capsule posterolaterally.

The large sphenethmoid, which forms the anterior roof of the braincase, completely occupies the frontoparietal fontanelle. Estes and Reig (1973), followed by Báez and Basso (1996), speak about a paired sphenethmoid, but its seemingly paired structure may be a result of post-mortem breakage and subsequent shift of both fragments (as can be judged by comparable movement of other cranial elements). Báez and Basso stated that the orbitonasal foramen was not surrounded by bone, even in the largest individuals. The sphenethmoid was ossified as far posteriorly as the foramen for the optic nerve. Most of the otic capsule was exposed. The columella auris (plectrum) is preserved in many specimens; its expanded pars interna plectri ("footplate") continues laterally as a slender curved rod (pars media plectri). The fenestra ovalis is surrounded by an unossified part of the capsule; the extent of this cartilaginous area is dependent on the degree of ontogenetic development. The prootic and exoccipital were connected synchondrotically. The exoccipitals were separated ventrally by cartilage but coalesced dorsally. The quadrate was ossified. Parahyoid bones (thyrohyals) were well developed.

The lower jaw consisted of the prearticular, dentary and mentomandibular. The prearticular is provided with a well developed coronoid process.

The vertebral column consists of nine amphicoelous presacrals with prominent spinal processes that may be thickened at their ends, and imbricate neural arches. A notochordal canal, although varying in width, was present. In most specimens, the atlas has neither ribs nor transverse processes, but short transverse processes were observed in one individual by Báez and Basso (1996). Free ribs are present on vertebrae two through five (sometimes also on the sixth), and a posterior rounded process occurs on the second pair of ribs. The sacral vertebra possesses only moderately dilated transverse processes. One postsacral vertebra with transverse processes, which in large individuals coalesces with the urostyle, remains well defined. The urostyle has a dorsal longitudinal crest, probably divided by a fissure.

The shoulder girdle is probably arciferal, with the clavicle slightly curved medially but nearly straight laterally. The coracoid has an extremely broad medial end. The scapula is short and has its acromial and glenoidal parts separated by a deep narrow cleft; it was completed by a large suprascapular cartilage, the anterior margin of which was invested by a large cleithrum. The humerus has a relatively small and weakly ossified caput, the fossa cubitalis is absent but the epicondyli are well developed and equally expanded. The ventral crista is prominent; its length is about 90 to 95% of the length of the tibiofibula. The radioulna is shorter than the humerus. The carpus has nine to eleven bones, with the ulnare, intermedium and radiale in the proximal row (the latter bone seems to be formed by two contiguous elements). Centralia one and two may be fused or not. The phalangeal formula is 2-2-3-3, with a prepollex consisting of two elements.

The iliac shaft is stout, with only a weak tuber smoothly confluent with the dorsal margin of the bone. The ischia have not coalesced even in the largest individuals. The pubes were probably cartilaginous. The femur is slightly sigmoidal and moderately longer than the tibiofibula. The tibiale and fibulare have not coalesced and the more distal portion of the tarsus is not ossified, even in the largest individuals. The phalangeal formula is 2-2-3-4-3.

Estes and Reig (1973) concluded that *Notobatrachus* was a primitive member of the Leiopelmatidae, a view that is now widely accepted (see also Sanchíz 1998).

Anurans were also reported (Seiffert 1973), but not yet described, from the Lower Kimmeridgian lignites of Guimarota, Portugal.

Fragmentary anurans were discovered in new localities in the Purbeck Limestone Formation (Upper Jurassic or, according to Rage, pers. comm., possibly Lower Cretaceous) of Dorset, England (Ensom 1988). This new material is assigned to the Discoglossidae (Ensom *et al.* 1991). There is also an unconfirmed record of a frog in the Purbeck Beds of Swindon, Wiltshire (Hudleston 1876).

According to Evans (pers. comm.; 1998), two localities in the Jurassic/Cretaceous Tetori Group in central Honshu, Japan, have revealed vertebrae and ilia of a primitive discoglossid grade.

V. LOWER CRETACEOUS FROGS

Frogs from the Lower Cretaceous (Upper Berriasian or Lower Valanginian) (Sanchíz 1998) were recovered from the lithographic limestones of Sierra del Monsech, north of Lerida, Spain. The best represented is *Eodiscoglossus santonjae* Villalta 1956 (Fig. 7); the type specimen was collected by L. Ferrer-Condal in the middle 1940s in the Santa María de Meya Formation near the village of Rubies, and first figured by Piveteau (1955). Later, additional material, consisting of both articulated and isolated bones, was recovered from the type locality and from Galve (Province of Teruel, Spain). It was re-described and discussed by Reig (1957), Hecht (1963, 1970), Estes and Reig (1973), Vergnaud-Grazzini and Wenz (1975), Estes and Sanchíz (1982a), and Wenz (1991). The holotype specimen consists of two parts, one deposited in the Paleontology Department of the Museo Nacional de Ciencias Naturales in Madrid, its counterpart in a private collection of L. Ferner in Lerida.
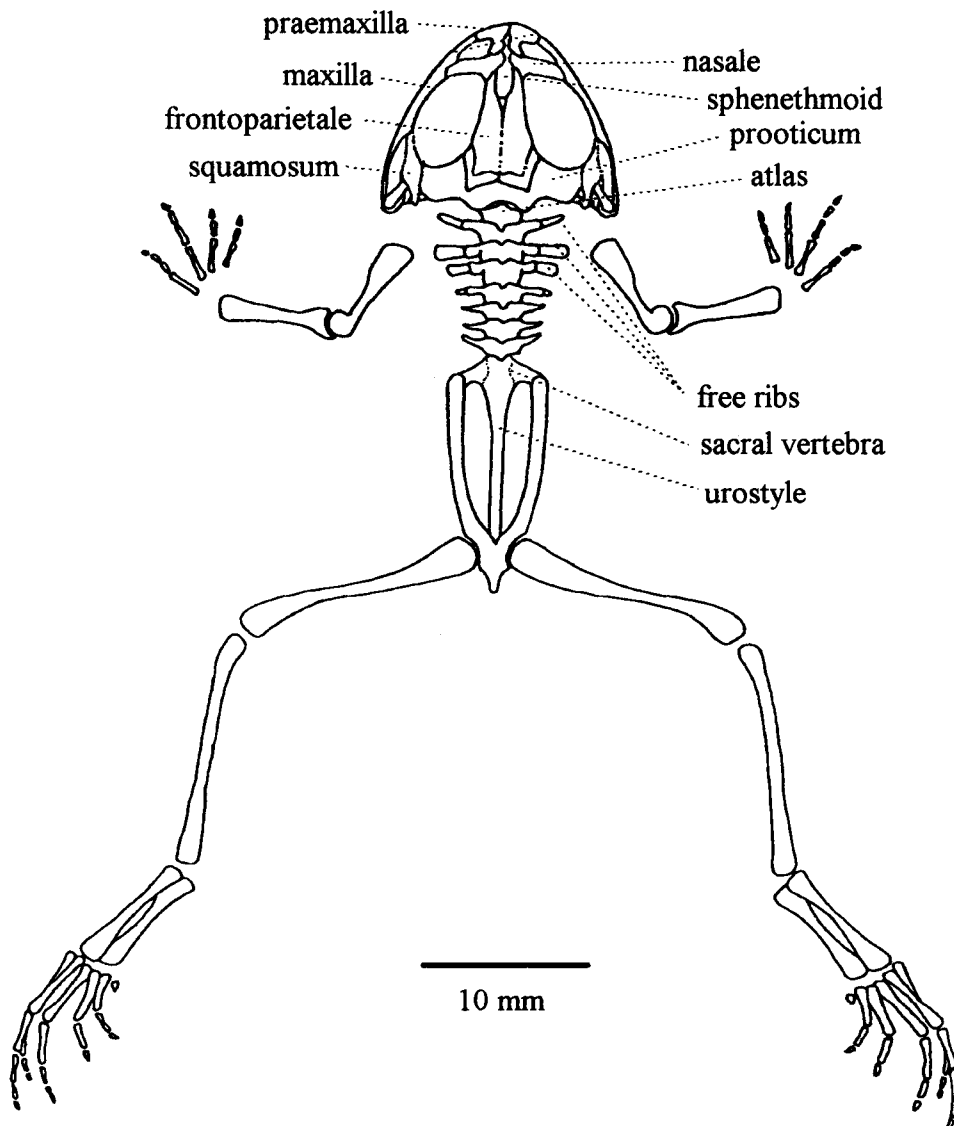
Fig. 7. Restoration of the skeleton of *Eodiscoglossus santonjae* Villalta 1957 in dorsal view. Late Jurassic/Early Cretaceous boundary, Spain; Discoglossidae. Based on the holotype. Compare the shape of sacral and other vertebrae with those in the restoration by Estes and Reig (1973).

Eodiscoglossus santonjae is small to medium-sized. The snout-vent length of the type specimen is nearly 28 mm, but another specimen from the same locality is nearly double this size. A further specimen has a snout-vent length of only 15 mm. The frontoparietals are smooth and paired, separated anteriorly by a large fontanelle that reached between the posterior part of the nasals (at least in small to medium-sized individuals). The premaxillae and maxillae bear teeth (in the former bone they number about 18). The vomers bear one row of 7–8 teeth. The parasphenoid has distinct but short posterior alae. A plectrum is present, as are ossified thyrohyals.

The vertebral column consists of eight presacral vertebrae, probably opisthocoelous with slightly imbricate neural arches. The sacral vertebra is biconvex with posterolaterally directed diapophyses only slightly dilated towards their distal ends. The impression of the left sacral diapophysis on the type specimen is hatchet-shaped resembling an expanded diapophysis but comparison with the counterpart (figure 7 in Hecht [1970]) shows that this is not the case. The urostyle has a pair of transverse processes. Vertebrae two through four bear free ribs.

The pectoral girdle is arciferal, consisting of arcuate clavicles dilated close to their medial end, a nearly straight coracoid, a short scapula with no cleft between the acromial and glenoidal parts, a suprascapula, and a large cleithrum. The humerus has a prominent ventral crista. At least four proximal and four distal carpals are present in some specimens. There are five digits (counting the prepollex), with a nuptial pad on the first, second and third (in the holotype). The phalangeal formula of the manus is 2-2-2-3-3.

The iliac shaft has a dorsal blade, the pubes are ossified, and the ischia have coalesced. The femur is about the same length (type specimen) or shorter (young individuals) than the tibiofibula, the tibiale and fibulare remain unfused, the prehallux consists of two elements, and the phalangeal formula of the pes is 2-2-3-4-3.

As was noted above, *Eodiscoglossus* is no doubt a discoglossid, with close morphological similarities to the genus *Discoglossus*.

A single specimen of a second frog from the same formation was recognized as a new species, *Neusibatrachus wilferti*, by Seiffert (1972) (Fig. 8) who considered it to be an ancestor of the Palaeobatrachidae and Ranidae. Estes and Reig (1973) considered it to be a definitive palaeobatrachid. Recently Sanchíz (in press), evaluating characters of this small anuran (snout-vent 21 mm) in the context of ontogenetic development among living *Discoglossus galganoi*, came to the conclusion that *Neusibatrachus wilferti* is a synonym of *Eodiscoglossus santonjae* (see also Sanchíz 1998). Estes and Reig (1973) also listed striking differences between *Neusibatrachus* and palaeobatrachids (e.g., *Neusibatrachus* had single sacral vertebra, a quadratojugal, free ribs, and a high number of maxillary teeth). On the other hand, Vergnaud-Grazzini and Wenz (1975) emphasized other characters of *Neusibatrachus*, including the undivided frontoparietal, parasphenoid lacking posterior transverse wings, and the presence of procoelous vertebrae that, if correctly interpreted, would contradict Sanchíz's opinion. Hence, relationships of *Neusibatrachus* remain uncertain.
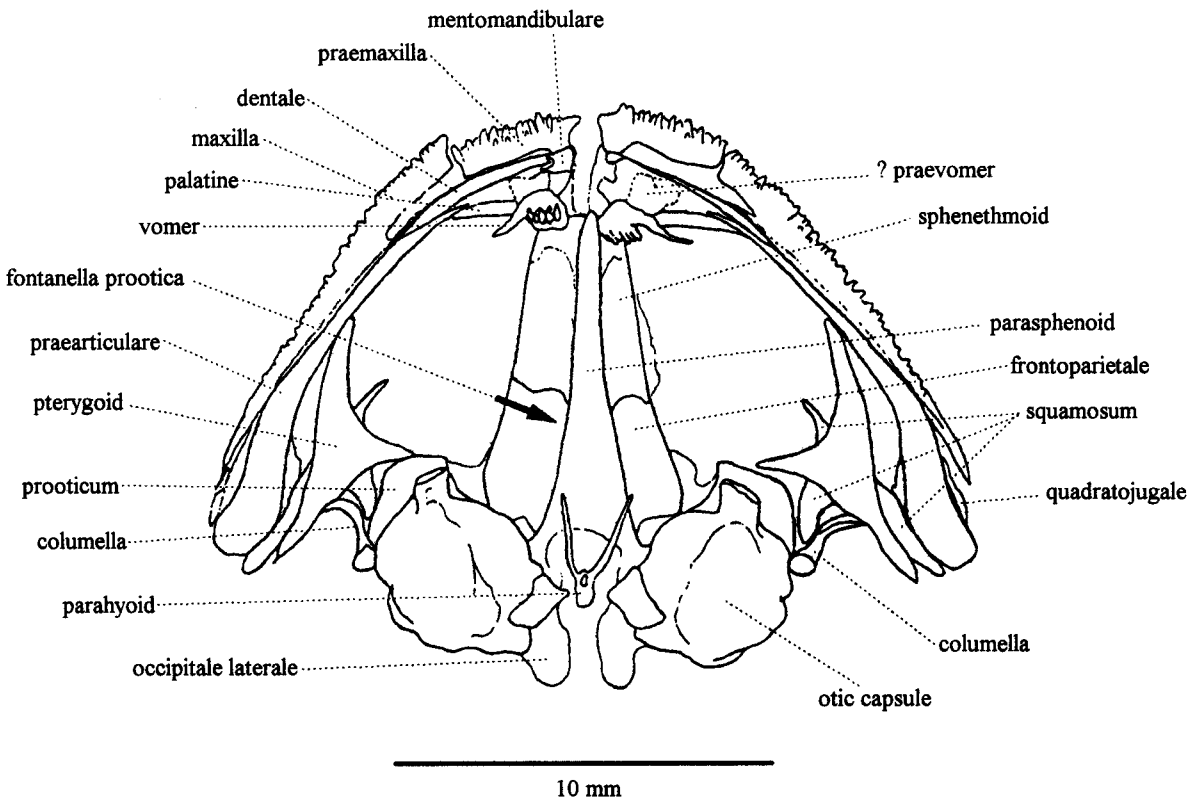

10 mm

Fig. 8. Neusibatrachus wilferti Seiffert 1972. Late Jurassic/Early Cretaceous boundary, Spain; phylogenetic relations uncertain. Skull of the holotype in ventral view. From Seiffert (1972).

Monsechobatrachus gaudryi is a third frog from the same formation as *Eodiscoglossus santonjae* and *Neusibatrachus wilferti*. Whereas the former two can be distinguished from one another, *Monsechobatrachus* is represented by only a very poorly preserved natural cast. Its poor state of preservation was the reason why Sanchíz (1998) placed this taxon within the *nomina vana* (see also Sanchíz and Roček 1996). It was found at La Pedrera and was originally described as *Palaeobatracus* (incorrectly written for *Palaeobatrachus*) by Vidal (1902). The name *Monsechobatrachus* was introduced by Fejérváry (1921) who recognized that this was not a palaeobatrachid. Only a few characters can be distinguished: snout-vent length slightly exceeding 25 mm, sacral diapophyses as in *Eodiscoglossus*, paired frontoparietals. These characters seem to contradict Estes and Reig's (1973) suggestion that *Monsechobatrachus* could be a palaeobatrachid. It is more probably a discoglossid (see also Vergnaud-Grazzini and Wenz 1975), if not even *Eodiscoglossus*. Another poorly preserved specimen from the same region was mentioned by Seiffert (1972, his figure 4–2).

From the Santa María de Meya Formation also comes a poorly preserved tadpole with a body length of over 20 mm (Sanchíz, pers. comm.). This is the earliest known fossil tadpole.

Borja Sanchíz and the late Richard Estes kindly allowed the study of the following specimens from the Early Cretaceous (Barremian) of Las Hoyas, Province of Cuenca, Spain that have not yet been formally described. These specimens consist of articulated skeletons, described in a preliminary manner as *Eodiscoglossus* sp. (Sanchíz 1998). They are very small, with a snout-vent length less than 20 mm. Their frontoparietal is paired (Fig. 9) (see also Roček 1988), they have a long, toothed maxilla, a quadratojugal, eight presacral vertebrae, discoglossid-like atlas, vertebrae two through six bear free ribs, the sacral vertebrae has narrow and posterolaterally inclined diapophyses, the urostyle probably had anterior transverse processes, and the tibiale and fibulare are not fused. These characters suggest that these tiny frogs belong to the Discoglossidae. However, their assignment to *Eodiscoglossus santonjae* does not seem to be justified in view of the different proportions of the tibiofibula and ilium in the specimen illustrated in Figure 8 and the restoration of *Eodiscoglossus santonjae* (Fig. 7) made after the holotype.

Disarticulated anuran bones closely resembling those of *Discoglossus* occur in the Lower Barremian (Mohr 1987) locality of Galve (Province Teruel, Spain) and were assigned to *Eodiscoglossus* by Estes and Sanchíz (1982a) and to *Eodiscoglossus santonjae* by Sanchíz (1998).

Possibly of early Barremian (Mohr 1987; Fey 1988) or Hauterivian age (Sanchíz 1998) is *Wealdenbatrachus jucarense* (Fig. 10), described by Fey (1988) from the Uña locality (Province of Cuenca, Spain). It is based on disarticulated skeletons collected in 1970 and deposited in the Paleontological Institute of the Free University of Berlin. This species is probably also present in Las Hoyas (Sanchíz 1998). This medium sized anuran (estimated snout-vent length up to 60 mm) can be diagnosed by the following characters: frontoparietals not fused, toothed maxilla, possibly amphicoelous vertebrae with imbricated neural arches, vertebrae two through four bearing free ribs, that of vertebra three (?) is forked, leiopelmatid-like scapula, ilium with dorsal crista and prominent tuber superius, tibiale and fibulare co-ossified. Fey (1986, 1988) assigned it (although with some doubt) to the Discoglossidae.

Lower Cretaceous deposits (Hauterivian?) of the Taysir Volcanics in the Shomron region of Israel yielded numerous tadpoles that were described by Estes *et al.* (1978) under the name *Shomronella jordanica* (Fig. 11). These tadpoles range between stages 57 and 61 of Nieuwkoop and Faber (1967), and are essentially complete. Many of the articulated specimens preserve the soft anatomy, including blood vessels and nerves. *Shomronella* was referred to the Pipidae on the basis of the large mouth, the presence of the angular in the lower jaw, the separation of inferior and superior perilymphatic foramina, and a narrow, lanceolate parasphenoid. These tadpoles differ from all other pipids in having a parasphenoid with a relatively large, diamond-shaped posterior end, and a cleithrum with
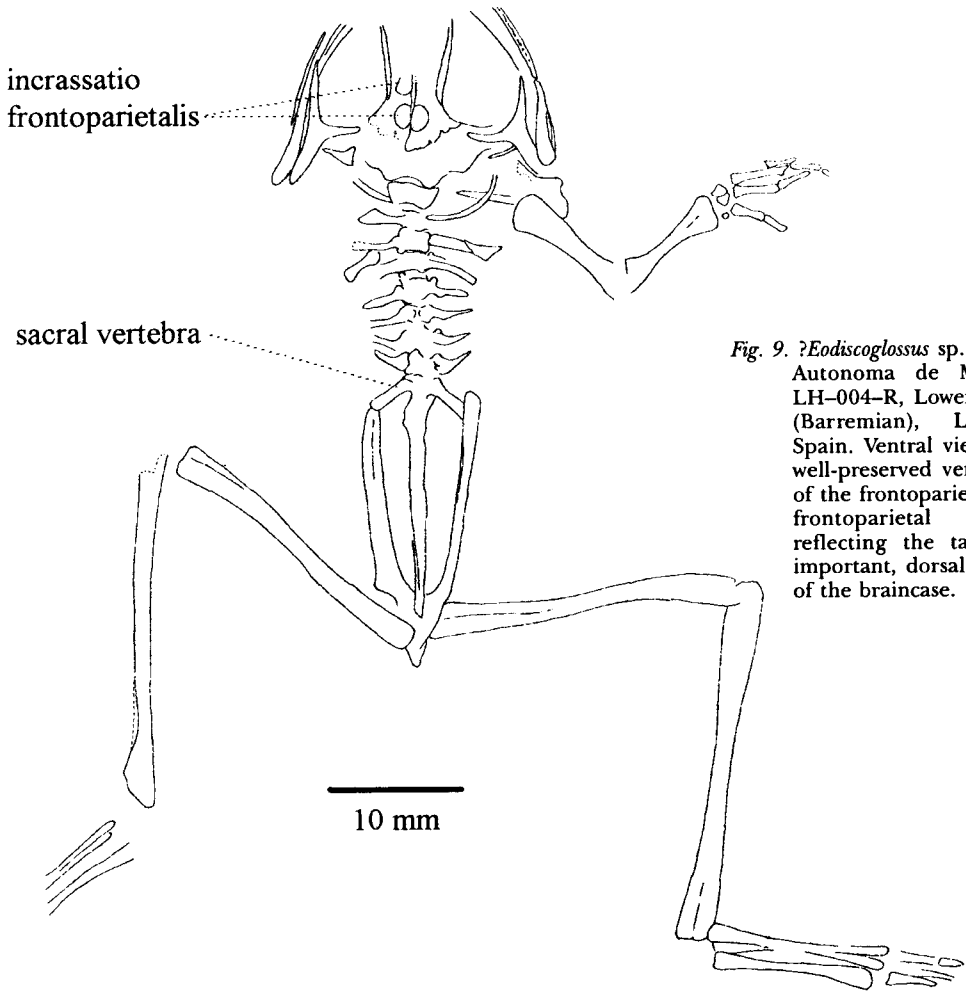
incrassatio
frontoparietalis

sacral vertebra

Fig. 9. ?Eodiscoglossus sp. Universidad Autonoma de Madrid No. LH–004–R, Lower Cretaceous (Barremian), Las Hoyas, Spain. Ventral view. Note the well-preserved ventral surface of the frontoparietals with the frontoparietal incrassation reflecting the taxonomically important, dorsal fenestration of the braincase.

10 mm

a prominent lanceolate anterior process and a much smaller posterior process. The angle subtended by the anterior cleithral border and the scapular border is at least 90 degrees. They represent the earliest fossil record of pipids.

From the same region but slightly younger (Barremian) are frogs from Makhtesh Ramon, Negev Desert, Israel mentioned by Nevo (1956), Griffiths (1963) and Hecht (1963), described by Nevo (1968) and later briefly discussed by Estes and Reig (1973). The type specimens are deposited in the Hebrew University of Jerusalem. Nevo interpreted this material (about 850 specimens of articulated adult individuals, among them only one tadpole) as forming two genera and three species. *Thoraciliacus rostriceps* (Nevo 1968) (Fig. 12) is a pipid with a free monocondylar sacro-urostylar articulation and one or more discrete postsacral vertebrae, fused frontoparietals, nasals extending over the premaxillae, dentate maxillae and premaxillae, sword-like parasphenoid, triangular transverse processes of vertebrae six through eight and with the articulation of the tips of the ilia with the ribs. This genus was also reported (as aff. *Thoraciliacus*) by Van Dijk (1985) from the Upper Cretaceous locality of Marydale in South Africa.

Cordicephalus gracilis and *C. longicostatus* (Nevo 1968) (Fig. 13) differ from *Thoraciliacus* in that they are more slender, with the tips of the ilia articulating with the sacral diapophyses, the ilia diverge to form a triangle, the skull is heart-shaped, rostrum not prominent, third rib longer than the second, transverse processes of vertebrae seven and eight arcuate, one or two postsacral vertebrae, and some morphometric differences. The two species differ from each other principally in that *C. longicostatus* has longer ribs and
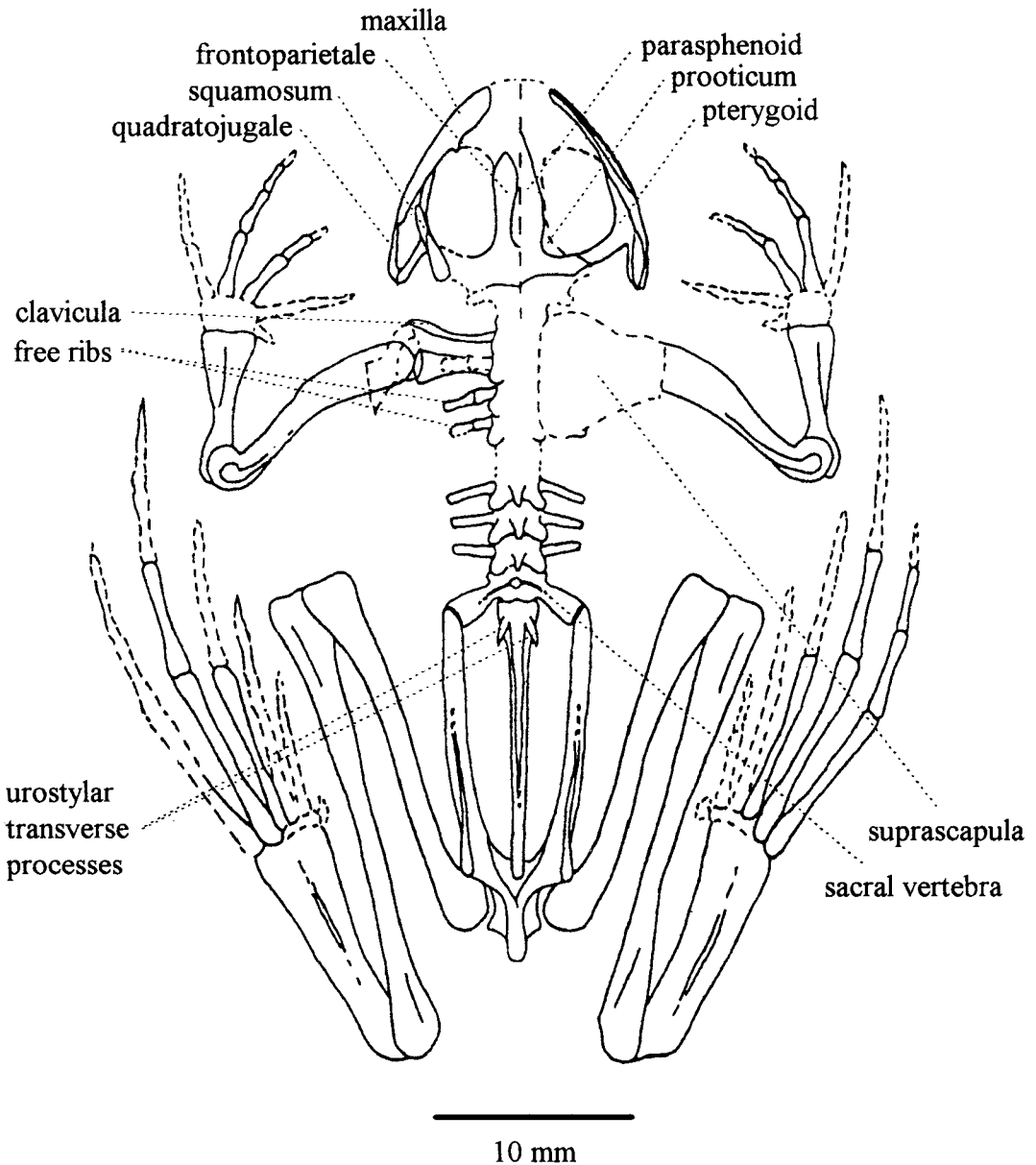
Fig. 10. Wealdenbatrachus jucarensis Fey 1988. Early Cretaceous, Spain; probably Discoglossidae. Restoration of the skeleton in dorsal view, with the left half of the skull in ventral view. From Fey (1988).

in the shape of the skull and of some cranial bones. All these pipids show a high degree of aquatic adaptation. Nevo (1968) suggested that *Cordicephalus* might be related to *Xenopus* whereas *Thoraciliacus* was closer to *Saltenia* (see below) and some Tertiary pipids (*Eoxenopoides, Shelania*). However, Estes and Reig (1973) did not exclude *Thoraciliacus* being related to *Xenopus* as well.

Zangerl and Denison (1950), Patterson (1951, 1956), Goin and Auffenberg (1958), Hecht (1963), Estes (1970), Estes and Reig (1973) and Winkler *et al.* (1990) reported on the Early Cretaceous (Comanchean) anurans from central Texas. Winkler *et al.* came to the conclusion that at least part of this material belongs to the Discoglossidae. Other anurans that were not referred to any family are remarkable in their maxillae showing distinct pitted ornamentation and in having amphicoelous and procoelous vertebrae. Pitted ornamentation and amphicoelous vertebrae are characteristic of Central Asian Cretaceous anurans considered as belonging to a separate family, Gobiatidae by Roček and Nessov
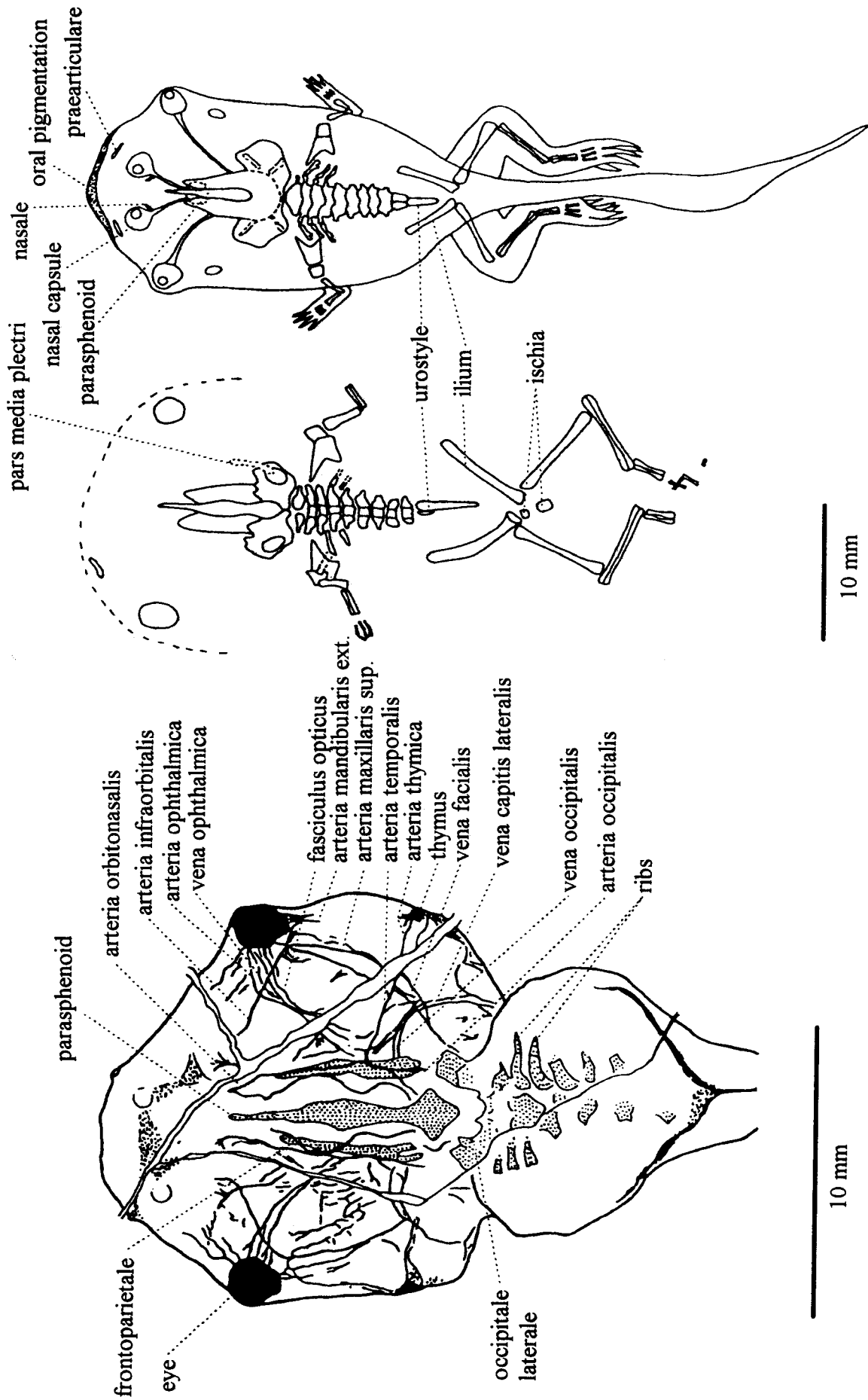
Fig. 11. Shomronella jordanica Estes, Špinar and Nevo 1978. Early Cretaceous, Israel; Pipidae. Interpretation of the nerves and vessels in developmental stage 50–51 (left). Metamorphosing individuals in stages 60–61 and 59 (right). Stages after Nieuwkoop and Faber (1967). From Estes *et al.* (1978).
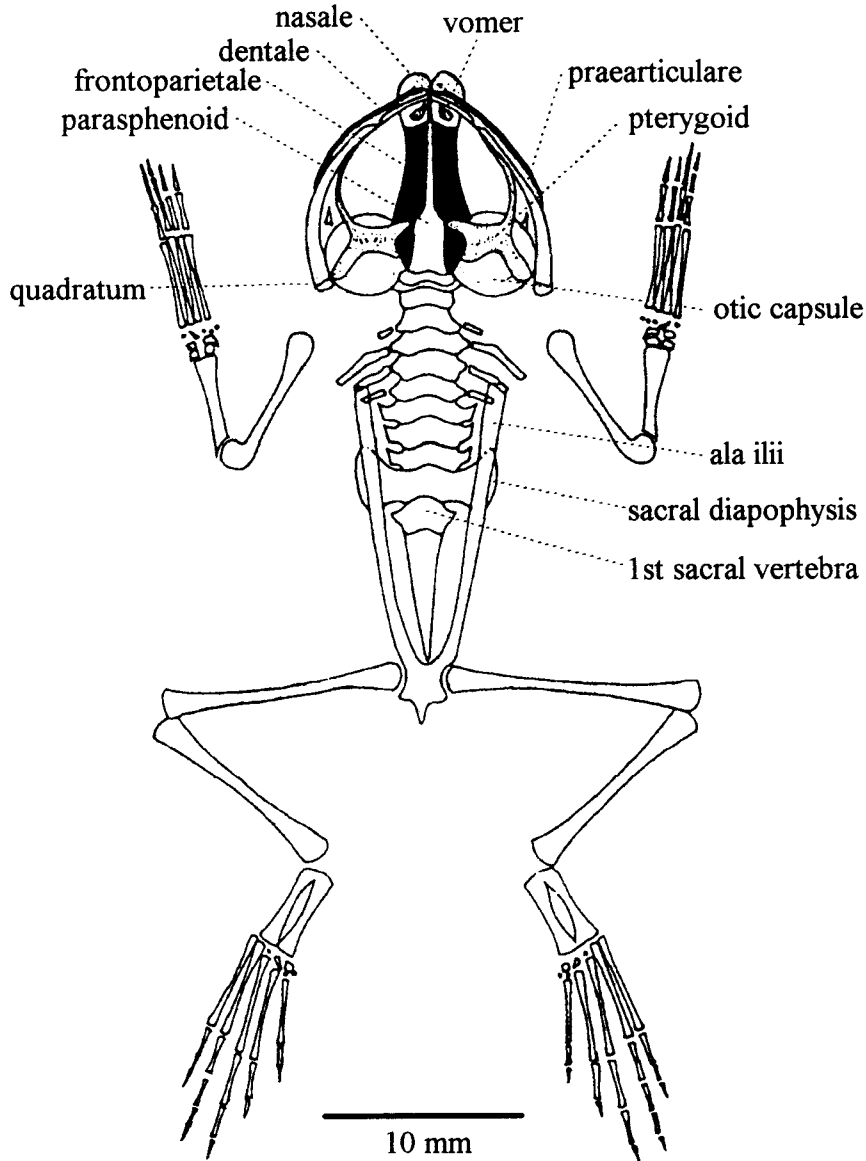
Fig. 12. Thoraciliacus rostriceps Nevo 1968. Early Cretaceous, Israel; Pipidae. Restoration of skeleton in ventral view. From Nevo (1968).

(1993). These authors suggested that at least some specimens described by Winkler *et al.* (1990) might belong to the Gobiatidae.

An unidentified Early Cretaceous anuran was found in the Chapada de Araripe region (Santana Formation), of north-east Brazil. The only specimen available represents a small frog with dentate upper jaw, quadratojugal, anteriorly arched clavicles, relatively narrow and mediolaterally extended sacral diapophyses, and the hind limb with a phalangeal formula of 2-2-3-4-3 (Kellner and Campos 1986; Maisey 1991; Báez 1991).

Abundant anuran material is reported, without closer determination, from the late Early Cretaceous of Koum Basin, Cameroon (Jacobs *et al.* 1988; Flynn and Brunet 1989). Four adult morphotypes can be preliminarily recognized; part of the material appears to resemble *Xenopus*. These frogs are currently being studied by Max Hecht. Aptian anurans (not determined but representing at least two taxa; Gomani 1994, pers. comm.) were found also in Malawi (Jacobs *et al.* 1990).
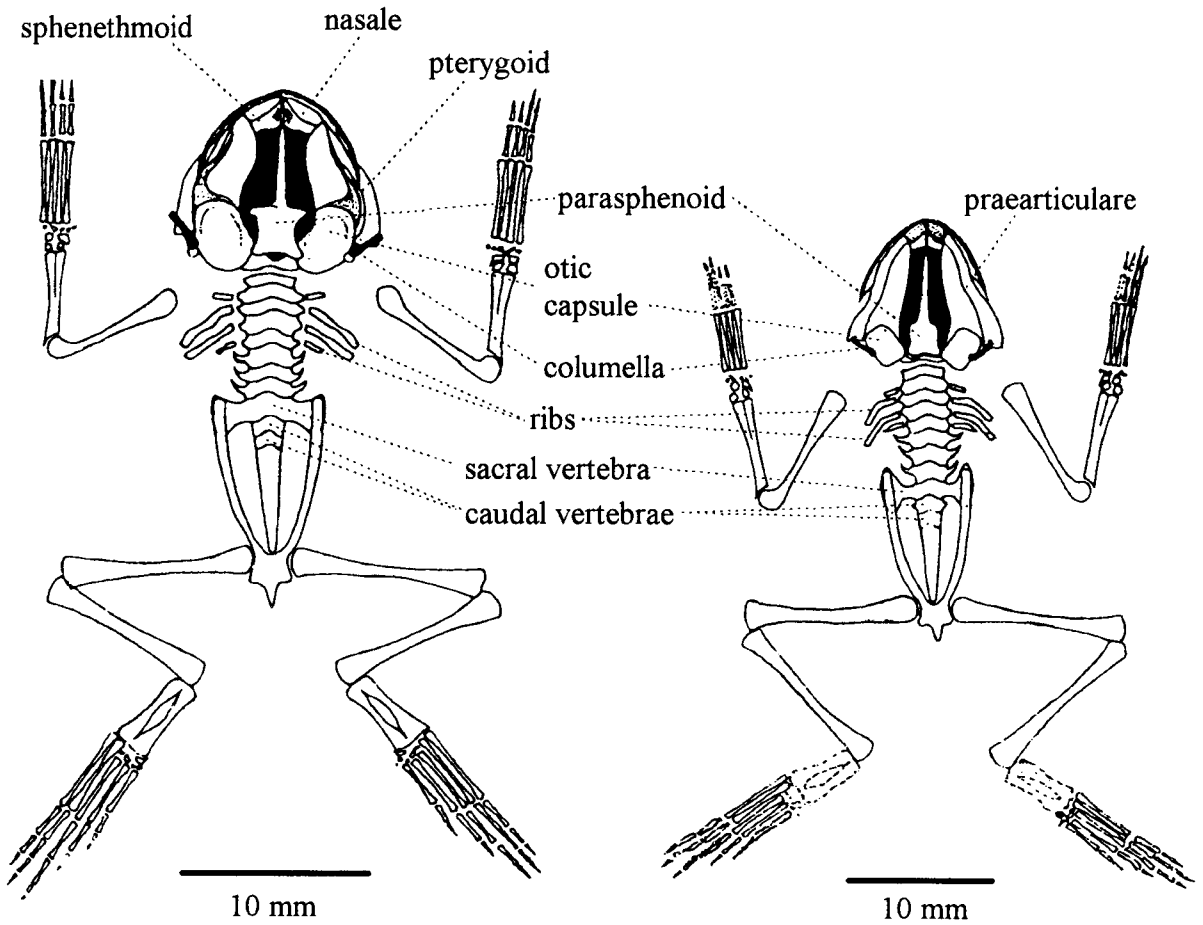
Fig. 13. Restoration of skeletons of *Cordicephalus gracilis* Nevo 1968 (left) and *C. longicostatus* Nevo 1968 (right) in ventral view. Early Cretaceous, Israel; Pipidae. From Nevo (1968).

Báez and Calvo (1989) published a preliminary report on a presumed pipid from the Rio Limay Formation (middle Cretaceous, Albian-Cenomanian) of the Rio Negro Province, north east Patagonia, Argentina. If assignment of this anuran to the Pipidae is confirmed, it will be the oldest known representative of this family in South America. Another pipid may be present in the mid-Cretaceous (Cenomanian) of Wadi Milk, northern Sudan (Evans *et al.* 1996).

VI. UPPER CRETACEOUS FROGS

The Late Cretaceous genus *Gobiates* Špinar and Tatarinov 1986 (Fig. 14) was originally considered a pelobatid because of its pitted ornamentation, arciferal pectoral girdle, and long cleft scapula (Borsuk-Białynicka 1978; Nessov 1981a, 1981b, 1985, 1988; Roček 1981). Špinar and Tatarinov (1986) described a similar anuran from the ?middle Campanian red beds of Khermeen Tsav, Gobi Desert, Mongolia as *Gobiates kermeentsavi*, recognized that it was not a pelobatid, and transferred it to the Discoglossidae. They also transferred the specimen described by Borsuk-Białynicka (1978) to this genus as *G. leptocolaptus* (Borsuk-Białynicka 1978). These two species differ from one another in the shape of the squamosal and the length of the quadratojugal (Fig. 15). Nessov (1981a), and Roček and Nessov (1993) studied large series of disarticulated bones from several middle to Upper Cretaceous (Late Albian through Santonian-Campanian boundary) localities of central Asia (Uzbekistan, Kazakhstan). Much of this material belongs to *Gobiates* and related forms. Although the original descriptions by Borsuk-Białynicka and by Špinar and Tatarinov are based on
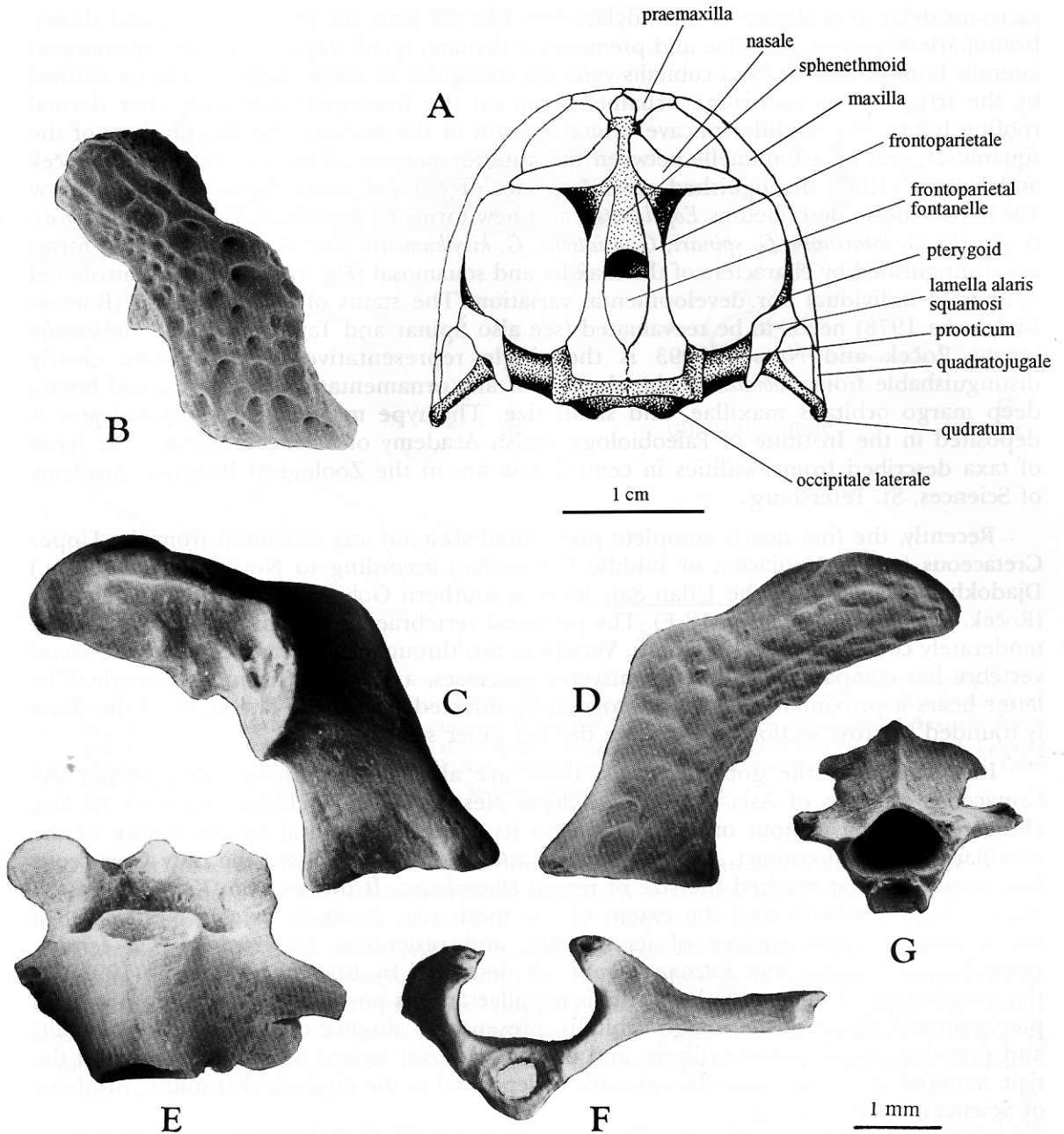
Fig. 14. Gobiates Špinar and Tatarinov 1986. Late Cretaceous, Asia; Gobiatidae. **A.** Restoration of skull in dorsal view. After Borsuk-Białynicka (1978) and Špinar and Tatarinov (1986). **B.** *G. spinari* Roček and Nessov 1993. Right lamella alaris squamosi in lateral view. **C, D.** *G. spinari* Roček and Nessov 1993. Left lamella alaris squamosi in medial (**C**) and lateral (**D**) views. **E.** *Gobiates* sp. V6 or V7 in ventral view. **F.** V 3 in posterior view. **G.** V3 or V4 in anterior and slightly dorsal view.

articulated skulls, large series studied by Roček and Nessov made it possible to examine the range of variation of some elements. This allowed recognition of several forms of *Gobiates* and required description of a new genus, *Gobiatoides*. All of these frogs display a complex of characters that is morphologically intermediate between the Leiopelmatidae and Discoglossidae. This intermediate condition was used to justify defining a separate family, Gobiatidae. The following characters are diagnostic of this family: amphicoelous vertebral centra, sometimes with notochordal canal; neural arches either do not join one another or fuse and roof the neural canal dorsally, in the latter case they are imbricate;

sacro-urostylar articulation is bicondylar; free ribs (at least on vertebrae two and three); frontoparietal paired; maxillae and premaxillae dentate; quadratojugal present; epicondylus lateralis humeri absent, fossa cubitalis ventralis triangular in shape. *Gobiates* may be defined by the irregular pit-and-ridge ornamentation on the frontoparietals and other dermal roofing bones, the slightly concave orbital margin of the maxilla, the morphology of the squamosal, and by a fontanelle between the anterior portion of the frontoparietals. Roček and Nessov (1993) distinguished several species of *Gobiates* including *G. sosedkoi* (Nessov 1981a), formerly described as *Eopelobates*, and new forms *G. bogatchovi*, *G. dzhyrakudukensis*, *G. fritschi*, *G. tatarinovi*, *G. spinari*, *G. asiaticus*, *G. kizylkumensis* and *G. furcatus*. These forms are distinguished by characters of the maxilla and squamosal (Fig. 15) that can be attributed neither to individual nor developmental variation. The status of *G. leptocolaptus* (Borsuk-Białynicka 1978) needs to be reevaluated (see also Špinar and Tatarinov 1986). *Gobiatoides parvus* Roček and Nessov 1993 is the single representative of the genus, clearly distinguishable from *Gobiates* by the absence of any ornamentation on the dermal bones, deep margo orbitalis maxillae, and small size. The type material of *G. leptocolaptus* is deposited in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw; the types of taxa described from localities in central Asia are in the Zoological Institute, Academy of Sciences, St. Petersburg.

Recently, the first nearly complete postcranial skeleton was recovered from the Upper Cretaceous (upper Coniacian or middle Campanian according to Novikov, pers. comm.) Djadokhta Formation of the Udan Sair locality, southern Gobi Desert, Mongolia (Fig. 16) (Roček and Nessov 1993, fig. 18 F). The presacral vertebrae are amphicoelous, their centra moderately constricted at mid-length. Vertebrae two through four bear free ribs. The sacral vertebra has comparatively broad transverse processes, and is free from the urostyle. The latter bears a proximal pair of posterolaterally directed processes. The shaft of the ilium is rounded in cross section, but bears a distinct tuber superius.

In addition to the gobiatid frogs, there are also typical discoglossids among the Cretaceous anurans of Asia. *Kizylkuma antiqua* Nessov 1981a is characterized by its low, elongated maxilla without ornamentation on its outer surface and by the nature of the maxillary-pterygoid contact. *Aralobatrachus robustus* Nessov 1981a was the only Cretaceous frog from Asia that reached the size of recent *Discoglossus*. It differs from *Kizylkuma* in the slightly rugose maxilla and the extent of the tooth row. *Itemirella cretacea* Nessov 1981a has a smooth outer surface of its maxilla, and resembles *Soevesoederberghia egredia*, *Procerobatrachus paulus* and *Estesina elegans*, all described by Roček and Nessov (1993), in the morphology of the lamina horizontalis maxillae and its posterior termination (processus pterygoideus), shape of the margo orbitalis, presence or absence of the processus frontalis and processus zygomaticomaxillaris, and by the posterior extent of the tooth row. All the type material of central Asian discoglossids is deposited in the Zoological Institute, Academy of Sciences, St. Petersburg.

A supposed anuran, *Altanulia alifanovi*, was described by Gubin (1993) from the Nemegt Formation (upper Campanian to lower Maastrichtian) of the Altan-Ula II locality, southern Gobi Desert, Mongolia. The taxon is based on a single maxilla with an estimated length of 20 mm. The number of tooth positions is about 45 to 47. The maxilla is smooth on its labial surface, with a horizontal triangular depression tapering anteriorly in its posterior moiety. The lamina horizontalis is deep but narrow anteriorly, with the processus pterygoideus widely rounded. In contrast to Gubin who placed it in the Discoglossidae, Sanchíz (1998) questioned its assignment to the Anura.

Anurans from the early Late Cretaceous of Utah were reported in a preliminary fashion by Eaton and Cifelli (1988).

Other late Cretaceous frogs of North America are represented by isolated bones from the Lance, Hell Creek, and Tongue River Formations of Wyoming and Montana, U.S.A. described or reviewed by Estes (1964, 1969, 1970), Estes, Berberian and Meszoely (1969), Estes and Reig (1973), Estes and Sanchíz (1982b). Several taxa are currently recognized
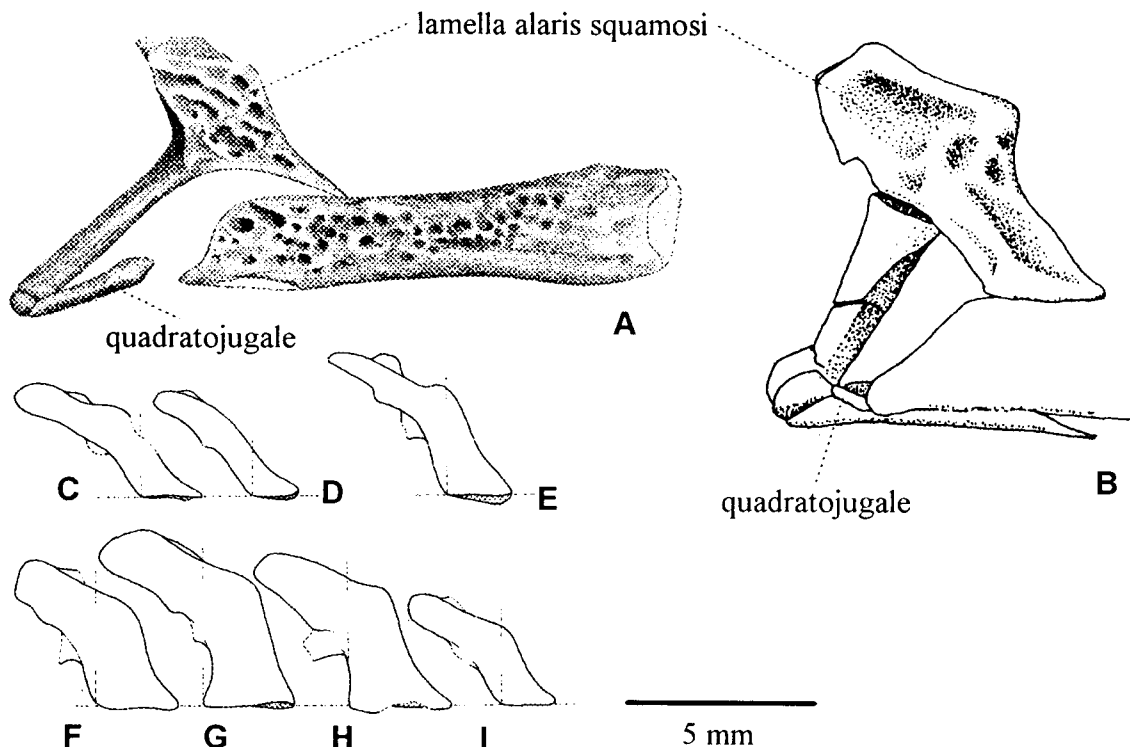
Fig. 15. The cheek region in *Gobiates* Špinar and Tatarinov 1986. **A.** The cheek region of *Gobiates kermeentsavi* Špinar and Tatarinov 1986. **B.** The cheek region of *Gobiates leptocolaptus* (Borsuk-Białynicka 1978). **C, D.** Lamella alaris in two specimens of *Gobiates asiaticus* Roček and Nessov 1993. **E.** Lamella alaris of *Gobiates kizylkumensis* Roček and Nessov, 1993. **F-H.** Lamella alaris in three specimens of *Gobiates spinari* Roček and Nessov 1993. **I.** Lamella alaris in *Gobiates* cf. *sosedkoi* (Nessov 1981). Note the difference in size of the quadratojugals in **A** and **B**. From Roček (1981), Špinar and Tatarinov (1986), and Roček and Nessov (1993).

among this material. *Paradiscoglossus americanus* Estes and Sanchíz 1982 from the Lance Formation is based on the ilium, characterized by a well developed dorsal crest on the iliac shaft, elongated tuber superius, and a very deep and large supraacetabular fossa. *Scotiophryne pustulosa* Estes 1969 (Fig. 17) is also based on an isolated ilium and some other elements. Estes (1969) diagnosed this taxon by the morphology of its ilium, humerus, and the pustular sculpture of the dermal skull bones. It was later discussed by Vergnaud-Grazzini and Wenz (1975) and Estes and Sanchíz (1982b); the latter authors concluded that it is distinct from *Paradiscoglossus* as well as from *Theatonius* (see below), and most probably belongs to the Discoglossidae.

Beside these discoveries in Wyoming and Montana, another record is from the Late Cretaceous locality of El Gallo, Baja California del Norte, where undescribed skull and postcranial elements have been found (Estes and Báez 1985). Recently, *Scotiophryne* was reported from the late Campanian Fruitland Formation of New Mexico (Hunt and Lucas 1992, 1993) and from the latest Maastrichtian-early Paleocene (Lancian-Torrejonian) Tullock Formation of Montana (Bryant 1989). Estes and Sanchíz (1982b) suggested that humeri from the Hell Creek Formation described by Estes, Berberian and Meszoely (1969) might indicate the presence of a third discoglossid in the Late Cretaceous of North America.

Palaeobatrachus occidentalis (Estes and Sanchíz 1982b), another anuran from the Lance and Hell Creek Formations of Wyoming and Montana, is also based on the morphology of its ilium, the only element available. It was originally identified as cf. *Barbourula* sp. by Estes (1964). This is the only discovery of a paleobatrachid in North America. Recently, Sanchíz (1998: 39) questioned its generic assignment. Estes and Sanchíz (1982b) also reported on the presence of *Eopelobates* sp. in the Lance and Hell Creek Formations. This evidence is based on the ilia, fragments of maxillae, nasal, and squamosal. *Eopelobates* sp.
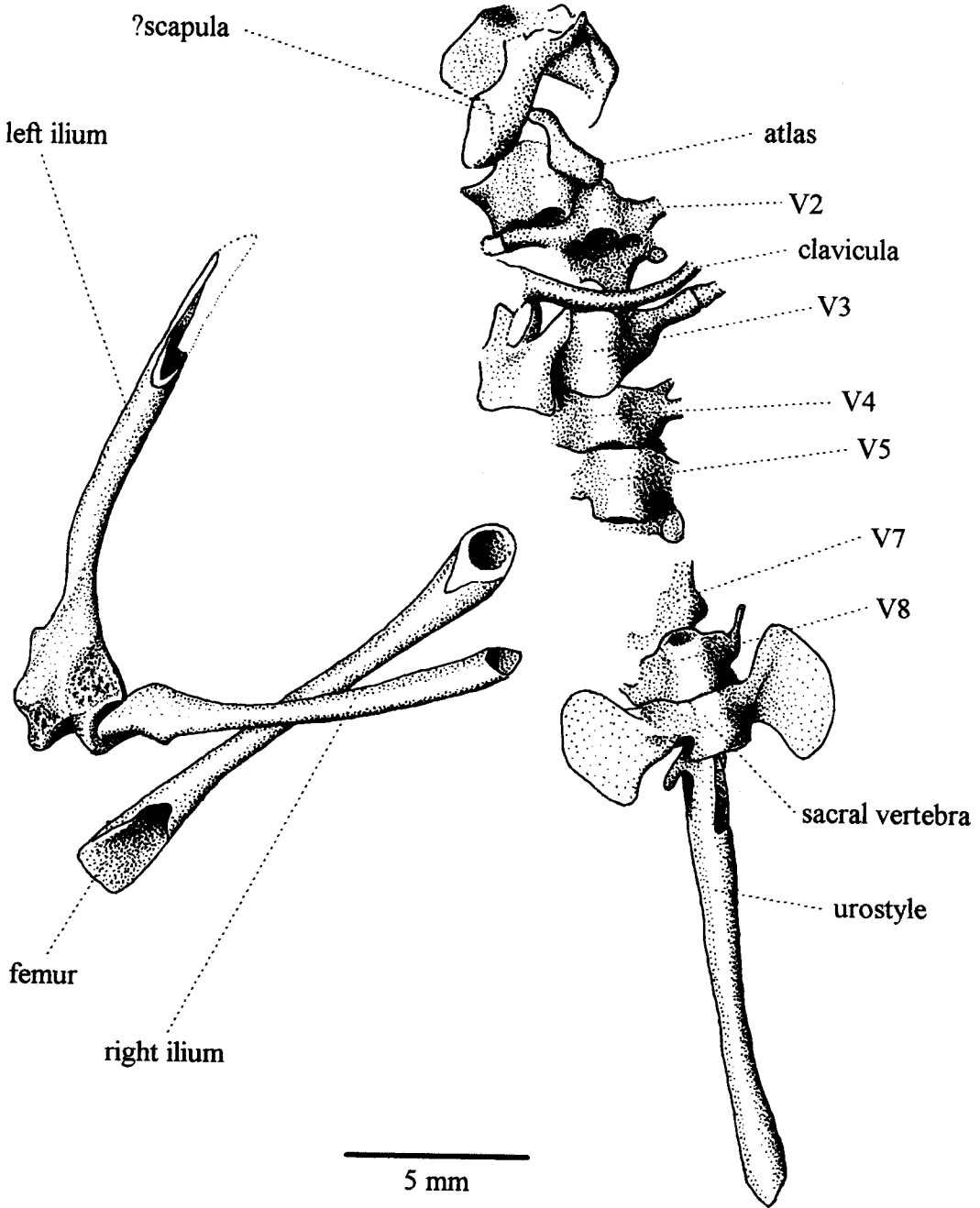
Fig. 16. Postcranial skeleton of *Gobiates* sp. Špinar and Tatarinov 1986. Specimen PIN 3907/10 from the Upper Cretaceous (Upper Coniacian or Middle Campanian) Djadokhta Formation, Mongolia.

was also reported by Hunt and Lucas (1992, 1993) from the late Campanian Fruitland Formation of New Mexico.

The latest known frog from the Late Cretaceous of North America is *Theatonius lancensis* Fox 1976, from the Lance Formation of Wyoming. This distinctive frog is based on maxillae and a presumed squamosal. Its maxilla is short, edentulous and distinctive in shape; the posterior margin of the squamosal bears spines, and the squamosal possibly meets the frontoparietal. Its dermal skull is covered with tubercular sculpture that is better defined than in *Scotiophryne* and does not intergrade into pits or ridges. It was briefly discussed by Estes and Sanchíz (1982b) who, in common with Fox (1976), could not offer any suggestion as to its relationships. Hence, it is classified as an anuran *incertae sedis*.

Buffetaut *et al.* (1996) reported on a fragmentary frontoparietal from the early Campanian deposits of southern France (Villeveyrac, Hérault). Since assignment of *Palaeobatrachus occidentalis* to Palaeobatrachidae is still obscure, this is apparently the oldest known specimen that can be assigned to this family without doubt, and together with an indeterminate palaeobatrachid from the early Maastrichtian of Spain (Astibia *et al.* 1990) the only evidence of the Palaeobatrachidae in the Mesozoic.

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 (1972) from the middle Campanian of Montana, U.S.A.

Besides the "Rio Limay pipid," South American Mesozoic pipids are represented by *Saltenia ibanezi* Reig, 1959 (Fig. 18), from the vicinity of Alemania, Department of La Vina, Province of Salta, Argentina. The age of the frog-bearing beds is now estimated as Late Cretaceous (Santonian-Campanian). Thorough revision of the type material by Báez (1981),
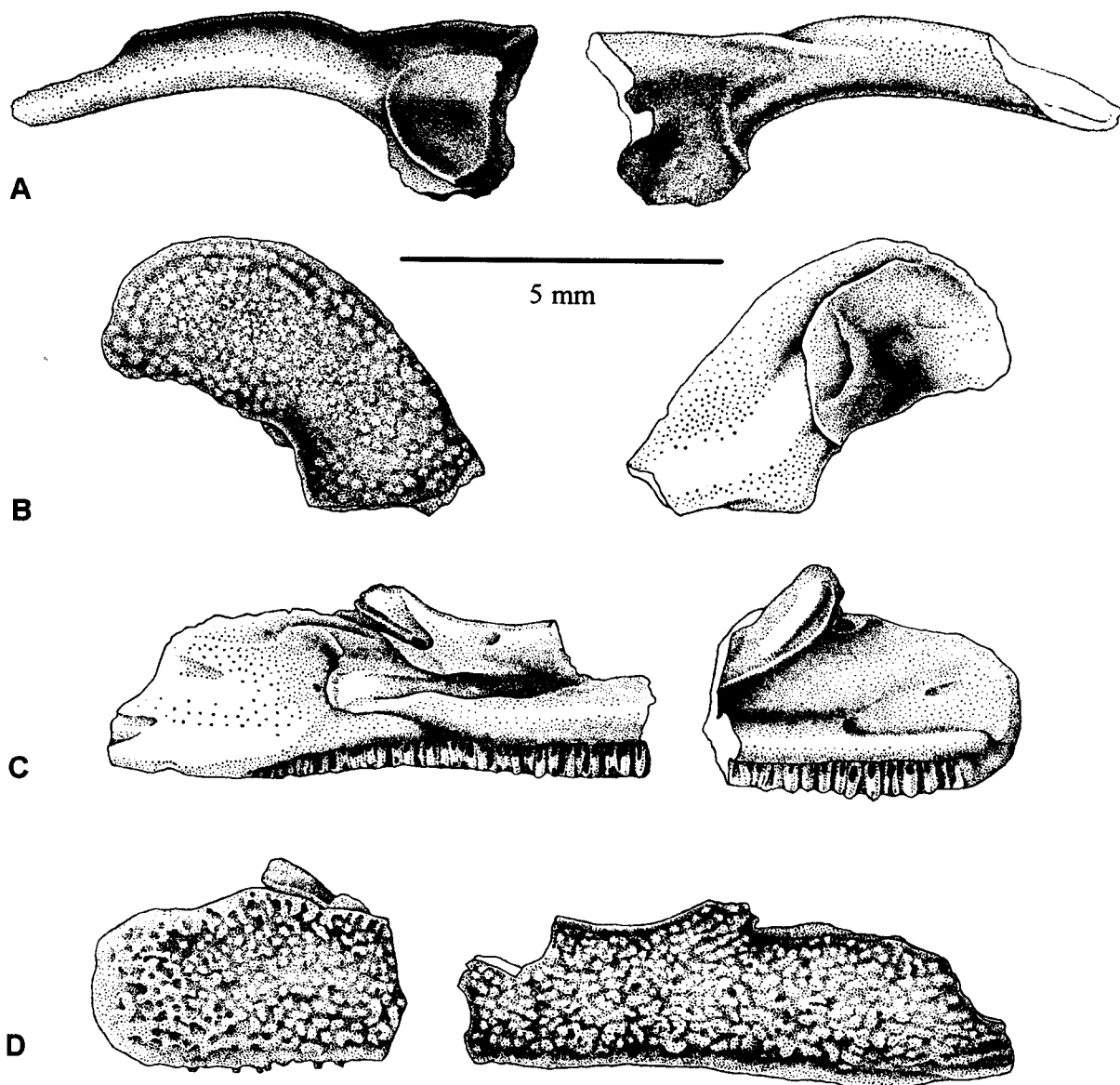

Fig. 17. Scotiophryne pustulosa Estes 1969. Late Cretaceous (Campanian and Maastrichtian) through Paleocene (Puercan), North America. **A.** Left ilium in outer (left) and inner (right) views. **B.** Lamella alaris squamosi in outer (left) and inner (right) views. **C.** Posterior (left) and anterior (right) parts of the maxilla in inner view. **D.** The same fragments as in **C,** but in outer view. From Estes (1969).

after previous studies by Reig (1959) and Parodi Bustos *et al.* (1960), revealed that this pipid frog can be distinguished from other members of this family in having a wide and flanged frontoparietal with the dorsal surface lacking parasagittal crests, edentulous maxillae and premaxillae, long and narrow parasphenoid, eight epichordal presacral vertebrae, the sacral vertebra and urostyle fused, no free distal carpal 4, free ribs in tadpoles and juveniles (occasionally present in adults), and fused tibiale and fibulare.

Pipids were also reported from the Upper Cretaceous (Coniacian-Santonian) In Beceten site, 90 km E of the town of Tahoua, Niger (de Broin *et al.* 1974; Báez and Rage 1998). The first form (Fig. 19) ("In Beceten pipid I unidentified genus and species" in Báez and Rage [1998]) has a well ossified braincase with dermal bones fused to it. The prootics and exoccipitals are fused with one other as well as with those on the other side of the skull so that the foramen magnum is completely rimmed with bone. A wide groove for the eustachian tube runs across the floor of each otic capsule. The sphenethmoid extends to the prootic foramen, so that the optic foramina pierce the bone. The frontoparietal is unpaired, with a small depression in the midline that possibly corresponds to the pineal foramen. The parasphenoid is lanceolate in shape, with a relatively narrow cultriform process. All these features exhibit superficial resemblance to *Xenopus*.

The second form was preliminarily reported by Báez and Rage (1988, 1989), and formally described by the same authors in 1998 as *Pachybatrachus taqueti* (Fig. 20). Similar to the previous form, it is a hyperossified pipid but unique in having dermal vermicular ornamentation on the upper surface of the skull and on the ventral surface of the vertebral centra. The grooves for the eustachian tubes on the floor of the otic capsules are deep and narrow. The nerve foramina between the fused atlas and next presacral are small and a bony accretion on the atlantal centrum forms an odontoid process that articulates with an excavation on the ventral surface of the braincase. Articular facets of the prezygapophyses of the presacral vertebrae are flat, whereas those of the postzygapophyses are curved ventromedially to form a groove. The vertebral centra are opisthocoelous. Due to hyperossification, the prootics and exoccipitals are fused, along with their counterparts of the other side, the optic foramina are enclosed in bone, the dermal bones are coalesced with the endocranium, and the sacral vertebra is fused with the urostyle. According to Báez and Rage (1998), *Pachybatrachus* is closely related to the living African forms *Hymenochirus* and *Pseudhymenochirus*.

Vergnaud-Grazzini (in de Broin *et al.* 1974) also identified ranid material from this locality; this material consists of a fragmentary sacral vertebra, urostyle, ilium and three fragmentary humeri (one of the latter illustrated in Rage 1984, fig. 1A). However, Rage (1984) denied assignment to the Ranidae because these specimens are too incomplete for familial identification.

Baurubatrachus pricei Báez and Perí 1989 (Fig. 21) from the late Cretaceous (Senonian, Marilia Formation) of a site near Peiropolis, Municipio Uberaba, State of Minas Gerais, Brazil was preliminarily described by Báez (1985), and Báez and Perí (1987). It is based on a single, partially complete skeleton of a large frog (snout-vent length about 100 mm). It is characterized by a skull exostosed by a pitted ornamentation, maxilla in extensive contact with both the nasal and the squamosal, subtemporal fenestra reduced or absent, quadratojugal expanded in a way similar to the pars facialis of the maxilla, squamosal and perhaps quadratojugal forming the boundary of a fenestra lateral to the crista parotica and dorsal to the ventral ramus of the former, ramus maxillaris pterygoidei bearing a ventral flange, extensive pterygoid-parasphenoid articulation, procoelous presacral vertebrae with their spinal processes well developed, transverse processes of vertebrae three and four longer than those of the posterior trunk and sacral vertebrae and dilated at their ends, sacral diapophyses moderately dilated, bicondylar sacro-urostylar articulation, and ilial shaft with dorsal crest. Undoubtedly this is a member of the Leptodactylidae, with some affinities to the Ceratophryinae.
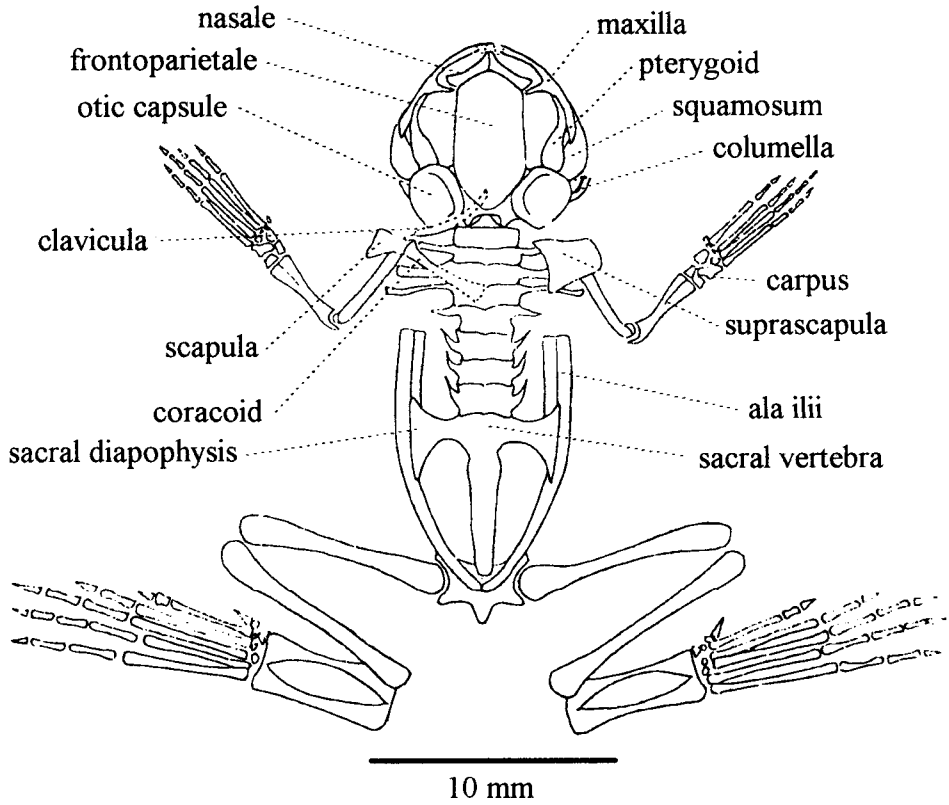
Fig. 18. *Saltenia ibanezi* Reig 1959. Late Cretaceous, Argentina; Pipidae. Restoration of the skeleton in dorsal view. From Báez (1981).
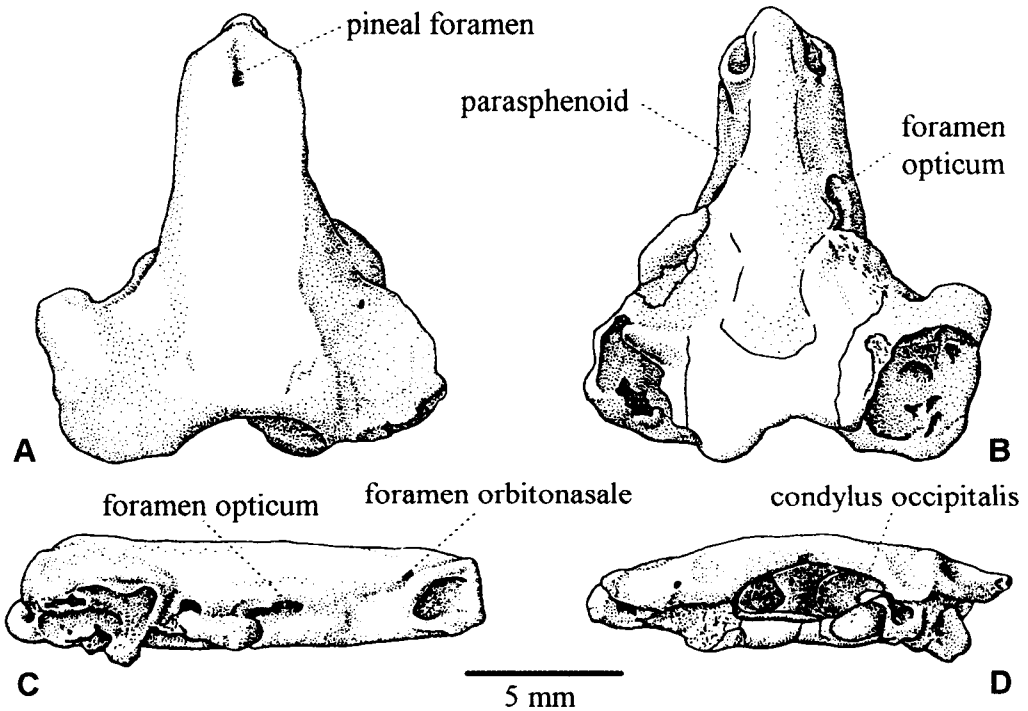
Fig. 19. Braincase of an unidentified pipid with affinities to *Xenopus* sp. from the Late Cretaceous (Coniacian-Santonian) of In Beceten, Niger. **A.** Dorsal view. **B.** Ventral view. **C.** Lateral view. **D.** Occipital view. From Báez and Rage (1998).
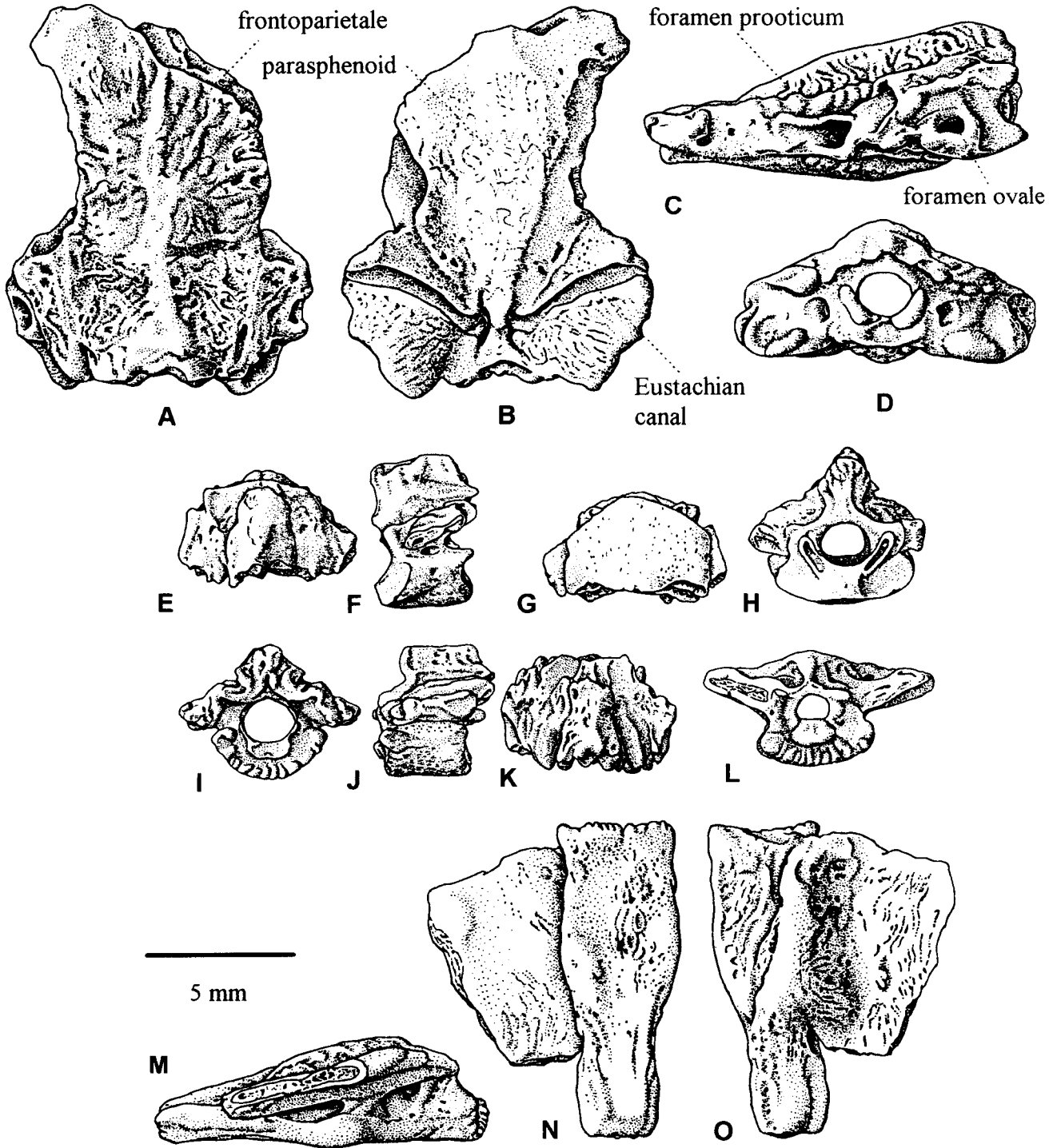
Fig. 20. *Pachybatrachus taqueti* Báez and Rage 1998. Late Cretaceous, Niger; Pipidae. **A–D**. The braincase and otic capsules in dorsal (**A**), ventral (**B**), sinistral (**C**), and posterior (**D**) views. **E–H**. Atlantal complex in dorsal (**E**), sinistral (**F**), ventral (**G**), and anterior (**H**) views. **I–L**. Presacral vertebra in posterior (**I**), sinistral (**J**), dorsal (**K**), and anterior (**L**) views (**I–K** is not from the same specimen as **L**). **M–O**. Sacro-urostylar complex in dextral (**M**), ventral (**N**), and dorsal (**O**) views. From Báez and Rage (1998).

Unidentified leptodactylid and pipid remains (the latter including also material identified as cf. *Xenopus* sp.) were found in the late Cretaceous (most probably Campanian) Los Alamitos Formation of southern Argentina (Bonaparte 1986; Báez 1987, 1991; Gayet *et al.* 1991). Quite recently, Rage, Marshall and Gayet (1993) found one indeterminate anuran vertebra in the material of Maastrichtian age from the Pajcha Pata locality in Bolivia. Another representative of the Leptodactylidae, *Estesius boliviensis* was reported from Tiupampa, south-central Bolivia (Báez 1991). Its age was considered Late Cretaceous (Maastrichtian) by De Muizon *et al.* (1983) but at present it is considered Paleocene (Báez 1991). Similarly, unidentified leptodactylids from Laguna Umayo, Peru (Sigé 1968; De Muizon *et al.* 1983) are presently regarded as early Paleocene (Báez 1991).

Sahni *et al.* (1982, 1983), Gayet *et al.* (1984) and Sahni (1984) reported on the Anura from the Maastrichtian of the Takli locality (= Gitti Khadan) in India. Among this material is an ilium that is exactly the same as that of the Tertiary pelobatid *Eopelobates*. Rage (1993, pers. comm,) recently confirmed this assignment. The Upper Cretaceous (Maastrichtian; see Thewissen *et al.* 1990) Pisdura locality yielded several fragmentary tibiofibulae and other distal limb bones (Jain and Sahni 1983). The material was assigned to the Pelobatidae. However, listed characters and illustrations suggest that it is indeterminate. From Naskal,
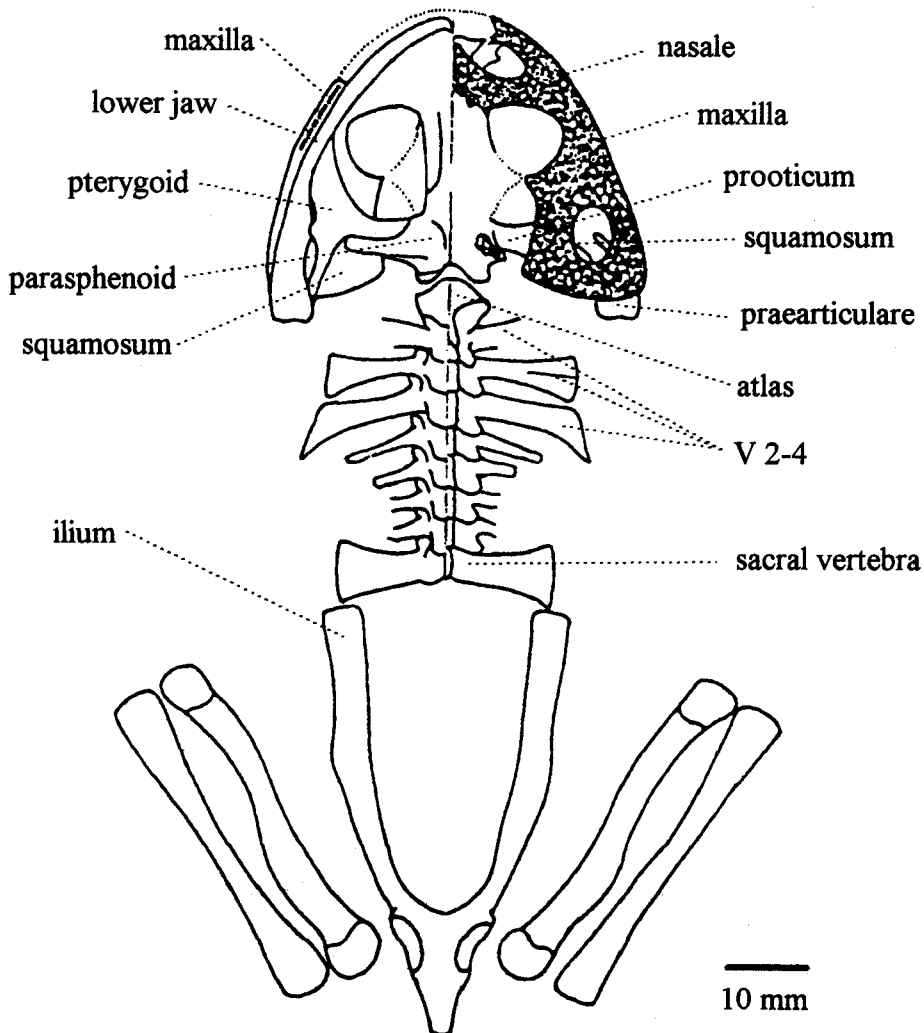

Fig. 21. *Baurubatrachus pricei* Báez and Perí 1987. Late Cretaceous, Brasil; Leptodactylidae. Partial restoration of the skeleton in dorsal view but with the left half of skull and pelvic girdle in ventral view. From Báez and Perí (1987).

another locality in India near the Cretaceous/Tertiary boundary (uppermost Maastrichtian), an anuran without explicit determination was mentioned by Prasad and Sahni (1988); it was later identified by Prasad and Rage (1991, 1995) as a discoglossid closely recalling those described by Roček and Nessov (1993) from central Asia. In addition to this discoglossid, a presumed hylid, based on a fragmentary ilium and humerus, and two or three other indeterminate anurans were recovered from the Naskal locality (Prasad and Rage 1995).

Recently, Late Cretaceous (probably Maastrichtian) discoglossids and paleobatrachids were reported from Laño, Basque Country, Spain (Astibia *et al.* 1990). Undescribed Upper Cretaceous anuran material consisting of isolated bones from the localities of Fontllonga and Moli Vell (both Province of Lerida) and Carlet (Province of Valencia) are deposited in the Institut de Paleontologia M. Crusafont at Sabadell. Although this material is waiting for thorough investigation it should be noted that frontoparietals from Fontllonga bear pit-and-ridge ornamentation which, together with tiny humeri, recall those of *Gobiates*. Massive, dorsoventrally compressed opisthocoelous vertebrae in the sample suggest the presence of discoglossids as well.

New material from the Upper Cretaceous of southern France was discovered by B. Sigé (University of Lyon) in 1998. This material was preliminarily assigned to the Discoglossidae and Palaeobatrachidae (Duffaud, pers. comm.).

Undescribed Late Cretaceous (or perhaps Paleogene) anurans are known also from Zaire (Estes 1986, pers. comm.).

VII. ZOOGEOGRAPHY AND EVOLUTION OF MESOZOIC ANURANS

The following conclusions can be inferred regarding the Mesozoic distribution of frogs and their phylogenetic diversification (Fig. 22, Table 1).

The earliest records of fossil frogs are from North America (*Prosalirus bitis* from Arizona) and South America (*Vieraella* from Argentina), both of Early Jurassic age (Table 1). If the Madagascar site where the proanuran *Triadobatrachus* lived 35–40 million years earlier is taken into account, then it is obvious that the early distributional area of frogs extended over the single large supercontinent Pangea. This early distribution was probably in regions with seasonally wet climate (Hallam 1985), and included parts of today's North America, South America, Africa, and most probably also Antarctica and India. The recent discovery of a form close to *Triadobatrachus* in Poland extends the range into Europe (Evans and Borsuk-Białynicka 1998). One should take into consideration that it would be highly improbable that these sites marked the limits of anuran distribution.

Vieraella was classified as a leiopelmatid but it might be considered as a structural ancestor of both the Leiopelmatidae and Discoglossidae (Estes and Reig 1973). The Middle Jurassic *Eodiscoglossus oxoniensis* (living about 20 million years later, which is a rather short period of time in terms of the rate of anuran structural evolution) is without doubt referred to the Discoglossidae which, except for some Tertiary immigrants to North Africa (*Latonia*) and interesting discoveries in the Late Cretaceous of India (see below), were not recorded in former Gondwana.

One question arising from the evaluation of the early zoogeographical history of anurans is why discoglossids, which are known as early as the Middle Jurassic, (at a time when southern and northern continents were still connected with each other) have not spread over the southern hemisphere? A possible answer is that their southward migration was prevented by a wide equatorial belt of arid climate (Hallam 1985). If this were true, the leiopelmatid-discoglossid mixture of characters in *Vieraella* may indicate the nature of the common Late Triassic anuran stock. On the other hand, *Notobatrachus* suggests that, like the Discoglossidae in the northern hemisphere, leiopelmatids were already well established in the Late Jurassic. Dispersal of the leiopelmatids towards the north may have already been prevented by changes in the configuration of the oceans. There is no evidence as to when or how *Ascaphus* reached North America.

The early Cretaceous picture differs in two aspects. The first pipids were recorded and the Laurasian continents became separated from Gondwana. Pipids no doubt had to arise before Africa and South America became separated from one another. This is evidenced by a mid-Cretaceous pipid from the Rio Limay Formation of Patagonia, Late Cretaceous *Saltenia* and Paleocene *Xenopus* (see Estes 1975) in South America, as well as by the recent distribution of the Pipidae. Buffeteaut and Rage (1993) distinguish an early dispersal, probably prior to the split between Africa and South America, and a late, probably Late Cretaceous and Palaeocene dispersal after the separation of the two continents. Curiously, pipids never penetrated into the northern continents, which they might have by using the same terrestrial routes at the end of the Cretaceous as did the Leptodactylidae and numerous other land dwellers. It is interesting that the first fossil record of pipids is in agreement with their estimated time of origin based on albumin data (130 million years ago; Bisbee *et al.* 1977). Anatomically, they can be derived neither from discoglossids nor from leiopelmatids, the only known families existing prior to that time. Their larval anatomical features differentiating them from other anurans (see e.g., Weisz 1945; Roček 1989) cannot be explained by their mode of larval feeding or other larval specializations. Evaluation of the taxonomic status of pipids is obscured by their paedomorphic nature (especially in their recent representatives) but the latent capacity of pipids to realize phenotypically ancestral features (Smirnov 1993) supports the view that they belong among primitive anurans.

Whereas the phylogenetic diversification of frogs was represented by only the Discoglossidae, Leiopelmatidae, and Pipidae for approximately 60 million years from the Early Jurassic to the Early Cretaceous, during the mid- and Late Cretaceous several new families appeared, including the Leptodactylidae in South America, and the Palaeobatrachidae, Gobiatidae, Pelobatidae and possibly also another group (represented by *Theatonius*), in Laurasia. The Palaeobatrachidae recall pipids in some features, but are clearly distinguished from them osteologically. It is theoretically possible that pipids could have dispersed around the oceanic barriers toward the north in the Late Cretaceous, using briefly existing land bridges, as in the manner of the Leptodactylidae (Rage 1981; Gayet *et al.* 1992). However, *Palaeobatrachus occidentalis* from the Late Cretaceous Lance Formation of North America suggests that the Palaeobatrachidae (if this assignment is correct) were already well established by that time. In contrast to the Palaeobatrachidae, the Gobiatidae have clear affinity to the discoglossid-leiopelmatid stem.

The earliest records of pelobatids (North America, India) represent a zoogeographical problem. If only one of these records were known, the history of this family would be easy to explain. However, this is not the case. The problem is the pre-Cretaceous position of the Indian subcontinent. No Mesozoic pelobatids have been found in the Eurasian continent. In contrast, presence of the "Naskal discoglossid" in India in the latest Cretaceous, which is similar to those described by Roček and Nessov (1993) from central Asia, suggests a terrestrial connection between the Indian plate and mainland Asia at that time (Prasad and Rage 1991; Klootwijk *et al.* 1992), and thus a probable invasion of discoglossids to India from Laurasia.
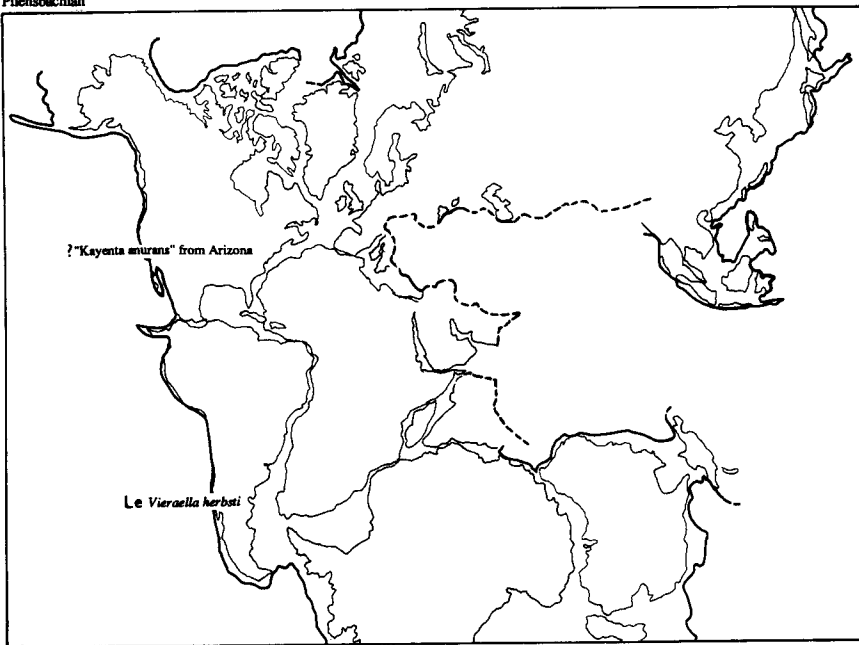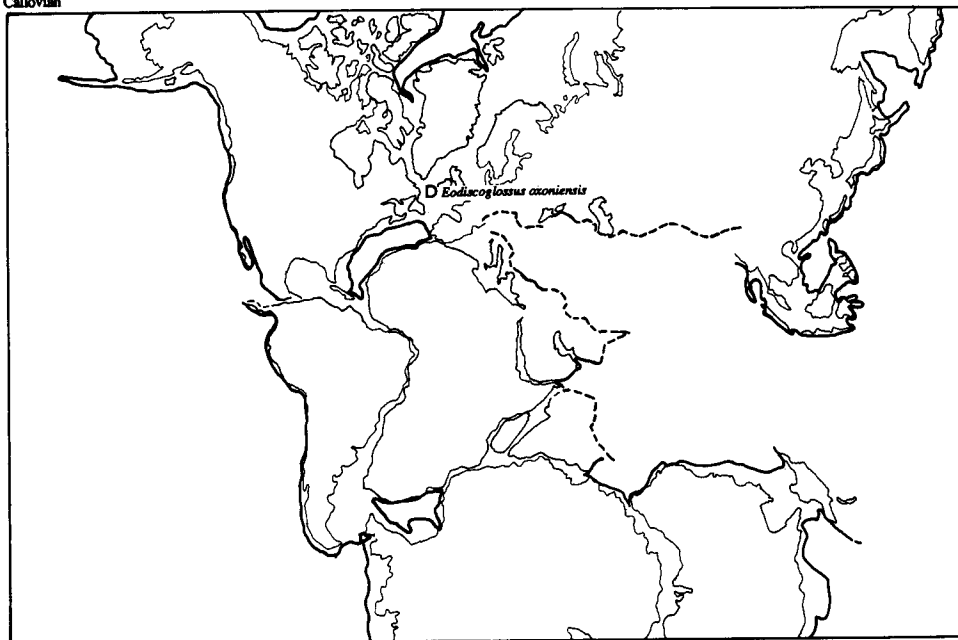
VIII. ACKNOWLEDGEMENTS

Fig. 22. Position of the continents in the Jurassic (exemplified by the Pliensbachian, Callovian and Portlandian — this page) and Cretaceous (Hauterivian, Cenomanian and Santonian — on opposite page), with records of Jurassic and Cretaceous anurans. Heavy line — ancient continents; thin line — present-day continents; D — Discoglossidae; G — Gobiatidae; Hy — Hylidae; L — Leptodactylidae; Le — Leiopelmatidae; Pa — Palaeobatrachidae; Pe — Pelobatidae; Pi — Pipidae; Rh — Rhinophrynidae; ? — taxonomic position uncertain. Arrow in Santonian map indicates the position and direction of movement of the Indian subcontinent.

Hauterivian

D "Comanchean discoglossid" from Texas
?G "Comanchean ?gobiatid" from Texas
? "Comanchean unident. anuran" from Texas
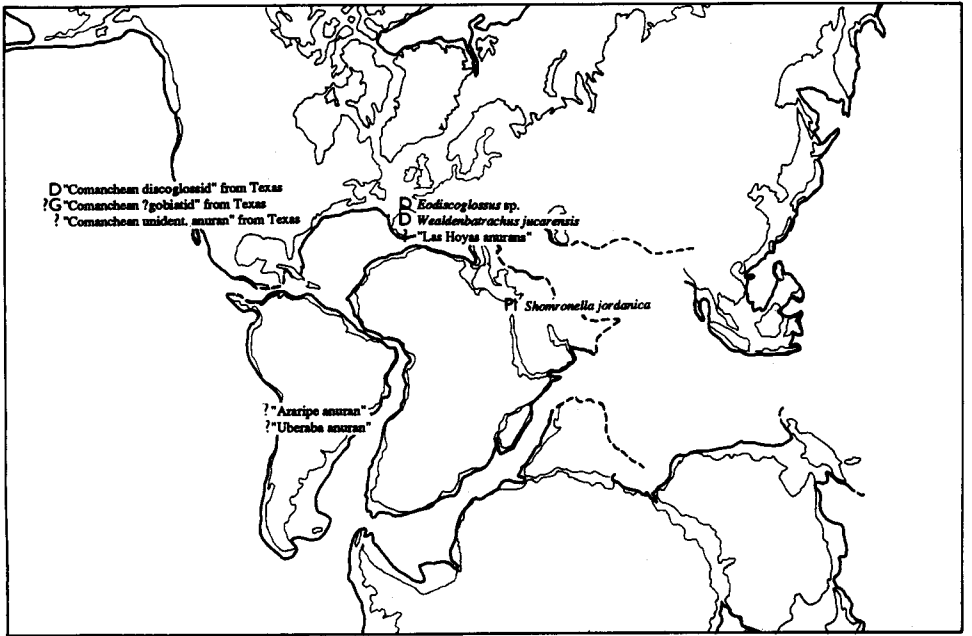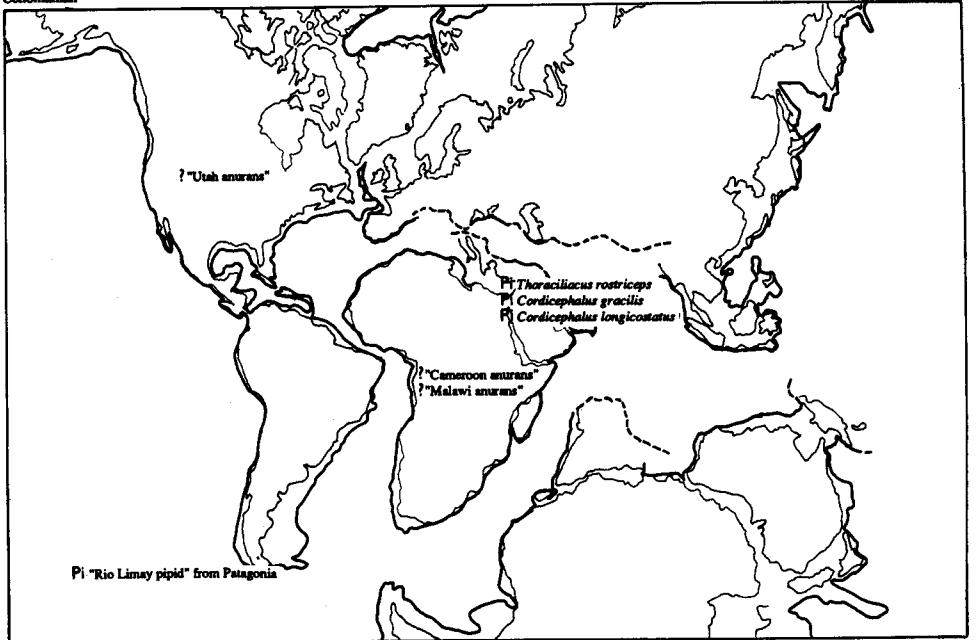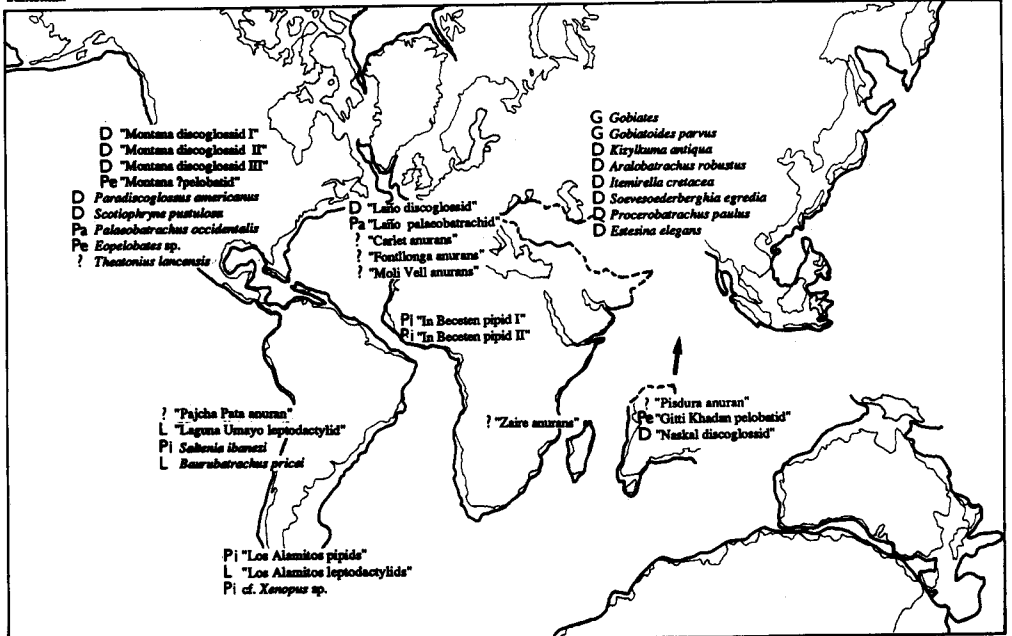
D *Eodiscoglossus* sp.
D *Wealdenbatrachus jucarensis*
"Las Hoyas anurans"

Pi *Shomronella jordanica*

? "Araripe anuran"
? "Uberaba anuran"

Cenomanian

? "Utah anurans"

Pi *Thoraciliacus rostriceps*
Pi *Cordicephalus gracilis*
Pi *Cordicephalus longicostatus*

? "Cameroon anurans"
? "Malawi anurans"

Pi "Rio Limay pipid" from Patagonia

Santonian

D "Montana discoglossid I"
D "Montana discoglossid II"
D "Montana discoglossid III"
Pe "Montana ?pelobatid"
D *Paradiscoglossus americanus*
D *Scotiophryne pustulosa*
Pa *Palaeobatrachus occidentalis*
Pe *Eopelobates* sp.
? *Theatonius lancensis*

D "Laño discoglossid"
Pa "Laño palaeobatrachid"
? "Carlet anurans"
? "Fontllonga anurans"
? "Moli Vell anurans"

G *Gobiates*
G *Gobiatoides parvus*
D *Kizylkuma antiqua*
D *Aralobatrachus robustus*
D *Itemirella cretacea*
D *Soevesoederberghia egredia*
D *Procerobatrachus paulus*
D *Estesina elegans*

Pi "In Beceten pipid I"
Pi "In Beceten pipid II"

? "Pisdura anuran"
Pe "Gitti Khadan pelobatid"
D "Naskal discoglossid"

? "Zaire anurans"

? "Pajcha Pata anuran"
L "Laguna Umayo leptodactylid"
Pi *Saltenia ibanezi*
L *Baurubatrachus pricei*

Pi "Los Alamitos pipids"
L "Los Alamitos leptodactylids"
Pi cf. *Xenopus* sp.

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