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CHAPTER 15

Tertiary Anura of Europe, Africa, Asia, North America, and Australia

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I. TERTIARY ANURA OF EUROPE

A. Introduction

Fossil anurans have been known in Europe since the end of the 16th century. This can be established from notes by Dan Herman published in 1580 and 1600, quoted by Wolterstorff (1886). In 1776, Andreae reported on a fossil anuran from Öhningen in southern Germany (middle Miocene, Astaracian, level MN7–8), which was later described by Tschudi (1839) under the name *Palaeophrynos gessneri*. The specimen (Fig. 3) is probably the earliest evidence of a fossil frog ever reported and still available for study. Another

early find of a fossil anuran also came from Öhningen; it was originally reported by Rudolf Schinz (in Lavater 1808) as a remnant of a bird (specimen illustrated by von Meyer [1845] his plate 5, figure 1). Later, on the basis of comparisons with a more complete specimen found in 1840, it was identified as an anuran, *Latonia* (von Meyer 1845). The third early discovery of a fossil frog from Öhningen was described by Agassiz in 1835 as *Bombinator oeningensis*; now it is known under the name *Pelophilus agassizi* (Tschudi 1839). Młynarski *et al.* (1982) considered it closely related to *Bombina* (see below).

Further early finds of European fossil frogs were made in Siebengebirge near Bonn (late Oligocene, level MP 30); the very first of them was published as *Rana diluviana* by Goldfuss (1831). Only later was it transferred to the genus *Palaeobatrachus*, erected by Tschudi (1839), along with other forms found in the underground oil shale mines of this region, and in the Tertiary deposits of north Bohemia (Czech Republic), published by von Meyer (1852a,b, 1857, 1860). In addition to these early finds in Germany and Bohemia, disarticulated material was found in a French site at Sansan, first mentioned by Blainville (1837). Lartet (1851) referred this material to several species assigned to *Rana*; however, since these names were accompanied by neither true descriptions nor diagnoses, most of them are considered *nomina dubia*. Part of this material belongs to *Latonia*, which was first recognized by Cope (1866).

Other early discoveries of European fossil frogs include *Rana antiqua* (Münster 1835), *Rana volhynica* (Eichwald 1835), "*Pipa*" (obviously *Latonia*) (Pomel 1844), *Rana aquensis* (Coquand 1845), later quoted by Gervais (1859) as *Rana dumerili* Barth, and a large number of other species, published in the second half of the last century by various authors (see Roček 1994a). Unfortunately, most of the specimens were either lost or destroyed. This also includes material described by Pomel (1853) as *Batrachus lemanensis*, *B. naiadum*, *B. lacustris* and many others. According to Hoffstetter (1970, pers. comm. to Špinar), Pomel's material was lost without ever being revised. On the other hand, the earliest finds mentioned above are preserved and deposited in the Paläontologisches Institut in Zürich (see below).

See table 1 for stratigraphic ranges of all European anurans.

B. Discoglossidae

In Europe, the family Discoglossidae is present throughout the entire Cenozoic. The middle Palaeocene deposits of Hainin (levels MP 1–5; Danian), Belgium, have yielded one vertebra which unquestionably belongs to a discoglossid (Groessens-Van Dyck 1981). The cylindrical opisthocoelous centrum, the long neural arch of the imbricate type which bears a relatively strong neural ridge, and the postzygapophyses which clearly project postero-laterally, point to the *Discoglossus* group. A humerus from the same locality was referred to this family by Groessens-Van Dyck (1981). However, this bone is fragmentary and its referral is questionable.

An ilium, a vertebra and a humerus from the late Palaeocene of Cernay (level MP 6), France, were referred to the Discoglossidae by Estes *et al.* (1967). However, the ilium belongs to a palaeobatrachid frog as demonstrated by the presence of a strong interiliac tubercle and the low tuber superius (Vergnaud-Grazzini and Hoffstetter 1972). The same confusion between ilia of the Discoglossidae and the Palaeobatrachidae occurred in the study of anurans from the earliest Oligocene of Belgium by Hecht and Hoffstetter (1962; see below). The vertebra is amphicoelous; it was only tentatively referred to the Discoglossidae on the basis of its resemblance to those of the earliest Oligocene of Belgium which were erroneously assigned to the family by Hecht and Hoffstetter (1962). The morphology of the vertebrae from Belgium is quite unusual; these vertebrae do not belong to the Discoglossidae. The humerus seems to be referrable to the Palaeobatrachidae (Vergnaud-Grazzini and Hoffstetter 1972) but this cannot be confirmed.

To sum up the situation in the European Palaeocene, only one vertebra is referrable to the Discoglossidae.

Indeterminate discoglossids were reported from the lower Eocene of Portugal (Antunes and Russell 1981) and Belgium (Godinot *et al.* 1978). *Opisthocoelellus weigelti* from the middle Eocene of Geiseltal was described and figured by Kuhn (1941). It should be noted that the specimen he illustrated in his plate IV, figure 2 as *Opisthocoelellus* is in fact a pelobatid, *Eopelobates* cf. *wagneri* (see below). Špinar (1976) gave the following diagnostic features of *Opisthocoelellus*: head one-third of the body length, the frontoparietal with large anterior and/or posterior fontanelle, large and strongly dentate vomers. Other characters (all on the postcranial skeleton) are diagnostic only for the family Discoglossidae. It is noteworthy that no discoglossids were found in Messel, which is approximately of the same age (lower Geiseltalian according to Franzen and Haubold [1986]). According to Vergnaud-Grazzini

Table 1. Stratigraphic ranges of European anurans (dubious taxa omitted).

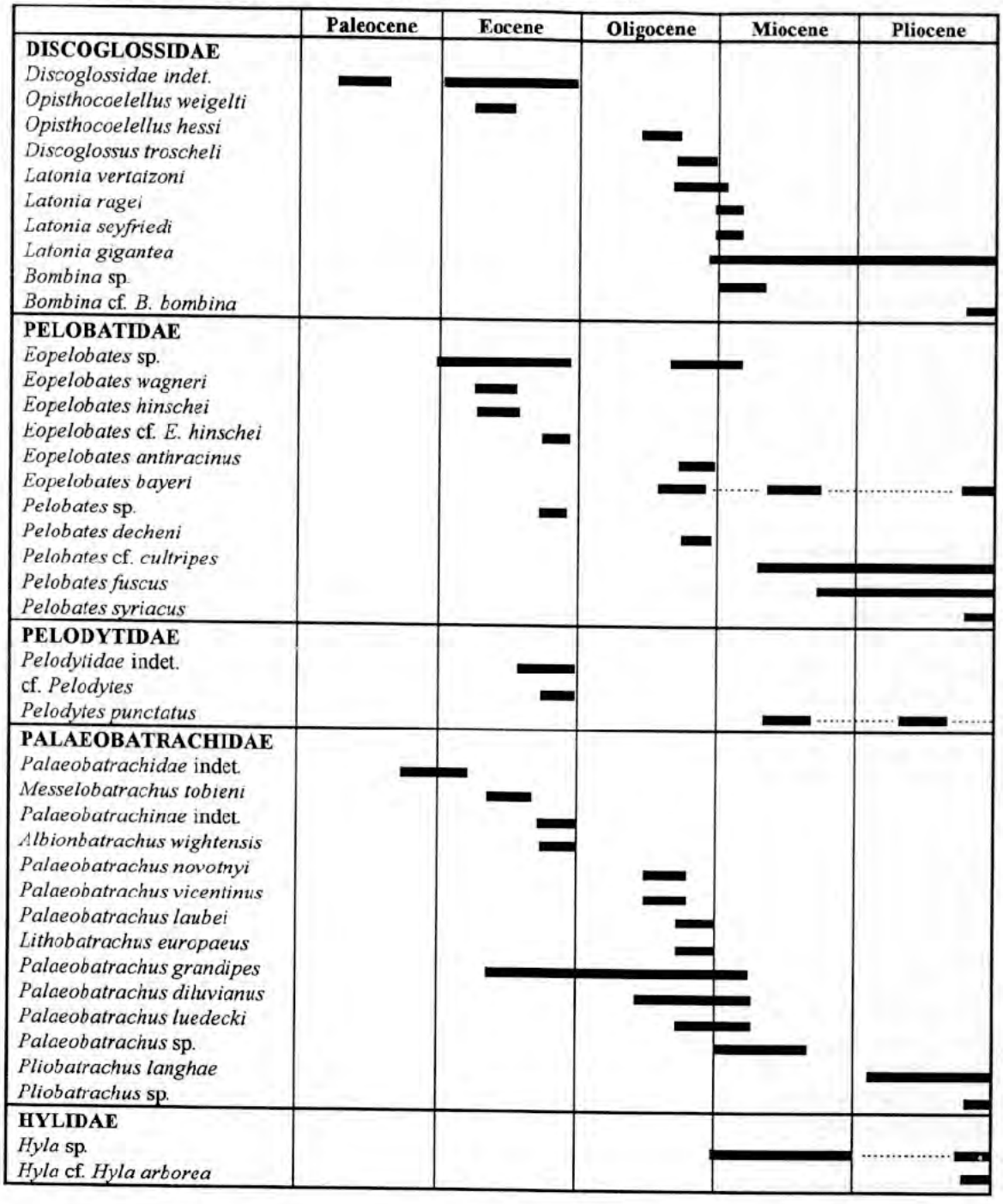

Table 1 — *continued*

	Paleocene	Eocene	Oligocene	Miocene	Pliocene
BUFONIDAE					
Bufo cf. *Bufo viridis*				———	·····
Bufo cf. *Bufo bufo*				———	·····
Bufo sp.				———	
RANIDAE					
Ranidae indet.		———			
Rana noeggerathi			———		
Rana meriani			———		
Rana pueyoi				———	
Rana straussi					———
LEPTODACTYLIAE					
Thaumastosaurus bottii		———			
ANURA INC. SEDIS					
Palaeophrynos gessneri				———	
Lutetiobatrachus gracilis		———			

and Wenz (1975), one of the Geiseltal anurans, described by Kuhn (1941) as *Rana carbicola*, is actually a discoglossid. Its taxonomic status should be restudied, but, as is the case for other Geiseltal material, it is not available at present.

A single discoglossid vertebra was recovered from the middle Eocene of England (Milner 1986). The family Discoglossidae (without closer determination) was reported from the upper Eocene of the Isle of Wight (England) by Rage and Ford (1980) on the basis of opisthocoelous vertebrae. Small (based on jaws, opisthocoelous vertebrae and ilia with prominent iliac crests) and large (heavily sculptured dermal skull roof, opisthocoelous vertebrae and characteristic ilia) discoglossids were found in the upper Eocene (Ludian) of Hordle Cliff (Hampshire, England). According to Milner *et al.* (1982), the latter appears to be distinct from *Latonia* and *Opisthocoelellus*.

Another discoglossid, the earliest evidence of which is from the middle Oligocene of France, is *Latonia*, originally published under the name *Discoglossus* cf. *giganteus* (de Bonis *et al.* 1973; Rage 1984a). A similar taxonomic history holds for the upper Oligocene findings of *Latonia* from France (Crochet 1971). The earliest complete skeleton was described as *Prodiscoglossus vertaizoni* by Friant (1944); however, because it expresses important diagnostic characters of *Latonia*, specifically that it bears two coronoid processes on the prearticular and that the tibiale and fibulare are different in size and not fused, it was transferred to the genus *Latonia* as *L. vertaizoni* by Roček (1994b). It is smaller than other species of *Latonia* and its maxilla was not covered by secondary sculpture.

In addition to *Latonia vertaizoni*, found only in France and, possibly, in Gussenstadt, Germany (see Roček 1994b), there was another, more subtle discoglossid in the late Oligocene of Europe. This is *Discoglossus troscheli* (Figs 1, 2) (von Meyer 1860), which was originally described as a ranid (see below) but later transferred to *Alytes* by Cope (1865) and finally to *Discoglossus* by Boulenger (1891). It is based on only three specimens, all found in the upper Oligocene (level MP 30; Mörs 1995) deposits of Rott near Bonn. Its assignment to the living genus *Discoglossus* should be re-evaluated.

Still another discoglossid of middle to upper Oligocene age (Gaudant 1995, pers. comm.) was found in Bechlejovice, Czech Republic, and was described by Špinar (1976) as *Opithocoelellus hessi*. Later, Špinar (1983) referred to this taxon as *Eodiscoglossus hessi*. It should be noted that this taxon is based on a single specimen (Fig. 3), found after many years of excavations which yielded several hundred palaeobatrachids and pelobatids. Its snout-vent length was only about 40 mm, the skull comprises 1/3 of this distance; the dermal bones of the skull roof are smooth, except for several small tubercles on the

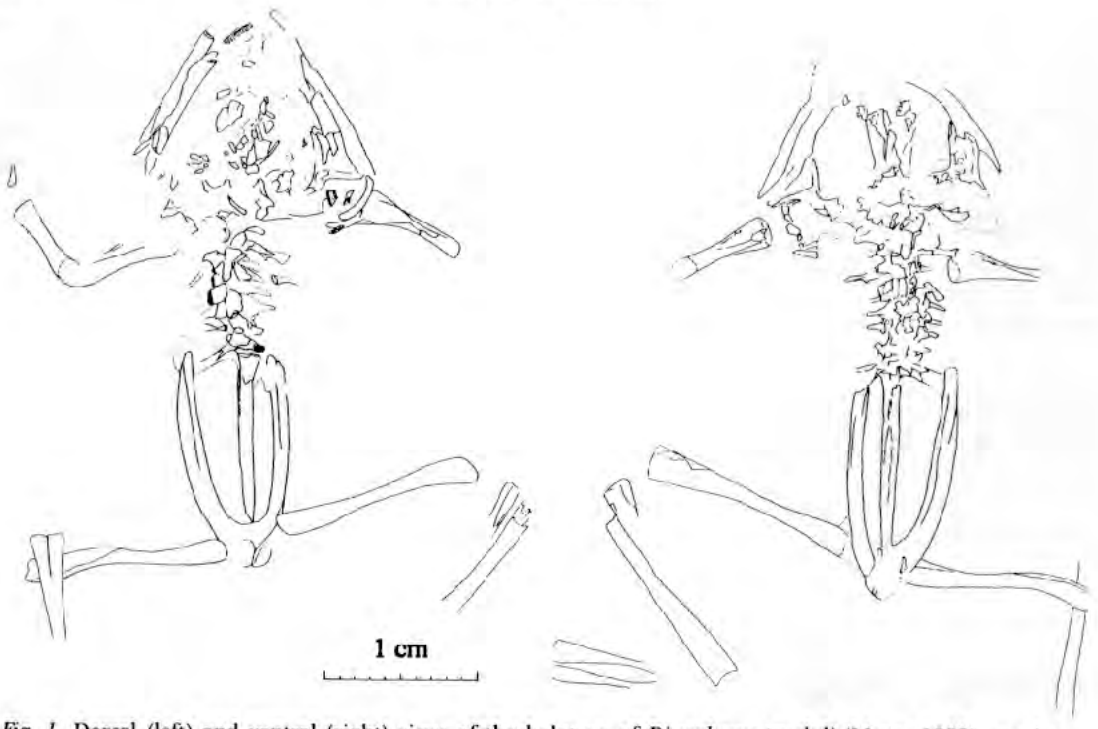

Fig. 1. Dorsal (left) and ventral (right) views of the holotype of *Discoglossus troscheli* (Meyer 1852), specimen Ro 4056, Institut für Paläontologie der Universität, Bonn, Germany.

frontoparietals; the latter bones were separated by a median suture and by a large rhomboid fontanelle anteriorly. A small foramen situated within this suture could be the pineal foramen. Other characters agree with those of the family as a whole. Although the general proportions of the head and body are similar to those of *Discoglossus troscheli*, this species differs in the shape of the transverse processes of the urostyle and in the humerus/tibiofibula ratio (0.82% in *O. hessi*, 0.87% in *D. troscheli*). The shape of the head cannot be compared because it is disarticulated in all specimens of *D. troscheli*. Hence, it is possible that *Opisthocoelellus hessi* and *Discoglossus troscheli* are conspecific.

Fig. 2. Dorsal view of a specimen of *Discoglossus troscheli* Meyer 1852, specimen Ro 4068, Institut für Paläontologie der Universität, Bonn, Germany.

Latonia vertaizoni, which was comparatively small and characterized by a smooth maxilla, was confined mainly to the late Oligocene and is present in only three French localities: Vertaizon (upper Oligocene), Coderet (uppermost Oligocene, level MP 30), and 'St. Gérand le Puy' (lowermost Miocene, levels MN 1 and MN 2). It was progressively replaced from the uppermost Oligocene to the middle Miocene by larger and more completely ossified species: *L. ragei*, *L. gigantea* and *L. seyfriedi*. *Latonia ragei*, described by Hossini (1993) from the lower Miocene (level MN 2b) of Laugnac (Lot-et-Garonne), France is characterized by its large size and smooth maxilla. It was described on the basis of disarticulated elements only. Recent findings from Germany (Hambach, late Orleanian or early Astaracian) (Mörs 1995, pers. comm.) and the Czech Republic (Merkur, early Miocene-Eggenburgian) (Hrazdíra 1995, pers. comm.) suggest that it was more widely distributed than had been supposed.

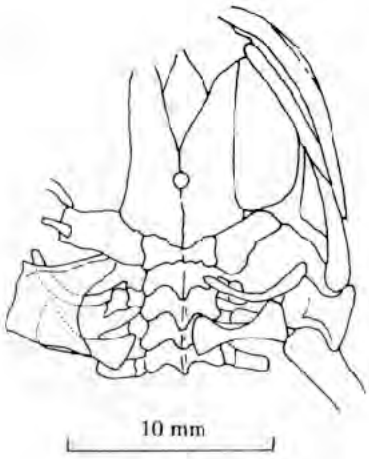

Fig. 3. Dorsal view of the skull and anterior part of the vertebral column, including some elements of the pectoral girdle of the holotype of *Opisthocoelellus hessi* Špinar 1976, National Museum Prague (Špinar's collection No. 2549a). Redrawn from Špinar (1976).

Younger than *Latonia ragei* was *Latonia gigantea*, originally described as *Rana gigantea* by Lartet (1851), and later published under various other names. It was attributed either to the Pelobatidae because of the sculpturing of the maxilla and frontoparietal, or to the Discoglossidae because of features of the postcranial skeleton, or to the Ranidae simply because of its size (e.g., *Pelobates robustus* Bolkay, *Rana batthyanyi* Bolkay, *Discoglossus giganteus* Wettstein-Westersheimb, *Miopelobates robustus* [Bolkay]). Adults were of medium to large size. The main diagnostic character is the secondary sculpturing on the posterior part of the maxilla and the frontoparietal. The sculpturing on the maxilla appeared in advanced postmetamorphic stages (Roček 1994b), whereas in early postmetamorphic stages the bone was smooth. The frontoparietal was covered with only indistinct pit-like sculpturing in young individuals. In large adults the sculpturing was of a dense tubercular nature. *Latonia gigantea* was widely distributed in Europe from the early Miocene to the late Pliocene, i.e., from the Orleanian, level MN 4, of Dolnice, Czech Republic, (sometimes cited as "*Miopelobates fejfari*" [Špinar 1975; Hodrová 1987]), through the Ruscinian, level MN 15, of Ivanovce, Slovakia (referred to as *Latonia "kolebabi"* [Špinar 1978]), and of Osztramos, level 1 E, Hungary (Venczel 1997). One of the last occurrences is from the Villanyian (level MN 16) of Arondelli, Italy, cited as *Discoglossus* cf. *D. giganteus* by Vergnaud-Grazzini (1970). An even later occurrence was suggested from the early Biharian (earliest middle Pleistocene) of Betfia 2/1–4 (formerly Püspökfürdö) in Romania, in which "*Pelobates robustus*" (Fejérváry 1917) was regarded as *Latonia* (Roček 1994b); in fact, this species belongs to the extant *Pelobates fuscus* (Venczel 1997).

With the exception of the holotype of *Latonia vertaizoni*, which is an articulated skeleton, other species of *Latonia* were based on dissociated bones. However, there is still another species of *Latonia* that was based on articulated skeletons. This is *Latonia seyfriedi*, the type species of the genus, published as early as 1843 (von Meyer 1843) and later described in full (von Meyer 1845). Five skeletons were found in the middle Miocene (Astaracian, MN 7–8) of Öhningen, Germany, including one that was originally interpreted as a remnant of a bird (von Meyer 1845). Unfortunately, all these skeletons are preserved in ventral aspect so that it cannot be decided whether the maxilla or the frontoparietal were smooth or sculptured. This is important because all other aspects of these skeletons agree with corresponding elements of *L. ragei* and *L. gigantea*. If it could be demonstrated that *L. seyfriedi* possesses or lacks ornamentation (at least on the maxilla), then either *L. ragei* or *L. gigantea* might be synonymous with *L. seyfriedi*.

Besides the material that is attributable to one of the above species of *Latonia*, there are many isolated bones found in various Neogene sites, especially parts of the postcranial skeleton that bear no diagnostic characters of the species; these remains can be only referred to as *Latonia* sp. For example, this is the case for the urostyle on which Depéret (1890) established "*Diplopelturus ruscinensis*" now considered a synonym of *Latonia* (Roček 1994b).

During the Neogene, *Latonia* was widely distributed and common in Europe. It was even suggested that *Latonia* reached northern Africa during the middle Miocene (Astaracian, level MN 7). This opinion rests on the description of a discoglossid from Beni Mellal (Morroco) by Vergnaud-Grazzini (1966). Subsequently, Sanchíz and Alcover (1984) and Roček (1994b) suggested that this discoglossid could be *Latonia*. In fact, this Moroccan fossil cannot be referred to *Latonia* (see section II of this chapter).

Latonia disappeared abruptly in the late Pliocene. The last occurrences of *Latonia* sp. are from the Ruscinian (level MN 15) of Serrat d'en Vacquer (= Perpignan) and Sète, France (Depéret 1890; Bailon 1991), Ivanovce, Slovakia (Špinar 1978), Osztrámos, level 1E, Hungary (Venczel 1997), the Villanyian of Arondelli, Italy (Vergnaud-Grazzini 1970), and the late Pliocene of Kaltensundheim/Rhön, Germany (Böhme 1989). In contrast, *Latonia* is absent in the earliest Pleistocene (lower Villafranchian) of Hajnáčka and Villanyian (MN 17) of Včeláre, Slovakia (Hodrová 1981, 1985) and from the early Biharian of Betfia, Romania (Venczel 1997).

Apparently, there was an abrupt disappearance of *Latonia* after MN 15; it was survived by *Discoglossus* and *Bombina*. Both genera can be derived from immature forms of *Latonia*. This can be judged from developmental series of cranial bones found in Miocene localities where there are large samples of adult *Latonia* and rare juvenile specimens that cannot be distinguished from the living genus *Discoglossus*. In the postcranial skeleton, no differences other than size can be found between *Latonia* and *Discoglossus*. Therefore, it was suggested by Roček (1994b) that the Neogene material of *Discoglossus* may, in fact, be juvenile *Latonia*, and that the *Discoglossus* that survived the Pleistocene glaciation may be a paedomorphic *Latonia*. According to recent investigations by Smirnov (1989), a similar evolutionary mechanism could lead to the origin of the living genus *Bombina*, which is structurally an underdeveloped *Discoglossus*. One may suppose that both of these extant genera evolved from *Latonia* by means of paedomorphosis, the main impetus of which was probably the continuous drop of annual mean temperatures that began in the late Oligocene and continued through the Plio-Pleistocene. That *Discoglossus* is not very old seems to be confirmed by discoveries by Lanza *et al.* (1986) that suggest continuing extensive evolutionary differentiation within the genus. If this were true, disarticulated bones from the Oligocene and Neogene described as *Discoglossus* and *Bombina* belong either to juvenile *Latonia* or to other discoglossids.

Whether postcranial elements recovered from the Miocene deposits of Germany and Poland (see below) were correctly assigned to *Bombina* may be decided only on the basis of cranial elements that bear diagnostic sculpturing.

It should be noted that Estes and Darevsky (1977) mentioned an incomplete opisthocoelous atlas found in the late Miocene (middle Sarmatian) from the northern Caucasus (valley of the Belaya River, Maikop District). Its centrum was flattened, with a prominent anteroposterior keel and anterior articular cotyles well separated at the midline. It is apparent that the vertebra may be attributed either to young *Latonia* or to *Discoglossus*; the latter was suggested by both authors. Similarly, one humerus recovered from the lower Pleistocene or upper Pliocene deposits of eastern Crete was assigned to *Discoglossus* sp. (Kotsakis 1982).

Bombina, a living genus, was first reported by Sanchíz and Schleich (1986) from the early Miocene (levels MN 2 and MN 3; late Agenian and early Orleanian) of Strubersheim 3 and Weissenburg 6, southern Germany on the basis of ilia and humeri. An incomplete ilium of *Bombina* sp. was reported, together with *Latonia*, by Młynarski *et al.* (1982) from the middle Miocene (MN 7) of Opole, Poland (see also Młynarskiv 1984). However, it is necessary that this determination be confirmed by discovery of cranial bones (see above). It was also suggested that the poorly preserved *Pelophilus agassizi* (Tschudi 1839) from the middle Miocene (MN 7–8) of Öhningen, described first as "*Bombinator oeningensis*" by Agassiz (1835), could belong to the genus *Bombina* (Vergnaud-Grazzini and Wenz 1975; Sanchíz and Młynarski 1979; Młynarski *et al.* 1982). That these genera are synonymous may be evidenced by the ilium which is the only element in the *Pelophilus* specimen that is of some diagnostic value, and the ratio between the humerus and tibiofibula (this is similar to living *Bombina*). The cranial and axial skeletons of *Pelophilus* are only indistinctly imprinted in the matrix (von Meyer 1845).

It may be noted that fossils close to the living *B. bombina* were present in the Pliocene of Central Europe: *B.* cf. *B. bombina* (*B. bombina* according to Sanchíz and Młynarski 1979)

from Poland (Sanchíz and Schleich 1986), from the latest Pliocene (Csarnotan) of Ivanovce, Slovakia (Hodrová 1981), and from the Ruscinian (level MN 15) of Osztrámos 1C (Venczel 1997). *Bombina* continued to the Pleistocene, as evidenced by findings from the Villanyian (MN 17) of Včeláre, Slovakia (Hodrová 1985).

Stromer (1940) referred three fragmentary humeri from the Miocene near Aumeister, Germany, to the genus *Alytes*, although with doubts. The main distinguishing character of this material was apparently the absence of the fossa cubitalis ventralis. This identification cannot be confirmed. In his plate III, figure 11 of the same paper, he misidentified the humerus of a bat as belonging to a palaeobatrachid. Hence, *Alytes* seems to be still unknown in the Cenozoic. *Ranomorphus similis*, from the late Pliocene of the Korotoyak locality in Russia, was founded by Ratnikov (1993a) on the basis of a single ilium, and assigned to the Discoglossidae. The ilium is apparently referrable to the genus *Rana*.

C. Pelobatidae

The earliest fossil record of this family in Europe is from the Eocene, when it is represented by the genus *Eopelobates*. It differs from *Pelobates* in that the frontoparietal complex does not contact the squamosal, the pars lateralis of the nasal is long and slender and bears neither the processes parachoanalis nor the processes paraorbitalis, and its margin between the processes anterior and pars lateralis is almost straight. The sternum is well ossified, the femur is shorter than the tibiofibula, the tibiale and fibulare are not fused, and the spade is absent (Špinar and Roček 1984). The first record (reported as *Eopelobates* sp.) is from the lower Eocene of Portugal (Antunes and Russell 1981).

Several fossils were described as pelobatids from the middle Eocene of Geiseltal (Germany) by Kuhn (1941), namely *Palaeopelobates geiseltalensis, Archaeopelobates efremovi, Archaeopelobates eusculptus, Amphignathodontoides eocenicus, Hallaeobatrachus hinschei*, and *Pelobatinopsis broili*. Although some of these forms turned out to be *Eopelobates* (Estes 1970) and even *Palaeobatrachus* (Špinar 1972), pelobatids were no doubt present in Geiseltal.

The middle Eocene (MP 11) pelobatids from Messel (Germany) are represented by *Eopelobates wagneri* (Weitzel 1938) (Fig. 4), originally described as *Propelodytes* (Wuttke 1988a). The holotype is of poor quality (now covered by pyrite decay, with some bones lost). This is why Wuttke (1988a) designated other specimens as paratypes. It is the largest representative of *Eopelobates* (see Wuttke [1988b]); some individuals reached a snout-vent length of about 75 mm, with the femur about 40 mm long. Its principal diagnostic characters are that the frontoparietal complex is broad in its interorbital part but becomes narrower in its otic section, it is paired anteriorly with the two parts widely separated by a median indentation that continues posteriorly as a short median suture, and it is covered by robust pit-like sculpture posteriorly but nearly smooth anteriorly. The nasals are widely separated and smooth. The sphenethmoid is exposed even in large (adult) individuals and its dorsal surface is smooth. The maxilla is smooth and the parasphenoid has a median keel on its ventral surface.

Eopelobates hinschei from Geiseltal was originally described as *Hallaeobatrachus* by Kuhn (1941) but was transferred to *Eopelobates* by Estes (1970). This species is conventionally regarded as valid but may be synonymous with *E. wagneri*. Pelobatids (determined on the basis of procoelous vertebrae with imbricate neural arches) were reported by Rage and Ford (1980) from the upper Eocene of Isle of Wight, England, and tentatively assigned to *Eopelobates* because of the pitted ornamentation of the maxillaries.

Eopelobates cf. *hinschei* was cited among the upper Eocene anurans of England by Milner (1986). Milner *et al.* (1982) found a pelobatid represented by a few cranial elements and several vertebrae and ilia in the Ludian of Hordle Cliff (Hampshire, England). The shape of the squamosal most closely resembles that of *Eopelobates hinschei* from Geiseltal. Further finds of *Eopelobates* are from the late Eocene of Quercy, France (Crochet *et al.* 1981)

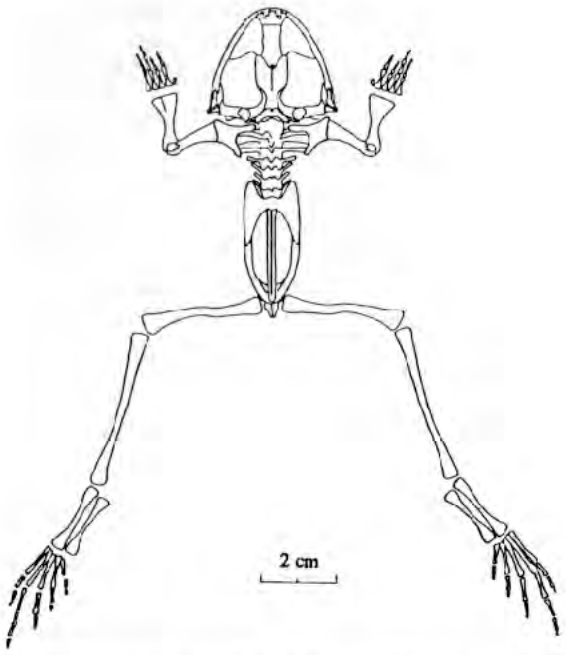

Fig. 4. Reconstruction of the skeleton of *Eopelobates wagneri* (Weitzel 1938) in dorsal view. Redrawn from Wuttke (1988a).

Eopelobates continued into the Oligocene, as evidenced by *Eopelobates bayeri* (Fig. 5) described by Špinar (1952) from the late Oligocene (Gaudant 1995, pers. comm.) of Bechlejovice, Czech Republic. It is smaller than *E. wagneri*, its frontoparietal is convex and broader in the middle than at the ends, and the medial margin of it pars facialis premaxillae is convex. The anterior margin of the sternum is simply convex and the sacral vertebra is fused with the urostyle. A large number of tadpoles is known from the same locality; development of the skeleton was described by Špinar (1963, 1972). The lower Oligocene pelobatid tadpoles from Sieblos, Germany, were attributed to *Eopelobates* sp. by Gaudant (1985); he based this assignment on impressions of dermal bones, the sculpture of which was more similar to *Eopelobates* than to *Pelobates decheni*. *Eopelobates neudorfensis*, published by Wettstein-Westersheimb (1955) from the middle Miocene (Astaracian, MN6) of Devínska Nová Ves (Slovakia) is a synonym of *E. bayeri*. It occurred in central Europe into the late Pliocene, as suggested by the material from Ivanovce (Hodrová 1981) as *Eopelobates* cf. *bayeri* and the unpublished findings of K. A. Tatarinov (ex Chkhikvadze 1981, 1984) described as *E.* cf. *bayeri* (*"bajeri"*) from the upper Pliocene site of Gorishnaya Vygnanka (western Ukraine).

Another pelobatid, *Eopelobates anthracinus*, was described by Parker (1929) from the upper Oligocene (MP 30) (Mörs 1995) of the Orsberg locality near Bonn, Germany (Fig. 6). The holotype (and one of two known specimens) consists of dorsal and ventral impressions. It differs from other species of *Eopelobates* in its small size. The sternum is distinctive in tapering posteriorly and in its medial convexities being larger than the more lateral ones. The medial margin of the pars facialis premaxillae is straight and bears no

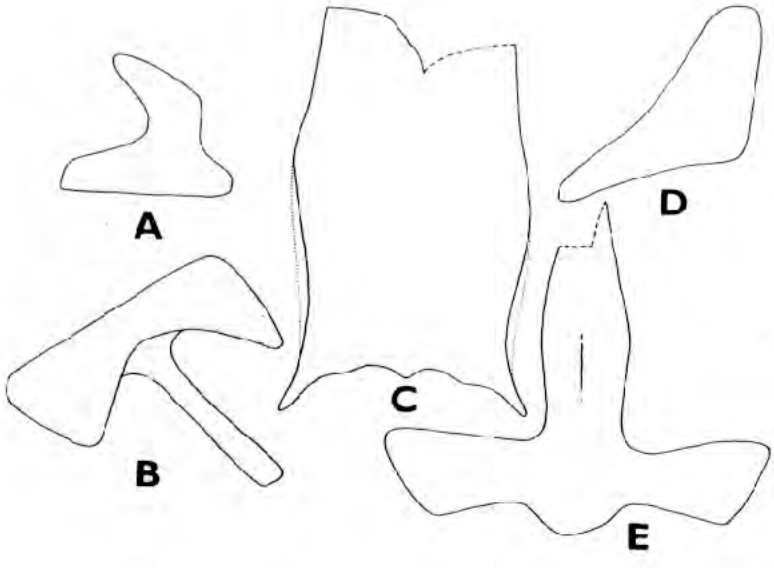

Fig. 5. Eopelobates bayeri Špinar 1952. Outlines of imprints of the premaxilla (A), squamosal (B), frontoparietal with the outline of the facies ventralis as a dotted line (C), nasal (D), and parasphenoid (E). Original specimens are deposited in the National Museum, Prague. Redrawn from Roček (1981).

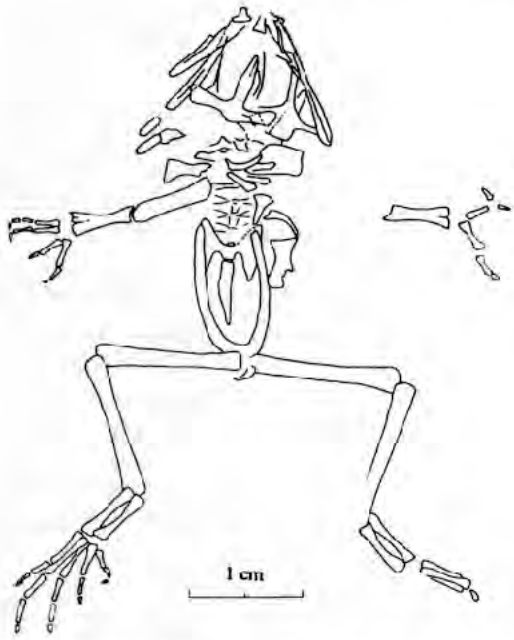

Fig. 6. Ventral view of the holotype of *Eopelobates anthracinus* Parker 1929, specimen Ro 4029, Institut für Paläontologie der Universität, Bonn, Germany. Redrawn from Špinar and Roček (1984).

convexity. The prearticular and maxilla are very slender. The sacral vertebra is not fused with the urostyle (Špinar and Roček 1984). Some features suggest that the specimen was not yet fully grown (Špinar and Roček 1984; Estes 1970; Zweifel 1956) but might be a juvenile individual of *Eopelobates bayeri*. However, another specimen from the same locality was recently found in the palaeontological collections of the University of Tübingen (Roček 1995) that is undoubtedly an adult. This specimen bears the diagnostic features of the type and therefore it can be demonstrated that *E. anthracinus* and *E. bayeri* are separate species.

Eopelobates is also known from the late Oligocene of central Europe (Böhme *et al.* 1982; Špinar 1972), lower Miocene (Vieux Collonges) of France (Hossini 1992), and from the Pliocene of Poland (Sanchíz and Młynarski 1979; Młynarski and Szyndlar 1989).

Contemporary with *Eopelobates, Pelobates* also occurred in the Oligocene of Europe, represented by *Pelobates decheni* based on a single specimen (Troschel 1861) from the uppermost Oligocene (MP 30) of Rott, Germany (Fig. 7). Recently, another articulated skeleton, differentiated from the holotype only by the width of the postorbital bridge, was recovered from the upper Oligocene (MP 28) deposits of the Enspel locality (between Mainz and Koblenz, Germany) by Michael Wuttke (in press). Tadpoles from the same locality and horizon, displaying pelobatid features and thus assigned to this species, reached a length of nearly 20 cm. Böhme *et al.* (1982) demonstrated that *Zaphrissa eurypelis*, from the same locality and horizon (Cope 1866), belongs to the same taxon, and therefore is a synonym of *P. decheni*. This species is distinguished by its broad postorbital bridge, the robust and sculptured quadratojugal, the pit-like sculpture, a distinct border between the quadrate and quadratojugal, free ribs, and the distinctly separate distal parts of the radioulnae in subadults, which fuse in the adults. Böhme *et al.* (1982) suggested that "*Pelobates cultripes*" from the Oligocene of Belgium (Hecht and Hoffstetter 1962), as well as the very similar *Pelobates* from the lower Oligocene (Tongrian), also from Belgium, might be referable to *P. decheni*. However, it should be noted that the material from Belgium (Hoeleden and Hoogbutsel; early Oligocene, level MP 21) that was referred to as *Pelobates cultripes* corresponds to the latter species only in its size; its precise determination should be based on a more detailed investigation.

The living species *Pelobates cultripes* may be known from the middle Miocene (cf. *P. cultripes*) to the upper Pleistocene of France (Bailon *et al.* 1988; Bailon 1991).

The extant *Pelobates syriacus* and *P.* cf. *syriacus* are known from the Pliocene of Poland (Młynarski and Szyndlar 1989).

Pelobatids from the upper Miocene and Pliocene deposits of the northern coastal region of the Black Sea recall *Pelobates fuscus*; similar material is known from Pliocene-Pleistocene localities in the Ukraine, Crimea, and in Bashkiria (Chkikvadze 1984 and references therein), as well as from the middle Pliocene of France (Bailon *et al.* 1988; Bailon 1991) and the upper Pliocene of Moldavia (Khosatzky 1985) and Poland (Młynarski *et al.* 1984; Młynarski and Szyndlar 1989).

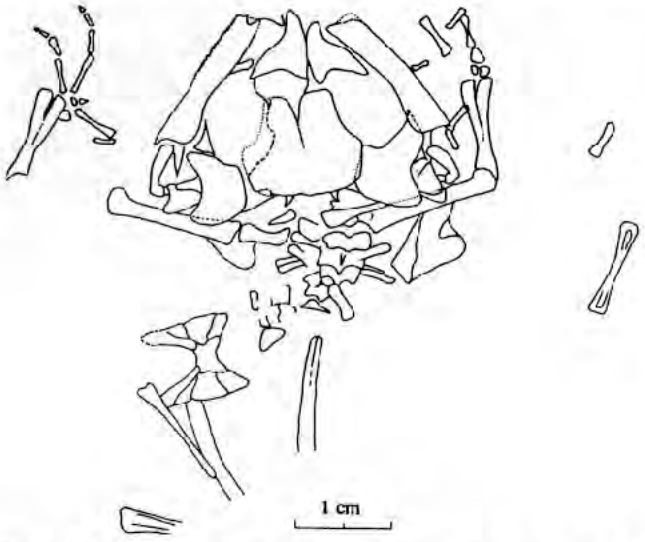

Fig. 7. Holotype of *Pelobates decheni* Troschel 1861, specimen Ro 4031, Institut für Paläontologie der Universität, Bonn, Germany. Redrawn from Böhme *et al.* (1982).

Pelobates sp. or *P.* cf. *fuscus* was recovered from the middle Sarmatian of the Gritsev locality, Ukrainia (Lungu *et al.* 1989; Zerova 1985), from the latest Pliocene of Ivanovce, Slovakia (Hodrová 1981) and Arondelli, Italy (Vergnaud-Grazzini 1970), and from late Pliocene to Holocene localities of Sinyakovo, Chortkova, Odessa, and Lvov, all in the Ukraine (see Chkhikvadze 1984 and references therein). *Pelobates* sp. was also reported on the basis of a fragmentary frontoparietal, maxilla, pterygoid, vertebra and urostyle, from the upper Pliocene locality of Korotoyak (Don River Basin) by Ratnikov (1990). Ratnikov reported on a small fragment of an ilium from the same locality that he assigned to *Eopelobates* sp.

Tatarinov (1970) erected a new genus and species, *Archipelobates giganteus*, for a late Pliocene anuran from the Gorishnaya Vygnanka locality (Ukraine). Since this new form was neither formally described nor type material stated, the name should be considered a *nomen nudum* (Chkhikvadze 1984). This taxon was considered a synonym of *Latonia* by Roček (1994b). *Pelobates praefuscus* (Khosatzky 1985) from the upper Pliocene of Moldavia does not differ in published diagnostic characters from those of *P. fuscus*. *Protopelobates gracilis* (Bieber 1880) is synonymous with *Palaeobatrachus* (Špinar 1972).

D. Pelodytidae

A new locality, Saint-Maximin, France, that appears to be late middle Eocene in age (?MP 13), has yielded a possible Pelodytidae (Rémy *et al.*, in progress). Unfortunately, this identification rests on a single fragmentary ilium. If this identification is correct, this fossil is the oldest pelodytid frog known.

Pelodytidae, close to the living *Pelodytes*, is present in the late Eocene of France from the standard levels MP 16 to MP 19 (Crochet *et al.* 1981; Rage 1984a, 1988).

Representatives of the family are absent in the Oligocene fossil record. It re-appears in the early Miocene (MN 1 or MN 2; Agenian) (Hossini 1992). Sanchíz (1978) described *Pelodytes arevacus* from the middle Miocene (MN 7+8; Astaracian) of Spain. He considered this species similar to the living *P. punctatus* based on the absence of fusion between the atlas and the second vertebra, the morphology of the anterior border of the scapula, the ventral face of the urostyle, and the middle part of the tibio-fibula. However, Hossini (1992) showed that in most *P. punctatus* the atlas and the second vertebra are not fused; therefore this character is not diagnostic. Moreover, the other differences result only from the difference in size (that is, age-dependent) between the fossil bones and the specimens used for comparisons (Böttcher 1994). Hence, *P. arevacus* is probably a synonym of the living *P. punctatus* but whatever the precise status of this Miocene *Pelodytes* may be, the fossil is closely related to the living species. The *P. punctatus* lineage was already in existence during the Miocene as were other extant amphibian lineages (Bailon *et al.* 1988). A fossil close to *P. punctatus* (*P.* cf. *punctatus*) has been found in the middle Pliocene (MN 15) of Sète, France (Bailon 1991).

E. Palaeobatrachidae

The Palaeobatrachidae is the only adequately known family of anurans to become extinct within the duration of the order. An indeterminate small palaeobatrachid from the late Palaeocene of Cernay, France, may be the earliest Tertiary record of the family in Europe (Vergnaud-Grazzini and Hoffstetter 1972). Indeterminate palaeobatrachids were reported also from the lower Eocene of Belgium (Godinot *et al.* 1978).

According to Špinar (1972), *Quinquevertebron germanicum* Kuhn, 1941 and *Pelobatinopsis hinschei* Kuhn, 1941 from the middle Eocene of Geiseltal (Germany) are synonyms of *Palaeobatrachus grandipes* (Giebel 1851). *Messelobatrachus tobieni* from the middle Eocene of Messel (Fig. 8) is most probably a palaeobatrachid (Wuttke 1988a,b). It has a broad skull, with the frontoparietal almost reaching the frontal processes of the premaxillae. The posterior tip of the maxilla reaches to about the posterior level of the orbit. There are eight presacral vertebrae, with the first two, and vertebrae 7–9 nearly fused with one another, the sacral diapophyses are slightly dilated and consist exclusively of those of the ninth vertebra. The transverse processes of fused vertebrae seven and eight are reduced or absent. The femur and tibiofibula are about the same length.

Palaeobatrachids, most probably belonging to the subfamily Palaeobatrachinae (as suggested by a characteristic frontoparietal), were reported by Rage and Ford (1980) from the upper Eocene of the Isle of Wight (England). Meszoely *et al.* (1984) described the species as *Albionbatrachus wightensis*. Milner *et al.* (1982) mentioned a single frontoparietal from the upper Eocene (Ludian) of Hordle Cliff (Hampshire, England) that can be assigned to the Palaeobatrachidae on the basis of the frontoparietal incrassation. The bone is thick and striated, and resembles that described by Rage and Ford (1980) from contemporaneous beds on the Isle of Wight.

In the Oligocene, the palaeobatrachids were dominant both in number of individuals and in number of species at some central European sites. The early Oligocene palaeobatrachids are known from Sieblos, Germany (*P. grandipes*) (Gaudant 1985) and Hoogbutsel and Hoedelen, Belgium (Vergnaud-Grazzini and Hoffstetter 1972). The palaeobatrachids occurred in the earliest Oligocene of Belgium, but Hecht and Hoffstetter (1962) did not recognize the family Palaeobatrachidae as valid (see below: Bufonidae); because the ilia of the Palaeobatrachidae show an interiliac tubercle similar to that of the discoglossid *Barbourula*, they confused them with the Discoglossidae. Palaeobatrachids are especially well represented in the upper Oligocene of Rott, Orsberg, and Stösschen, all in Siebengebirge near Bonn, Germany, and Bechlejovice, Czech Republic. Špinar (1972) revised the genus *Palaeobatrachus*, and among many species described under various names since the beginning of the last century, he recognized as valid the following: *Palaeobatrachus diluvianus* (Goldfuss 1831), originally described from the Orsberg locality but recovered also in Soulce (Oligocene, Switzerland) (Gaudant 1979), Seifhennersdorf (late Oligocene) (Gaudant 1995, pers. comm.) in Germany, and Bechlejovice, Markvartice, Veselíčko, and some other middle Oligocene through lower Miocene localities in the Czech Republic. *Palaeobatrachus luedecki* Wolterstorff 1886 is based on a specimen found in the lower Miocene of Markvartice (formerly

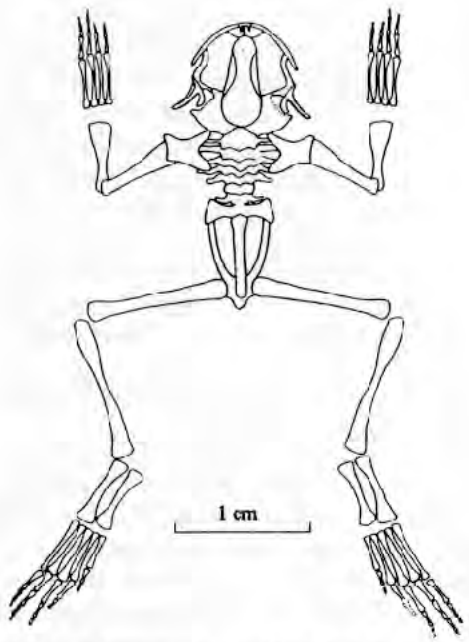

Fig. 8. Reconstruction of the skeleton of *Messelobatrachus tobieni* Wuttke, in press, in dorsal view. Redrawn from Wuttke (1988a).

Markersdorf), Czech Republic. It was also collected from the late Oligocene of Bechlejovice and Košťálov (? lower Miocene), both in the Czech Republic. *Palaeobatrachus rostae* Špinar 1972 was described from Bechlejovice. *Palaeobatrachus grandipes* (Giebel 1851) is the commonest palaeobatrachid present in the middle Eocene of Geiseltal (described as *Quinquevertebron* and *Pelobatinopsis* by Kuhn 1941) through the Oligocene (Orsberg, Bechlejovice) to the lower Miocene (Suletice, Odeř, Hájek; all Czech Republic). It was originally described as *P. goldfussi* (the latter species is a synonym of *P. diluvianus*). It reached a considerable size; Špinar (1972) considered *P. gigas* from Rott near Bonn conspecific with *P. grandipes*. *Palaeobatrachus novotnyi* Špinar 1972 was described from Bechlejovice. *Palaeobatrachus laubei* (Bieber 1880) is known only from Suletice (formerly Sulloditz; middle or late Oligocene) near Litoměřice, Czech Republic. In spite of Špinar's revision, some later authors (e.g., Schleich 1988) still used Wolterstorff's (1886, 1887) original synonyms. The morphology of shoulder girdle elements in some of these species was described by Maňourová (1976).

Lithobatrachus europaeus (Noble 1928) is another Oligocene palaeobatrachid; it was doubtfully referred to as *Rana meriani* by Lydekker (1890), then assigned to *Hyla* as *H. europaea* by Noble (1928), and later described by Parker (1929) as *Lithobatrachus*. As von Koenigswald *et al.* (1992) suggested, it might be a palaeobatrachid. It comes from the uppermost Oligocene (MP 30) of the Rott locality near Bonn, Germany. Its principal characters are: skull longer than the vertebral column, arciferous pectoral girdle, sacral diapophyses dilated, urostyle connected with the sacral vertebra by two condyles, teeth in upper jaw, femur longer than tibiofibula, tibiale and fibulare free, scapula nearly as long as coracoid, five to six procoelous presacral vertebrae, transverse processes even in posterior presacrals are slender and long, pubis ossified. The specimen needs a taxonomic revision and it is possible that it is conspecific with some other Oligomiocene palaeobatrachid.

Palaeobatrachus vicetinus from the middle or upper Oligocene of Ponte, Italy, was described by Peters (1877) as *Probatrachus vicetinus*, misspelled *vicentinus* by Portis (1885) and subsequent authors. It is represented only by one metamorphosing tadpole so that its precise taxonomic status is questionable. Palaeobatrachid tadpoles are known also from Monte Viale (? early Oligocene), Italy (Vergnaud-Grazzini and Hoffstetter 1972).

Miocene fossils of *Palaeobatrachus* are not so abundant; this genus was reported from Kaltennordheim/Rhön in Germany (? middle Miocene) under various names by Wolterstorff (1886, 1887), in the upper Aquitanian (MN 2) of Poncenat and Laugnac, and the Astaracian (MN 6) of Sansan (the latter three localities in France) (Vergnaud-Grazzini and Hoffstetter 1972; Hossini 1992), and in MN 7 of the Opole locality, Poland (Młynarski *et al.* 1982). Further evidence of Miocene Palaeobatrachidae is from the upper Vindobonian of Randecker Maar, Germany, originally described as "*Rana hauffiana*" by Fraas (1909) but later recognized as a palaeobatrachid by Vergnaud-Grazzini (Vergnaud-Grazzini and Hoffstetter 1972). This re-assignement was recently confirmed by discovery of a large palaeobatrachid tadpole from this locality in the collections of the Staatliches Museum für Naturkunde in Stuttgart (Roček, unpubl. obs.). Młynarski *et al.* (1984) reported *Palaeobatrachus* sp. from the early Pliocene (MN 15) of Węze II, Poland. The identification rests on a single ilium. If this identification is correct, then this fossil represents the only known post-Miocene *Palaeobatrachus*. However, the identification should be corroborated.

Pliobatrachus langhae was described by Fejérváry (1917) from the middle Pleistocene of Betfia (the former Hungarian name was Püspökfürdö) in Romania (Fig. 9) (Vergnaud-Grazzini and Młynarskiv 1969). No complete skeleton has yet been recovered. *Pliobatrachus tarloi* (originally described as *Bufo* by Młynarskiv 1960, 1962) has been synonymized with *P. langhae* (Vergnaud-Grazzini and Młynarski 1969). This species was also found in the lower Pliocene (MN 15) of Ivanovce (Slovakia) (Hodrová 1981) and Węze (Poland), and from the upper Pliocene of Rebielice Królewskie (MN 16), Poland (Młynarski1961, 1962) and Villány (MN 17), Hungary (Vergnaud-Grazzini and Młynarski 1969). *Pliobatrachus* cf. *langhae* was reported from the upper Pliocene of the Korotoyak locality in the Don River basin

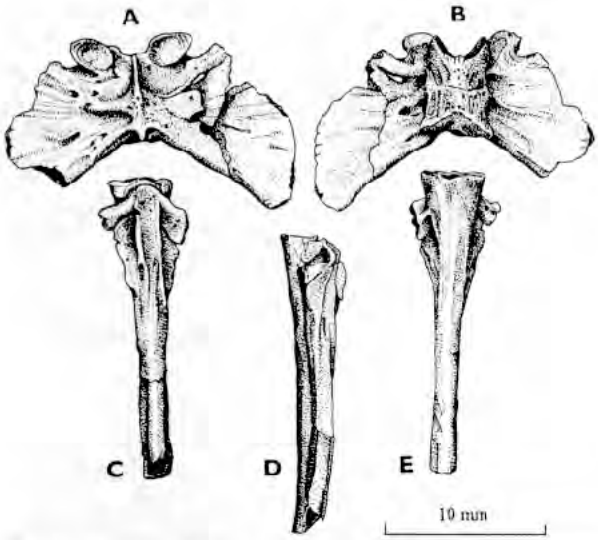

Fig. 9. Original elements on which the taxon *Pliobatrachus langhae* Fejérváry 1917 was based, Hungarian Geological Institute, Budapest. Synsacrum in dorsal (A) and ventral (B) views. C-E — Urostyle in dorsal (C), lateral (D), and ventral (E) views. Redrawn from Fejérváry (1917).

(Ratnikov 1990) and from the middle Pleistocene of Kozi Grzbiet, Poland (Sanchíz and Szyndlar 1984); the latter discovery is the latest Palaeobatrachidae known. *Pliobatrachus* sp. was also reported from the late Pliocene of the Don River basin (Ratnikov 1990, 1993b) and from the lower Pleistocene (lower Villafranchian) of the Hajnáčka locality, Slovakia (Hodrová 1981).

It was suggested that eastern populations survived the Mindel glaciation. In contrast, the palaeobatrachids disappeared as early as the middle Miocene or Pliocene from the western and southwestern Mediterranean region (Vergnaud-Grazzini and Hoffstetter 1972). Špinar (1987) tried to explain why palaeobatrachids, although common in central and western Europe, have never been found in southeastern Europe. This may be explained by the fact that during the Miocene, when the radiation of palaeobatrachids culminated, this region was isolated from other parts of Europe by a huge arm of the Tethys Sea.

Despite the fact that no complete skeleton has been found, Hodrová (1982) maintained that *Pliobatrachus* was, contrary to some earlier views (e.g., Młynarski 1977), primarily aquatic, as was the case with other palaeobatrachids. Strict adaptation to the water could be a reason for their extinction.

F. Hylidae

Pre-Neogene fossils have been referred to the Hylidae, but none belongs to this family. Unquestionable Hylidae appeared in Europe only in the Miocene. Fossils from the early Miocene (MN 4, Orleanian) of the Czech Republic (Hodrová 1987) and middle Miocene (MN 6 Astaracian) of Slovakia (Hodrová 1988) are referred to *Hyla* without specific identification. *Hyla* was also reported from the late Miocene of Ampudia 8 (MN 9), Spain, Ano Metochi 2 and 3 (MN 12/13), Greece (Sanchíz 1981a), the early Pliocene of Spilia 3 (MN 15), Greece (Sanchíz 1981b), Ivanovce (MN 15), Slovakia (Hodrová 1981), late Pliocene (MN 16) of Rebielice Królewskie I and II, Poland (Sanchíz and Młynarski 1979), and (as *Hyla* cf. *H. arborea*) from Arondelli, Italy (Vergnaud-Grazzini 1970). These disarticulated Neogene hylid bones (mainly ilia and humeri) are not distinguishable from living *Hyla*.

G. Bufonidae

Identification of bufonids from the Eocene of France (Filhol 1876), the middle Eocene of Geiseltal, Germany (Kuhn 1941; Estes 1970), and the earliest Oligocene of Hoogbutsel and Hoeleden, Belgium (Hecht and Hoffstetter (1962) are apparently all in error.

Unquestionable Bufonidae are first reported in the fossil record from the early Miocene. They appeared in the middle Orleanian (MN 4) and are documented in Spain and France: *Bufo* sp. and *Bufo* cf. *viridis* in Spain, *Bufo* aff. *viridis* in France (see below). As can be seen from the extensive Spanish record (Sanchíz 1977a,b), the Bufonidae have been continuously present, at least in the Iberian Peninsula, since the early Miocene. These early fossils already appear close to living species.

The *Bufo viridis* lineage appears to have been one of the first bufonid groups that colonized Europe. In Spain, it is represented by a single fragment of a urostyle from Córcoles (MN 4, Orleanian) referred to as *Bufo* cf. *viridis* by Alférez Delgado and Brea Lopez (1981). In France, *Bufo* aff. *B. viridis* from the early Miocene of Vieux-Collonges (MN 4, Orleanian) and the middle Miocene of La Grive (MN 7+8, Astaracian) is well documented by cranial and post-cranial bones. Only slight differences in the morphology of the frontoparietal, sphenethmoid, sacral vertebra and the scapula distinguish the latter fossil from living *B. viridis*. These differences are perhaps not significant at the specific level (Bailon and Hossini 1990). *Bufo viridis* was mentioned from the late Pliocene of Poland (Młynarski and Szyndlar 1989) and Italy (Vergnaud-Grazzini 1970).

Bufo priscus was described by Špinar *et al.* (1993) from the middle Miocene (MN 6) of Devínska Nová Ves, Slovakia. It differs from other species principally by sculptured frontoparietals and by other characters that may be assigned to individual variation. It may be synonymous with *B. bufo*. According to Hodrová (1980), *B. bufo* could be present in the middle Miocene (MN 6, Astaracian) of Slovakia. However, the nature of the remains did not permit her to ascertain their specific identity. Nevertheless, this species does appear very similar to *B. bufo*. This fossil might be more appropriately labelled *Bufo* cf. *bufo*. Similar remains were reported from the late Pliocene of Kaltensundheim/Rhön, Germany (Böhme 1989), Ivanovce, Slovakia (Hodrová 1981, 1985), Podlesice, Poland (Młynarski and Szyndlar 1989), Arondelli, Italy (Vergnaud-Grazzini 1970), and Korotoyak and Uryv, Russia (Ratnikov 1990). Among them are probably the oldest known representatives of *B. bufo*.

Sanchíz (1983) reported *Bufo* cf. *calamita* from the late Miocene (level MN 12) of Spain. This is the only report of a possible *B. calamita* from the Tertiary, which is somewhat surprising because the species is common in the Pleistocene.

Bufo raddei is an extant member of the family. Although its current distribution is limited to Asia, it was reported from the upper Pliocene localities of Kotlovina (Ruscinian, MN 15), Liventsovka (Villanyian, MN 17), and Zapadnaya Peshchera in the Ukraine (Chkhikvadze 1984; Ratnikov 1996, 1997).

Ratnikov (1993a) described three extinct species of *Bufo* from the late Pliocene of Russia and Ukraine: *B. belogoricus* based on a frontoparietal from the Korotoyak locality in the Voronezh Region, *B. planus* based on an incomplete humerus from the Kotlovina locality in the Odessa Region, and *B. albus* based on an incomplete humerus from the Liventsovka locality in the Rostov Region. Each species is poorly represented by few isolated bones. The status of these three taxa is questionable.

Bufavus meneghinii Portis, 1885 from the upper Miocene (Turolian, MN 12–13) of Sinigaglia (Italy) is a synonym of *Bufo* (Sanchíz 1998).

H. Ranidae

Pre-Eocene frogs have been referred to the Ranidae, but these fossils are either non-ranid amphibians or only possibly ranids. One possible ranid is represented by the distal part of a humerus from the late Palaeocene (MP 6, Thanetian) of Cernay, France. According to Estes *et al.* (1967), it is reminiscent of the Ranidae, Hyperoliidae, and Microhylidae. This humerus may indeed belong to the Ranidae, but this remains questionable. Possible Eocene ranids include *Rana carbicola* from the middle Eocene (MP 11–13) of Geiseltal, Germany, described by Kuhn (1941), and *Rana plicata* (Filhol 1876) from unknown localities of the phosphorites of Quercy (France). These fossils show an overall aspect consistent with that of the Ranidae, but this is not sufficient for assignment to the family.

The oldest doubtless ranids come from the late Eocene of France (Rage 1984b). They are represented by isolated bones (Fig. 10) and cannot be referred to a particular genus. The oldest were found at Grisolles (level MP 16), in the Paris Basin. Other ranid remains from the late Eocene were found in several localities of the Phosphorites of Quercy extending from levels MP 17 to MP 19. Two forms are present in the late Eocene; one of

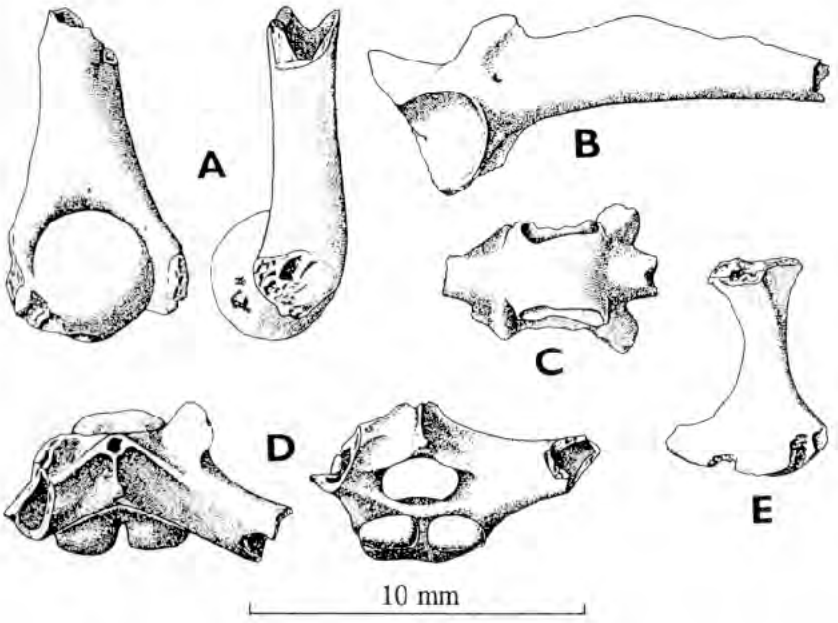

Fig. 10. Skeletal elements from the earliest European Ranidae. A. Right humerus in anterior (left) and medial (right) views. B. Right ilium. C. Eighth vertebra in ventral view. D. Sacral vertebra in dorsal (left) and posterior (right) views. E. Right coracoid in medial view. A and C-E are from the Late Eocene, Lavergne, France. B is from the Late Eocene, Perrière, France. Specimens are deposited in the Université des Sciences et Techniques du Languedoc, Montpellier, France: A as LAV 1251, B as PRR 2002, C as LAV 1252, D as LAV 1253, and E as LAV 1254. From Rage (1984b).

them resembles green frogs (Rage 1984b). From the late Eocene onwards, ranids has been present in Europe.

Rana meriani (Meyer 1853, 1860) is based on several specimens from the late Oligocene of Rott near Bonn, Germany. One specimen (Fig. 11), showing the general skeletal proportions, includes elements of the shoulder girdle and ventral cranium. Although ranids from the European Oligocene need taxonomic revision, this species seems to be better founded than most. *Rana noeggerathi* Meyer 1852, also from the late Oligocene of Rott, is much smaller (Fig. 12). It is possible that Wolterstorf (1901) was right when he considered it a juvenile of *Rana meriani* because carpal and tarsal elements and the epiphyses of the long bones are absent.

Two other Oligocene species have been described as ranids, but are of dubious attribution: *Rana aquensis* (Coquand 1845; Piveteau 1927) and *R. sieblosensis* (Meyer 1863; Gaudant 1985).

Indeterminate Miocene ranids include *Rana danubiana* (Meyer 1858, 1860), *R. jaegeri* (Meyer 1851, 1860), *R. salzhausenensis* (Meyer 1860; Sanchíz 1998), *R. rara*, and unnamed specimens from northern Italy (Morisi and Tropeano 1983; Kotsakis 1989).

Rana pueyoi (Navás 1922; Piveteau 1955) is based on complete specimens representing both adults and tadpoles, which include stomach contents suggesting that they fed on shelled gastropods (Werneburg 1995). This species was found in the Miocene of Spain where it was widely distributed (Sanchíz 1977a). Sanchíz (1998) assigned some of the specimens previously attributed to this species to *Rana esculenta*, the living green frog.

The late Pliocene deposits of the Willershausen locality, Germany, yielded a large number of well preserved (including soft parts) ranids which were described as *Rana straussi* by Špinar (1980a). Other Pliocene ranids include unnamed specimens from the early Pliocene site of Mandriola, Sardinia (Pecorini *et al.* 1973), and *Rana jalpugiensis* (*nomen dubium*) (Ratnikov 1993a) from the late Pliocene of Ukraine.

Rana temporaria, *Rana* cf. *arvalis*, and *Rana* sp. are reported from the late Pliocene of Kaltensundheim/Rhön, Germany by Böhme (1989). Ranidae that resemble *R. latastei* or *R. dalmatina* were found in the late Pliocene of Ivanovce (Hodrová 1981), and *Rana* cf. *latastei* and *R.* cf. *esculenta* are from the latest Pliocene of Arondelli, Italy (Vergnaud-Grazzini 1970). *Rana* cf. *nigromaculata* and *Rana* sp. were reported from the upper Pliocene locality of Korotoyak in the Don River Basin by Ratnikov (1990). However, because of their

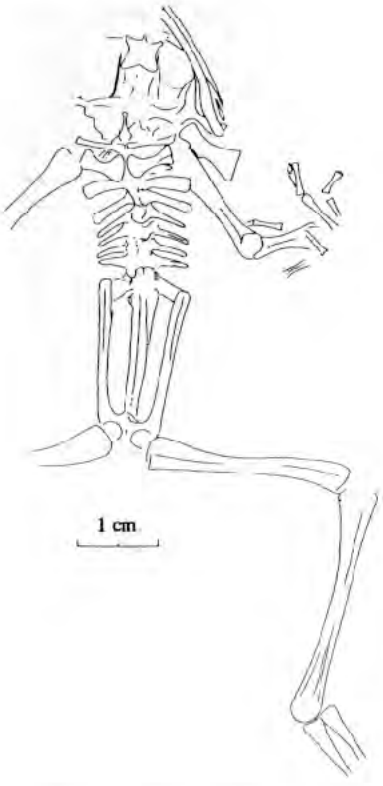

Fig. 11. Ventral view of *Rana meriani* Meyer 1853, specimen Ro 4134, Institut für Paläontologie der Universität, Bonn, Germany.

Fig. 12. Ventral view of the holotype of *Rana noeggerathi* Meyer 1852, specimen Ro 4059, Institut für Paläontologie der Universität, Bonn, Germany.

fragmentary nature their status is questionable. Ratnikov (pers. comm.) suggested that the sacral vertebra from Uryv-II, originally assigned to *Rana* sp. could be *Latonia*.

The genus *Ranomorphus*, described by Ratnikov (1993a) as a discoglossid (see above) from the upper Pliocene, is apparently a ranid and probably even the genus *Rana*.

Other forms described as *Rana* are either insufficiently described or were transferred to other genera. These include: *Asphaerion reussi* and *R. luschitzana* (Meyer 1852a; Špinar 1972), *Rana quellenbergi* (Navás 1922; Sanchíz 1977c), *Rana troscheli* (Meyer 1852b, 1860), *Rana batthyanyi* (Bolkay 1913), and *Rana volhynica* (Eichwald 1835).

The Ranidae can be well defined by osteological characters (see Rage 1974, 1984b; Bailon 1986); however, their infrafamilial determination is difficult. Most authors based their assignment to the genus *Rana* only on the fact that there is no other genus of Ranidae in Europe today.

I. Microhylidae and Rhacophoridae

Sanchíz (1990, 1998) reported undescribed Microhylidae and Rhacophoridae from the French upper Eocene (Escamps, Priabonian MP 17). A detailed study of this material is needed to verify this preliminary determination.

J. Leptodactylidae

In 1903, De Stefano erected the genus *Thaumastosaurus* for a supposed saurian reptile found in the phosphorites of Quercy, France. Nopcsa (1908) considered the similar name *Thaumattosaurus* von Meyer, 1841 a homonym, and so proposed the new name *Enigmatosaurus*. Hoffstetter (1945) correctly recognized that this animal is, in fact, an anuran, and Rage (1981) placed it in the Ceratophryinae (Leptodactylidae). The original

specimens from the localities "Caylux" and "Lamandine" described by De Stefano were lost but new material was collected in the La Bouffie site (level MP 17, upper Eocene) (Crochet *et al.* 1981). Roček and Lamaud (1995) argued that the first name is valid and gave a description of all skeletal elements of *Thaumastosaurus bottii* available at the time. The cranium of this frog is heavily ossified. Among the most important diagnostic characters are the heavily sculptured dermal roofing bones with pit-and-ridge sculpture, co-ossifications of the nasals and frontoparietals of the left and right sides in large individuals, and their coalescence with the sphenethmoid and prootico-occipitals; the frontoparietal is not in contact with the squamosal. *Thaumastosaurus bottii* is known in several localitites of late Eocene age in the phosphorites of Quercy (La Bouffie, Rosières 2, Escamps C [both latter are MP 19] and Gregols [MP 18]). This anuran is included among the taxa that are evidence of Gondwanan elements persisting in Europe until the Eocene.

K. Anura *Incertae Sedis* and *Nomina Dubia*

The following are considered as *incertae sedis* or *nomina dubia*: *Palaeophrynos gessneri* (Fig. 13) (Meyer 1845; Sanchíz 1998), *Lutetiobatrachus gracilis* (Fig. 14) (Wuttke 1988a), *Liventsovkia jucunda* (Ratnikov 1993a), and *Ranavus scarabellii* (Portis 1885; Gaudant 1996, pers. comm.; Sanchíz 1998).

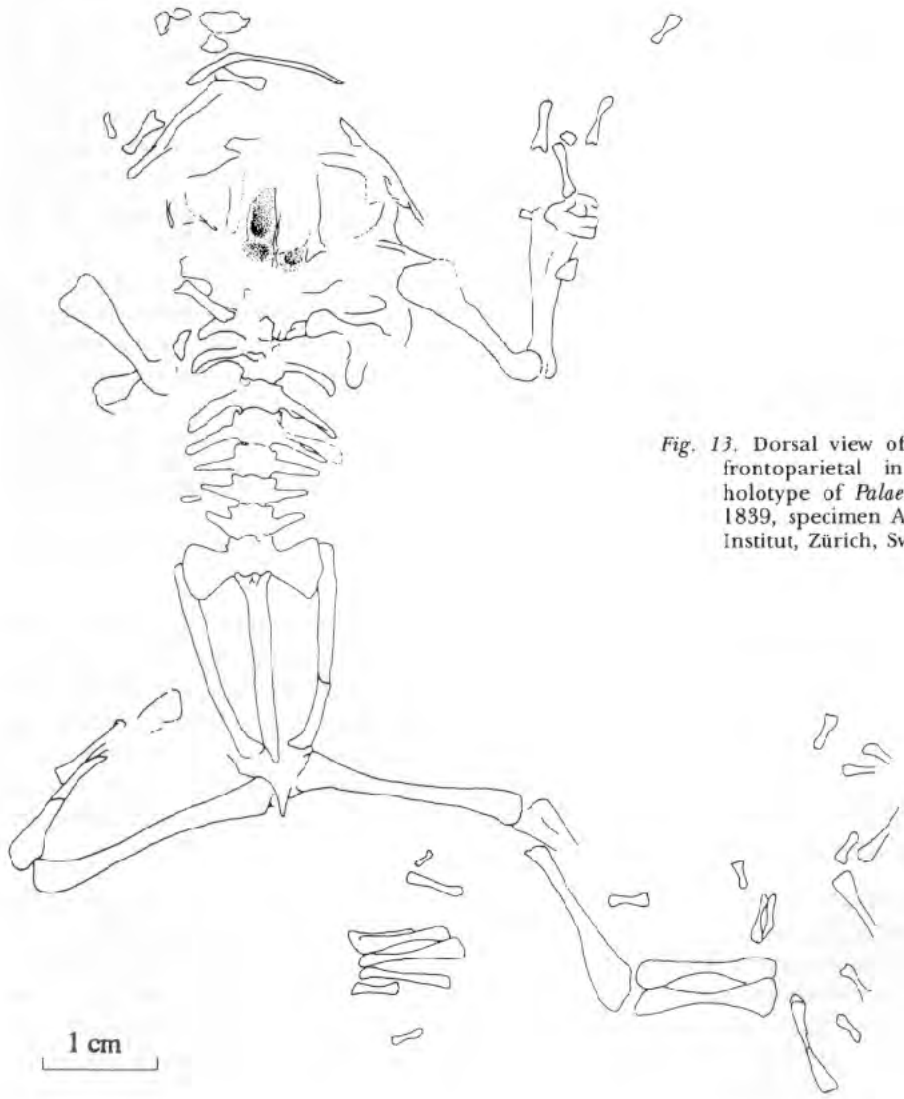

Fig. 13. Dorsal view of the skeleton (including frontoparietal in ventral view) of the holotype of *Palaeophrynos gessneri* Tschudi 1839, specimen A II 25, Paläontologisches Institut, Zürich, Switzerland.

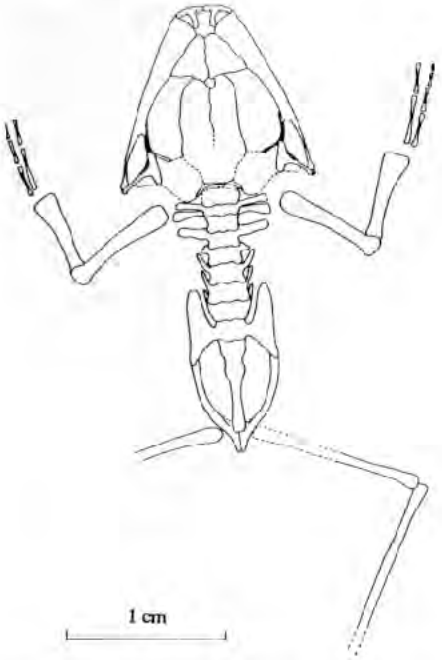

Fig. 14. Reconstruction of the skeleton of *Lutetiobatrachus gracilis* Wuttke, in press, in dorsal view. Redrawn from Wuttke (1988a).

II. TERTIARY ANURA OF AFRICA

Anura, as microvertebrates as a whole, are still poorly known in the Tertiary of Africa. Moreover, the African record appears to be somewhat unbalanced; the Pipidae represent the prevailing group.

A. Discoglossidae

The oldest discoglossid frog from Africa comes from the middle Miocene (MN 7+8) of Beni Mellal, Morocco. Vergnaud-Grazzini (1966) assigned it, on the basis of the urostyle, ilium, and humerus, to the living genus *Discoglossus*, although she noted that some characters of the ilium and urostyle are not consistent with *Discoglossus pictus*, the only species referred to the genus at that time. She also mentioned that the urostyle is reminiscent of a large discoglossid from the middle Miocene of La-Grive-Saint-Alban (France). This large discoglossid frog is now referred to the extinct European genus *Latonia*; therefore the fossil from Beni Mellal was referred to as *Latonia* sp. by Roček (1994b). However, the range of variation of the ilia and humerus is rather wide in living *Discoglossus* (Sanchíz and Pérez 1974) and the minor differences noted on the fossil bones fall within it. On the other hand, according to Vergnaud-Grazzini, only one character of the urostyle recalls *Latonia*: the individualization of the neural arch of the first postsacral vertebra, with its transverse processes dissymmetric and distorted. This is a relatively frequent anomaly in anurans and it cannot be used as a diagnostic character. Moreover, the referral of the urostyle to the Discoglossidae rests only on the presence of these transverse processes. Such processes can appear as an anomaly in other families (for example in the Ranidae, which are also present in the locality); as a consequence, the assignment of this urostyle to the Discoglossidae is uncertain. Nevertheless, the discoglossid frog from Beni Mellal appears to be referable to *Discoglossus*.

Discoglossidae may also be present in the late Miocene (level MN 10) of Oued Zra, Morocco (Hossini, work in progress).

B. Pipidae

Recently discovered anurans at the lower Eocene site of Mohenge in north-central Tanzania (Harrison 1996) most probably belong to the Pipidae based on the transverse processes of the sacral vertebra, extensive interiliac junction, and relatively short skull. Comparison of body proportions with *Xenopus (Lybicus) hasaunus* (see below) revealed that these frogs differ in the proportions of the tibiofibula and femur (the latter bone is much longer in the frogs from Tanzania). They differ from *Eoxenopoides* in having their femora markedly longer than their ilia. However, nothing more precise can be said until the specimens are more completely studied.

Eoxenopoides reuningi Haughton 1931 is based on several tens of complete or fragmentary specimens (Fig. 15) collected in the Eocene or Oligocene (probably the lower Eocene) of South Africa. It is not the oldest African pipid frog because this family is known from the Cretaceous onwards on this continent. According to Estes (1977), *E. reuningi* shows several character states that are more primitive than those in the living Pipidae: the conspicuously anterior position of the parietal foramen, relatively long scapula (however, this contrasts with the relatively short proportions of the scapula in his figure 8), and

presence of four separate distal tarsals. This taxon also displays a derived character: the presence of only six presacral vertebrae (the lack of maxillary teeth does not seem significant within the Pipidae). Estes (1977) considered *Eoxenopoides* to be closely related to *Xenopus*. Since that time, the genus *Silurana* has been resurrected (Cannatella and Trueb 1988); it was formerly considered as a junior synonym of *Xenopus*. Therefore, it should be added that *Eoxenopoides* retains vomers (azygous) as in *Xenopus*, but unlike *Xenopus* its nasals are paired. One derived character (atlas and second vertebra fused) is shared by *Eoxenopoides, Silurana* and the Pipinae. Because of this unusual combination of characters, the status of *Eoxenopoides*, at least at the generic level, is uncertain. Reig (1958) considered that *Eoxenopoides* should be placed in a family of its own ("Familia nueva para *Eoxenopoides*") but he did not name it. Subsequently, Parodi Bustos *et al.* (1960) and Casamiquela (1961) independently erected the new family Eoxenopoididae. Kuhn (1961) independently coined the name Eoxenopoididae in order to replace "Familia nueva para *Eoxenopoides*" in Reig's classification. Therefore, the family Eoxenopoididae was erected independently three times! Nevo (1968) demonstrated that *Eoxenopoides* does not deserve a separate family; Estes (1977) and Sanchíz (1998) did not recognize the family Eoxenopoididae.

The lower Oligocene of Jabal al Hasawnah (= Gebel Hasawnah), Libya, has yielded a fossil pipid frog described by Špinar (1980b). It was named *Xenopus (Libycus) hasaunus*. Špinar regarded this species as a representative of a new subgenus, *Libycus*, of *Xenopus* (at that time, *Xenopus* comprised *Silurana*). This species is based on seven complete and well-preserved specimens and some others that are poorly preserved. The frontoparietal is ovoid; this appears to be the only clear resemblance to *Eoxenopoides*. The paired nasals are reminiscent of *Silurana* but this is a primitive feature. However, the fused atlas and second vertebra in most specimens could suggest relationships to *Silurana*. Špinar indicated that ten vertebrae are present in two specimens; this surprisingly primitive feature is perhaps an individual anomaly. Finally, the generic allocation remains somewhat questionable. According to Báez (1996), this species appears to be more closely related to *Silurana* or the pipines than it is to *Xenopus*.

Xenopus stromeri from the Miocene (without more precision) of Namibia, was described by Ahl (1926) on the basis of various isolated bones (including braincases). This species is poorly known; unfortunately, the specimens which were in the Museum of the Humboldt University at Berlin are lost. According to Estes (1977), *X. stromeri* would be related to the living species *X. muelleri*.

The middle Miocene of Beni Mellal, Morocco, has yielded various bones of Pipidae that were referred to *Xenopus (Silurana* included) by Vergnaud-Grazzini (1966). She demonstrated that two forms are present in this locality. It does not seem possible to determine whether both genera (*Xenopus* and *Silurana*) or only one of them (with two

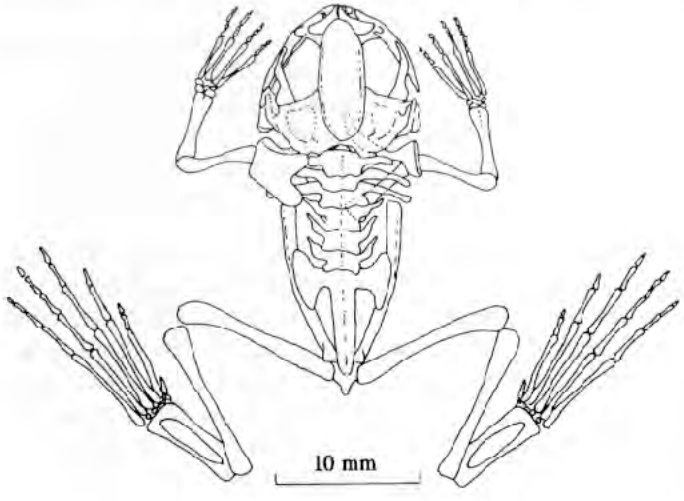

Fig. 15. Restoration of the skeleton of *Eoxenopoides reuningi* Haughton 1931 in dorsal view. The cleithrum and lower jaw are removed on the right side. Dashed line indicates extension of the elements of the shoulder girdle. Redrawn from Estes (1977).

species) are present. One fused atlas-second vertebra complex suggests the presence of *Silurana*, its presence is regarded as possible by Báez (1996).

The upper Miocene (MN 10) of Oued Zra, Morocco, has furnished a few remains of pipid frogs. They belong to either *Xenopus* or *Silurana* (Hossini, work in progress).

Stromer (1931), quoted here after van Dijk (1995), mentioned possible Pliocene fossil pipids from Namaqualand, South Africa, tentatively assigned to *Xenopus*.

C. Bufonidae

The middle Miocene of Beni Mellal, Morocco, has provided isolated bones that belong to the Bufonidae. Vergnaud-Grazzini (1966) referred them to the living genus *Bufo*. She distinguished two species among these fossils. The greatest resemblances of one of them lie with the living African *Bufo regularis*, but the fossil does not belong to this species. According to Vergnaud-Grazzini, the second form does not show resemblances to any known species; however, she did not name it. Bufonidae are perhaps present in the upper Miocene of Oued Zra, Morocco (Hossini, work in progress).

D. Ranidae

Ranid frogs were reported from the middle Miocene of Beni Mellal, Morocco, by Vergnaud-Grazzini (1966). Two genera are present in the locality: *Rana* and *Ptychadena*. Both genera are represented by various isolated bones. No attempt at a specific identification was made. The middle Miocene of Pataniak 6 (MN 7+8) and the upper Miocene of Oued Zra and Khendeck el Ouaich (MN 13), all localities in Morocco, have produced some anuran bones which could belong to the Ranidae (Hossini, work in progress).

E. Indeterminate anurans

Unpublished remains of anurans are known in the Palaeocene of Adrar Mgor (Morocco) and in the lower Eocene of El Kohol (Algeria).

III. TERTIARY ANURA OF ASIA

The first fossil anurans from Asia were recovered as early as the middle of the 19th century (Owen 1847). Since that time, several fossil sites have yielded anuran remains but most of them still remain unstudied.

A. ?Discoglossidae

Some rare anurans have been found in the Miocene of Li Mae Long (Thailand) (Rage and Ginsburg 1997). The vertebral arch of a large vertebra bears a long processus spinosus. This process and the postzygapophyses project markedly posteriorly. This configuration is reminiscent of the large discoglossid from the European Neogene. The referral of the material to this family could be confirmed by the presence of an opisthocoelous sacral vertebra that bears two cotyles for articulation with the urostyle. Li Mae Long was considered middle Miocene by Jaeger *et al.* (1985) but it appears to be early Miocene (Mein and Ginsburg 1985).

The distal extremity of a humerus and a fragmentary vertebra from the upper Miocene (Vallesian/Turolian transition) (Brandy 1979) of Sherullah, Afghanistan, may belong to the Discoglossidae. The fragmentary humerus is somewhat flattened dorso-ventrally and widened transversely; this morphology is reminiscent of discoglossids of the *Discoglossus* group. Moreover, the vertebra was apparently opisthocoelous. Both bones indicate a large anuran. If the referral of these remains from Thailand and Afganistan to the Discoglossidae proves correct, then these fossils are the only discoglossid frogs reported from the Cenozoic of Asia, although the Discoglossidae was widely distributed there during the Cretaceous.

B. Palaeobatrachidae

Claessens (1997) reported *Palaeobatrachus* sp. from the early Miocene of Anatolia, Turkey. If this identification proves correct, then this fossil represents the southernmost occurrence of the family.

C. Pelobatidae

Remains attributed to *Eopelobates* are reported, without any description, from the lower Oligocene, and indeterminate Pelobatidae from the middle Oligocene of the Zaisan Basin, Kazakhstan (Chkhikvadze 1985). An isolated maxilla from the lower Oligocene of the Ergilin-Dzo locality in the southern Gobi Desert, Mongolia, was described as *Uldzinia kurochkini* (Gubin 1996).

Paicheler *et al.* (1978) referred several well preserved tadpoles from the early or middle Miocene of Bes Konak in the Gürcü Valley (north of Ankara), Turkey, as *Pelobates* sp. The assignment rests on the large size of the tadpoles. Wassersug and Wake (1995) reported excellently preserved tadpoles from the same area, regarded as middle Miocene; they tentatively assigned these tadpoles to *Pelobates*, but not identical with any living species.

A few bones of an indeterminate pelobatid were collected in the lower Pliocene (level MN 15) of Calta (Turkey, Anatolia) (Rage and Sen 1976).

D. Scaphiopodidae

The genus *Macropelobates* was based on the American Museum of Natural History specimen No. 6252, illustrated in Noble (1924), Estes (1970), Roček (1981, 1984) from the Hsanda Gol Formation (Rupelian, middle Oligocene) of Isagan Nor Basin, central Mongolia. It was based on *Macropelobates osborni* and its principal characters are (Fig. 16) large size (estimated snout-vent length of the holotype 17–18 cm); columella developed, frontoparietal paired in early developmental stages; urostyle and sacral not coalesced, urostyle with a single condyle, and pubis ossified. On the basis of anatomical and palaeogeographical data, Roček (1981, 1984) referred the genus to the Scaphiopodidae, a taxon previously included within the Pelobatidae (as Scaphiopinae).

Another species attributable to *Macropelobates* is *Macropelobates cratus* (Gao 1986) from the Shanwang Formation (SW 2 and MN 5, middle Miocene) of the Linqu locality in Shandong Province, China (Fig. 17). Gao also included a second specimen in this taxon which was identified as *Bufo linquensis* by Yang (1977). The latter specimen is considered the paratype and was illustrated by Gao. *Macropelobates cratus* is characterized by its large size, skull much wider than long with sculpture on its dorsal surface, maxillary teeth well developed, vomerine teeth reduced, palatine present, eight procoelous presacrals, sacral

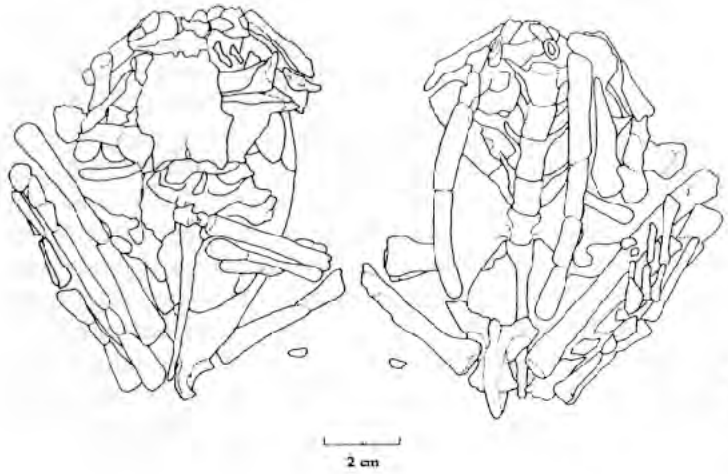

Fig. 16. Dorsal (left) and ventral (right) views of the holotype of *Macropelobates osborni* Noble 1924. Redrawn from Roček (1981).

Fig. 17. Skeleton of the holotype of *Macropelobates cratus* Gao 1986, holotype in ventral view. Redrawn from Gao (1986).

diapophyses strongly broadened, urostyle somewhat stocky and articulating with the sacral vertebra via a single condyle, crista ossis ilii absent, posterior legs short and massive, femur slightly longer than tibiofibula, and prehallux developed as a spade (Gao 1986).

E. Bufonidae

Indeterminate Bufonidae are reported, but not described, from the middle Oligocene and early Miocene of Zaisan Basin, Kazakhstan. *Bufo* sp. is mentioned from the middle Miocene of the same area (Chkhikvadze 1985). A bufonid frog from the early Miocene of Anatolia (Turkey) is referred to as *Bufo* aff. *viridis*, i.e., a living species, by Claessens (1997).

Bufo linquensis was described by Yang (1977) from the middle Miocene (Shanwang Formation, SW2 and MN5) of the Shanwang locality near Linqu, Shandong Province, China. However, the description was insufficient and one of the two specimens was later referred to *Macropelobates cratus* by Gao (1986). Gao gave the following emended diagnosis of the species and confirmed its original assignment to the Bufonidae: large size, head strikingly wider than long, snout wide and rounded, maxillary and vomerine teeth absent, parasphenoid blade shorter than its half width across alae, alae well developed and perpendicular to blade, eight procoelous presacrals (their diapophyses massive), urostyle-sacral articulation by double condyles, sacral diapophyses strongly dilated, pectoral girdle arciferal, no iliac crest, short legs, and a tibiofibula shorter than the femur.

Various isolated bones from the lower Pliocene (MN 15) of Calta (Turkey, Anatolia) belong to a Bufonidae. This fossil was referred to as *Bufo* cf. *viridis* by Rage and Sen (1976). Another representative of the genus *Bufo* is *B. raddei*, which was recovered from the upper Pliocene deposits of the Bural-Obo locality in northern Mongolia (Hodrová 1986). This finding confirms the view expressed by Sanchíz and Młynarski (1979) that the present-day Eurasian Bufonidae took their origin as early as the Pliocene.

F. ?Myobatrachidae

The intertrappean black shales of Bombay, India, have produced numerous complete or nearly complete specimens of a small frog described as *Rana pusilla* by Owen (1847). Subsequently, Noble (1930) allocated this species to a genus of its own, *Indobatrachus*. The geological age of this fossil taxon is generally considered to be Eocene or even lower Oligocene, but according to Khajuria *et al.* (1994) the intertrappean beds of Bombay "should not be younger than early Paleocene". Two other species from the same fossiliferous beds were referred to *Indobatrachus: I. trivialis* and *I. malabaricus* by Chiplonker (1940) and Verma (1965), respectively. Špinar and Hodrová (1985) demonstrated that the three species are synonymous. *Indobatrachus* was referred to the Ranidae by Owen (1847) and Stoliczka (1869), to the subfamily Crininae (which was included in the Bufonidae at that time) by Noble (1930, 1954), and to the subfamily Myobatrachinae (that is to the Leptodactylidae) by Lynch (1971). In fact, the opinions of Noble and Lynch are identical. Špinar and Hodrová (1985, 1986) corroborated Lynch's opinion and they referred *Indobatrachus* to the Myobatrachinae, a taxon which is now often considered as a family (Myobatrachidae). However, this referral does not seem well established. The features on which this assignment is based are not conclusive, except perhaps the reduced transverse processes of the presacral vertebrae and the presence of free intervertebral discs. But the latter character is apparently questioned by Špinar and Hodrová (1985); thus the allocation to

the Myobatrachidae would rest only on the size of the transverse processes of the presacral vertebrae. As a result, although the referral of *Indobatrachus* to the Myobatrachidae may be accurate, the problem of the family assignment of this genus cannot be considered settled.

G. Ranidae

Indeterminate Ranidae are reported, but not described, from the middle Oligocene of Zaisan Basin, Kazakhstan (Chkhikvadze 1985) and from the early Miocene of Li Mae Long, Thailand (Rage and Ginsburg 1997).

Paicheler *et al.* (1978) referred several articulated skeletons from the early or middle Miocene of Bes Konak (Anatolia, Turkey) to *Rana* sp. The ilia of these ranids show an iliac crest similar to that of living green frogs, *Rana esculenta*.

Rana basaltica was described, on the basis of both adults and tadpoles, from the Miocene of Shanwang (= Wanchuanshue) near Lingchühsien (= Linqu), Shantung (= Shandong) Province, China, by Young (1936). According to the original, not very informative, description, the articulated skeleton may be characterized by nine vertebrae and by a skull that is broader than long.

Rana kisatibensis was described by Riabinin (1928) from the Neogene (Pliocene) diatomites near the village of Kisatibi, Tiflis Region, Azerbaydzhan. It was based on two counter-parts of the same individual. One of these parts (illustrated in Riabinin [1928]) was described earlier as *Rana macrocnemis angeloi* by Bogachev (1927) and consequently the former name (i.e., *Rana kisatibensis*) should be considered a synonym. Undoubtedly, the fossil is related to *R. macrocnemis* but as is the case for other fossil ranids, it needs taxonomic revision. Currently, *R. macrocnemis angeloi* is considered a *nomen dubium* by Sanchíz (1998).

Some fragmentary bones from the upper Miocene of Sherullah, Afghanistan (see above: ? Discoglossidae), probably belong to a large ranid frog.

Indeterminate Ranidae were reported from the lower Pliocene (MN 15) of Calta (Turkey, Anatolia) (Rage and Sen 1976).

Rana hipparionum Schlosser 1924 is another fossil frog reported as a ranid from two Chinese localities, the upper Miocene (MN 13) locality of Ertemte which is close to the Miocene/Pliocene transition (Qiu and Qiu 1995; Storch 1995) and the lower Pliocene locality of Olan Chorea (Bohlin 1942). The taxon is based on isolated bones that were illustrated but not adequately described by Schlosser. Since the deposition of the original material is unknown, its taxonomic revision is not possible.

The maxillae of an indeterminate species of *Rana* similar to modern species were recovered from the upper Pliocene deposits of the basal Pinjor Formation (upper Siwaliks) at Chandimandir, Haryana, India (Raghavan 1991).

IV. TERTIARY ANURA OF NORTH AMERICA

A. Introduction

According to current lists, more than 60 anuran species are known from the Tertiary deposits of North America (Table 2). Compared with Europe, this number is greater, despite the fact that the search for fossil amphibians began in Europe much earlier, at the beginning of the 18th century. However, this disparity is largely the result of many North American fossil anurans (especially bufonids, hylids, and ranids) being based on isolated ilia or sacrum-urostyle complexes. Identification has been further confused by the association of these bones with other disarticulated elements, both from the same site and especially from other localities. Another problem is that original descriptions were in many cases too vague to provide sufficient diagnostic information. This is why a considerable number of taxa based on isolated skeletal elements should be designated *nomina dubia* or *nomina vana* until detailed taxonomic revision, using more informative material, becomes possible.

Nevertheless, the fossil record of the Tertiary anurans in North America provides an important contribution to the knowledge of the phylogeny of these amphibians, especially when this is seen from the point of view of palaeogeography. Special attention should be paid to the absence of palaeobatrachids and discoglossids in the Tertiary of North America, which casts some doubts on Mesozoic and Palaeocene discoveries (Estes and Sanchíz 1982;

Table 2. Stratigraphic ranges of North American anurans (dubious taxa marked by question marks).

	Paleocene	Eocene	Oligocene	Miocene	Pliocene
DISCOGLOSSIDAE					
(?) "undescribed genus and species"	- -				
RHINOPHRYNIDAE					
Eorhinophrynus sp.	—				
Eorhinophrynus septentrionalis Hecht 1959		—			
Chelomophrynus bayi Henrici 1991		—			
Rhinophrynus canadensis Holman 1963			—		
PELOBATIDAE					
"Green River pelobatid"		—			
Eopelobates grandis (Zweifel 1956)			—		
SCAPHIOPODIDAE					
Scaphiopus guthriei (Estes 1970)		—			
Scaphiopus skinneri Estes 1970			—		
Scaphiopus neuter Kluge 1966				—	
Scaphiopus hardeni Holman 1974				—	
Spea studeri (Taylor 1938)				—	
Scaphiopus wardorum Estes *et* Tihen 1964				—	—
Spea alexanderi (Zweifel 1956)				- -	—
Spea bombifrons (Cope 1863)				—	—
Spea cf. *S. hammondi* (Baird 1859)					- -
PELODYTIDAE					
Tephrodytes brassicarvalis Henrici 1994			—	—	
Miopelodytes gilmorei Taylor 1941				—	
LEPTODACTYLIDAE					
(?) *Eorubeta nevadensis* Hecht 1960		- -			
(?) *Eleutherodactylus* sp.		- -			
BUFONIDAE					
Bufo praevius Tihen 1951				—	
Bufo kuhrei Holman 1973				—	
Bufo pliocompactilis Wilson 1968				—	—
Bufo suspectus Tihen 1962				—	—
(?) *Bufo marinus* (Linnaeus 1758)				- -	- -
Bufo hibbardi Taylor 1942				—	—
Bufo alienus Tihen 1962				—	
Bufo holmani Parmley 1992				—	
cf. *Bufo* (*americanus*) sp.				- -	- -
Bufo aff. *compactilis* Wiegmann 1833				- -	- - —
Bufo cognatus Say in James 1823				- -	- - —
Bufo campi Brattstrom 1955					—
Bufo speciosus Girard 1854					- -
Bufo spongifrons Tihen 1962					—
Bufo tiheni Auffenberg 1957					—
Bufo rexroadensis Tihen 1962					—
Bufo woodhousii Girard 1854					—
Bufo cf. *alvarius* Girard 1859					- -

Table 2 — *continued*

	Paleocene	Eocene	Oligocene	Miocene	Pliocene
HYLIDAE					
Hyla swanstoni Holman 1968					
Acris sp.					
Acris barbouri Holman 1967					
Proacris mintoni Holman 1961					
(?) *Hyla miofloridana* Holman 1967					
Hyla squirella Bosc 1800					
Hyla miocenica Holman 1966					
Pseudacris nordensis Chantell 1964					
Pseudacris sp.					
Hyla cf. *H. versicolor*					
(?) *Hyla chrysoscelis* Cope 1880					
Acris cf. *A. crepitans* Baird 1854					
Hyla cf. *cinerea* (Schneider 1799)					
Hyla cf. *gratiosa* LeConte 1856					
Pseudacris cf. *clarki* (Baird 1854)					
Acris cf. *gryllus* (LeConte 1825)					
Hyla cf. *H. regilla* Baird *et* Girard 1852					
RANIDAE					
Rana miocenica Holman 1965					
Rana johnsoni LaRivers 1953					
Rana pipiens Schreber 1782					
Rana cf. *R. catesbeiana* Shaw 1802					
Rana cf. *clamitans* Latreille 1801					
Rana pliocenica Zweifel 1964					
Rana areolata Baird *et* Girard 1852					
Rana feyae Taylor 1942					
Rana palustris LeConte 1825					
Rana rexroadensis Taylor 1942					
Rana sylvatica LeConte 1825					
Rana cf. *R. aurora* Baird *et* Girard 1852					
MICROHYLIDAE					
Gastrophryne cf. *carolinensis* (Holbrook 1836)					

Estes 1975). The presence of chronologically limited genera (middle Eocene through early Oligocene) closely related to the European *Pelobates* (some apparently paedomorphic) is also of considerable interest, especially in the context of the relatively rich record of *Scaphiopus* and *Spea*, which continues to the present. Although the presence of leptodactylids is a matter of discussion (except for *Eleutherodactylus* found in Eocene amber of the Dominican Republic, i.e., beyond the North American continent), their possible occurrence in the North American Tertiary is not excluded, especially in the context of finds of leptodactylids in the European Eocene.

The occurrence of pelobatids (excluding *Scaphiopus* and *Spea*; see below), pelodytids, and possibly leptodactylids on the North American continent was only a temporary episode that did not last beyond the Chadronian, and the Barstovian or Clarendonian, respectively. The presence of these anuran groups on the North American continent was probably a result of penetration from the European part of Laurasia and from South America, before they were isolated from North America in the Late Cretaceous. As for pelobatids and pelodytids, one can speculate on their unsuccessful competition with *Scaphiopus* that occupied the same ecological niche.

It is also interesting to note that hylids appeared in North America as early as the early Oligocene, but their diversification occurred only in the early Miocene, as is the case with European hylids. The early Miocene was also the period when the earliest bufonids and ranids appeared, although diversification of the former was delayed until the middle Miocene, and that of ranids until the late Pliocene.

On the basis of the Tertiary record, the family Rhinophrynidae appears to be the most ancient lineage in the contemporary anuran fauna rooted in the late Palaeocene-early Oligocene interval (i.e., roughly 50 million years ago). *Scaphiopus* also is very old, with its earliest record from the early Eocene; only in the late Miocene (i.e., about 40 million years later) did the latter give rise to the paedomorphic *Spea* (which may be characterized as a hypo-ossified *Scaphiopus*). It is surprising that the first hylids appeared earlier than the bufonids, ranids and microhylids, and that this first record (about 35 million years before present) was represented by the extant genus *Hyla* (if it can be reasonably diagnosed on the basis of only the ilium and tibiofibula; see below). However, the substantial part of the contemporary North American anuran fauna took its origin in the early Miocene (Hemingfordian) in the case of hylids and microhylids, and middle to late Miocene (Barstovian through early Hemphillian) in the case of bufonids and ranids. Nevertheless, it was only in the late Pliocene that ranids became numerous and diversified, whereas in Europe they were common as early as the late Oligocene; the earliest record is from the late Eocene.

B. Discoglossidae

Estes (1975) identified a discoglossid from the late Palaeocene (Tiffanian, Fort Union Formation) at the Princeton Quarry, Park County, Wyoming, on the basis of a single distal part of the right humerus. It was referred to the Discoglossidae on the basis of resemblance to the living European genus *Alytes*, and was obviously so derived from the general discoglossid morphology that Estes published it as "undescribed genus and species". If his identification proves to be correct, this specimen would represent the last known surviving discoglossid from the Cretaceous in North America. However, the available material is too limited and its identification too questionable to draw firm conclusions at present.

It should be noted that the Mesozoic genus *Scotiophryne*, questionably referred to the Discoglossidae (see Chap. 14), was identified as cf. *Scotiophryne* from the Paleocene (Estes 1969, 1976; Estes and Sanchíz 1982).

C. Rhinophrynidae

The earliest fossil of this family was recognized from the late Palaeocene (Tiffanian, Fort Union Formation), Princeton and Fritz Quarries, Park County, Wyoming, by Estes (1975). In contrast to the isolated, distal part of the humerus identified as a discoglossid, this material is more informative, consisting of humeri (one of them nearly complete), sacral vertebra, and tibiale (fibulare according to Henrici 1991). The humerus was assigned to the Rhinophrynidae on the basis of its relatively short total length, large size of the ventral crest, small size of the medial epicondyle, raised olecranon scar flanked by shallow channels, and strongly angulated shaft; the sacral vertebra shows a general resemblance to those of living *Rhinophrynus*. Estes (1975) called this Palaeocene rhinophrynid *Eorhinophrynus* sp.; see also Krause (1980).

Two other rhinophrynids were recorded from the middle Eocene. *Eorhinophrynus septentrionalis* Hecht 1959 was originally based on a single atlas from the middle Eocene (Bridgerian) Bridger Formation at Tabernacle Butte, Sublette County, Wyoming. Later, this material was completed by a topotypic right exoccipital-prootic complex, a right scapula, a partial left humerus, and a partial right tibiofibula (Henrici 1991). According to her revised diagnosis it differs from all other rhinophrynids in having a long atlantal neural arch that is laterally broad with a square posterior margin (Fig. 18A) and a well-developed crista lateralis humeri. Estes (1975) figured a left fibulare (tibiale according to Henrici 1991) from the same locality that he referred to *E. septentrionalis*.

The second known rhinophrynid from the middle Eocene is *Chelomophrynus bayi* Henrici 1991, a burrowing representative of the family with two digging spades on each hind limb. It was based on a large sample (several hundred) of partial to almost complete

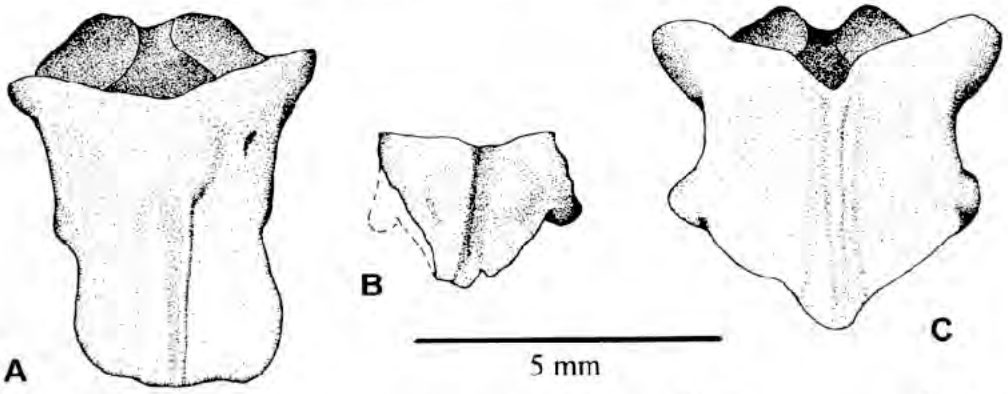

Fig 18. Shape of atlas of the Rhinophrynidae in dorsal view. A. *Eorhinophrynus septentrionalis* Hecht 1959; middle Eocene (Bridgerian), Wyoming. B. *Chelomophrynus bayi* Henrici 1991; middle Eocene (Uintan), Wyoming. C. Contemporary *Rhinophrynus dorsalis*. From Henrici (1991).

skeletons from the Bridgerian-Uintan Wagon Bed Formation at Battle Mountain, in the Lysite Mountain Area, Hot Springs County, Wyoming. It is unique among rhinophrynids in having the following combination of characters (Figs 18B, 19): broad, triangular processus frontalis premaxillae, anterior notch on the maxilla, elongate posterior process and posterior choanal process of the vomer, laterally oriented transverse processes of the last three presacral vertebrae, caput humeri round, atlantal neural arch tapering posteriorly, and prominent crista lateralis humeri. A growth series, representing at least six developmental stages ranging from tadpoles beginning metamorphosis to adults, is present in this sample, which is the largest sample of any fossil anuran species described from a single locality in North America. Later, Henrici and Fiorillo (1993) reported on an unusual bone accumulation found in the same quarry, consisting exclusively of bones of young postmetamorphic individuals of *Chelomophrynus bayi*.

The last representative of the family is *Rhinophrynus canadensis* Holman (1963a) from the lower Oligocene (Chadronian) Cypress Hills Formation, Calf Creek locality near Eastend, Saskatchewan, Canada, which was based on a right ilium (Fig. 20A). In addition to the ilium of the holotype, it is represented by numerous other disarticulated bones (Holman 1963a, 1968, 1972). It can be distinguished from the living species, *R. dorsalis*, by the well developed tuber superius of the ilium (Fig. 20B), and the elongate oval space between the tibiale and fibulare (Henrici 1991). It is known only from the type locality.

D. Pelobatidae

The genera *Pelobates* and *Eopelobates* are considered here as taxonomically separate from *Scaphiopus* and *Spea* because of ontogenetic features including the development of the frontoparietal complex (see below) or fusion of the palatine (either with the maxilla or vomer), which are different in both groups (even in three groups, if megophrynids are taken into account). These developmental processes are undoubtedly independent of environmental influences and, consequently, phylogenetically more important than those characters of adults that might arise by convergent evolution, such as a vertical pupilla, spade, or extended transverse processes of the sacral vertebra.

Eopelobates grandis Zweifel 1956 was described from the lower Oligocene Chadron Formation (middle part of Ahern member) in the area of the divide between the West Fork and the Main Fork of Indian Creek, Pennington County, South Dakota on the basis of a nearly complete skeleton lacking only part of the skull and distal limb bones (Fig. 21). It is large (estimated snout-vent length 110 mm), with a broad frontoparietal that is not in contact with the lamella alaris squamosi.

The original generic assignment (Zweifel 1956) to *Eopelobates* was based primarily on the shape of the squamosal, sacral diapophyses, absence of a bony prehallux, urostyle free

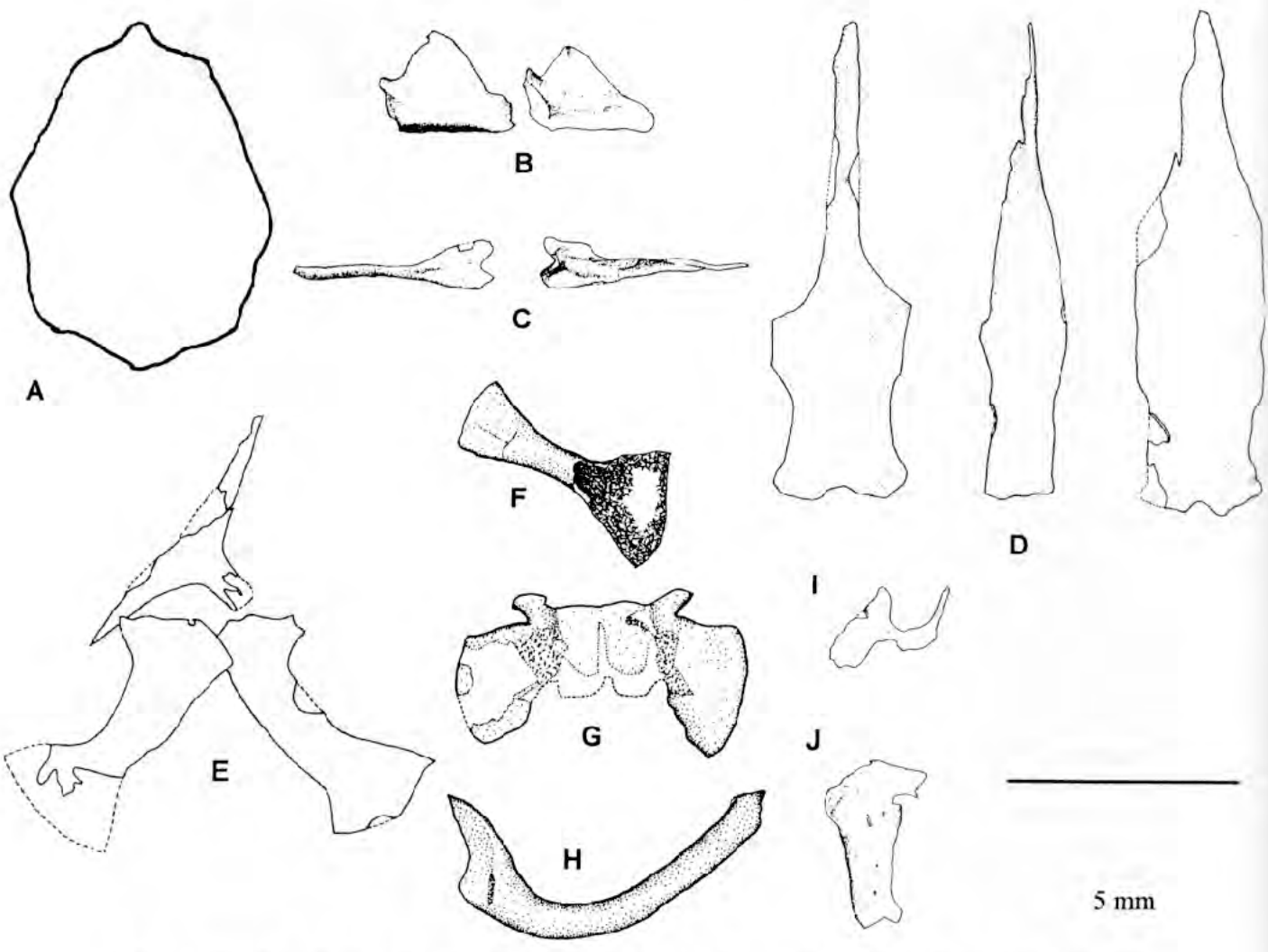

Fig. 19. Chelomophrynus bayi Henrici 1991. A. Frontoparietal. B. Left premaxilla in outer (left) and inner (right) views. C. Right maxilla in outer (left) and inner (right) views. D. Three parasphenoids, to show variation in shape. E. Somewhat displaced, unpaired parahyoid bone and paired ossa thyroidea. F. Coracoid. G. Sacral vertebra in dorsal view. H. Clavicle. I. Vomer. J. Squamosal. From Henrici (1991).

from the sacral vertebra, presence of maxillary teeth, the femur and tibiofibula of about equal length, and the (incorrect) presupposition that there was a broad contact between the frontoparietal and the squamosal over the temporal region. Some of these characters cannot be accepted as good diagnostic criteria of *Eopelobates*, whereas others were misinterpreted (e.g., restoration of the original shape of the orbits suggests that the squamosal and frontoparietal were well separated; the processus posterolateralis squamosi is indicated as a quadrate in Zweifel's figure 2). Because the frontoparietal was considered by Estes (1970) as paired, Roček (1981) expressed some doubt as to its generic assignment. This was followed by Sanchíz (1998), who referred to it as "*Eopelobates*" *grandis* (and placed it among the Megophryinae). In the meantime, Henrici (1998, pers. comm.) re-investigated the specimen and prepared parts hitherto covered by matrix. This revealed that the frontoparietal lacked a median suture (although illustrated as paired by Estes [1970]). The posterior margin of the bone forms a median apex lacking sculpture and does not bear a median suture. This demonstrates that the frontoparietal developed a posteromedian ossification during its ontogeny that prevented the median suture from reaching the posterior margin of the bone. A large palatine process of the maxilla projects medially, and the quadratojugal is present. This bone was misinterpreted by Zweifel as a stapes.

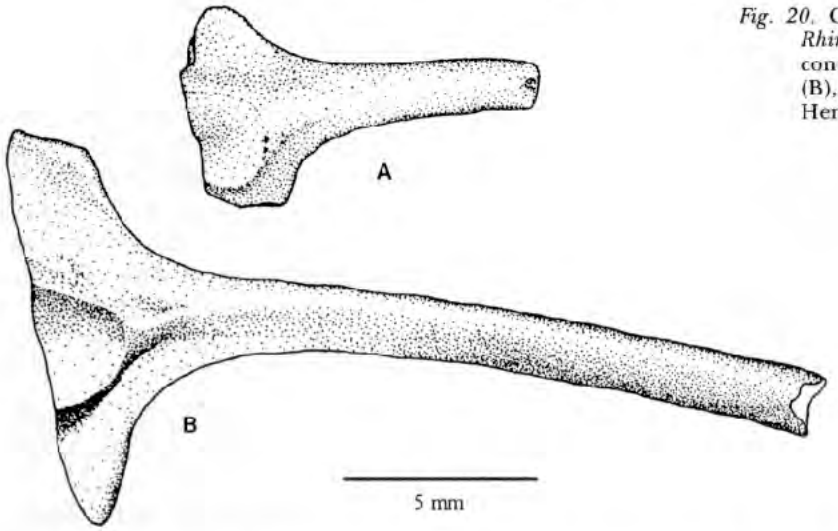

Fig. 20. Comparison of the right ilia of *Rhinophrynus canadensis* (A) and contemporary *Rhinophyrnus dorsalis* (B), both in lateral view. From Henrici (1991).

However, the quadratojugal was correctly identified by Estes (1970). Despite Zweifel's original errors in anatomical interpretation, most features suggest his original taxonomic assignment was correct.

Eopelobates grandis is known only from the type locality, although an exception may be an incomplete sacral vertebra described from the middle Eocene (late Bridgerian) of Wyoming by Hecht (1959) which bears, according to him, peculiar resemblance to *E. grandis*. According to Lynch (1971) it is clear that this is a megophryine pelobatid, as was originally suggested also by Hecht.

The only other representative of North American pelobatids is a not yet formally described anuran from the middle Eocene Green River Formation (Lancy Member) near Farson, Wyoming, first mentioned by Grande (1984) as "a complete pelobatid frog . . . probably a new species of the genus *Eopelobates*" (Fig. 22; compare with Grande's [1984]

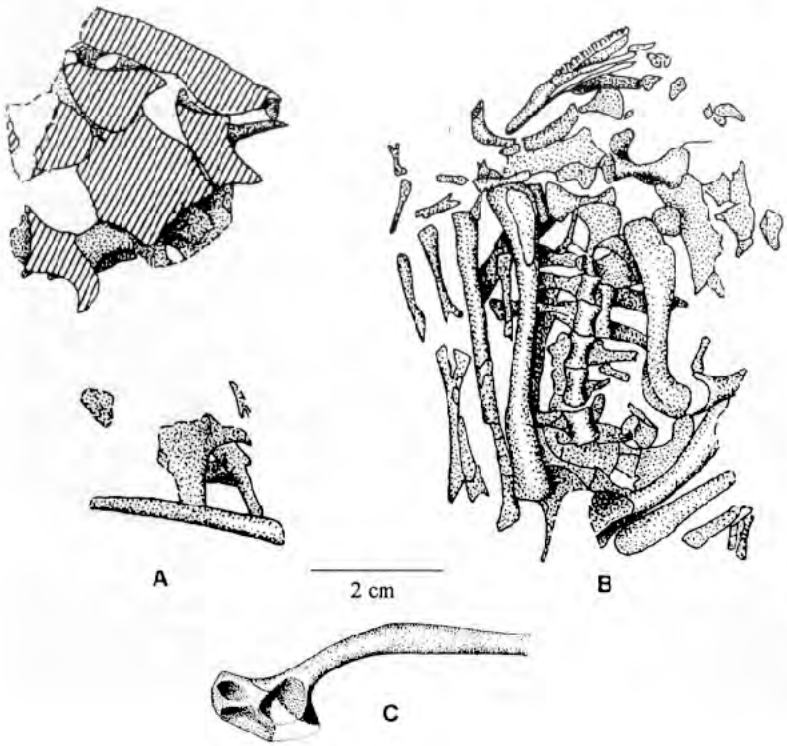

Fig. 21. Eopelobates grandis Zweifel 1956. A. Dorsal view with sculptured dermal bones hatched. B. Ventral view. C. Right ilium in lateral view. Redrawn after Zweifel (1956).

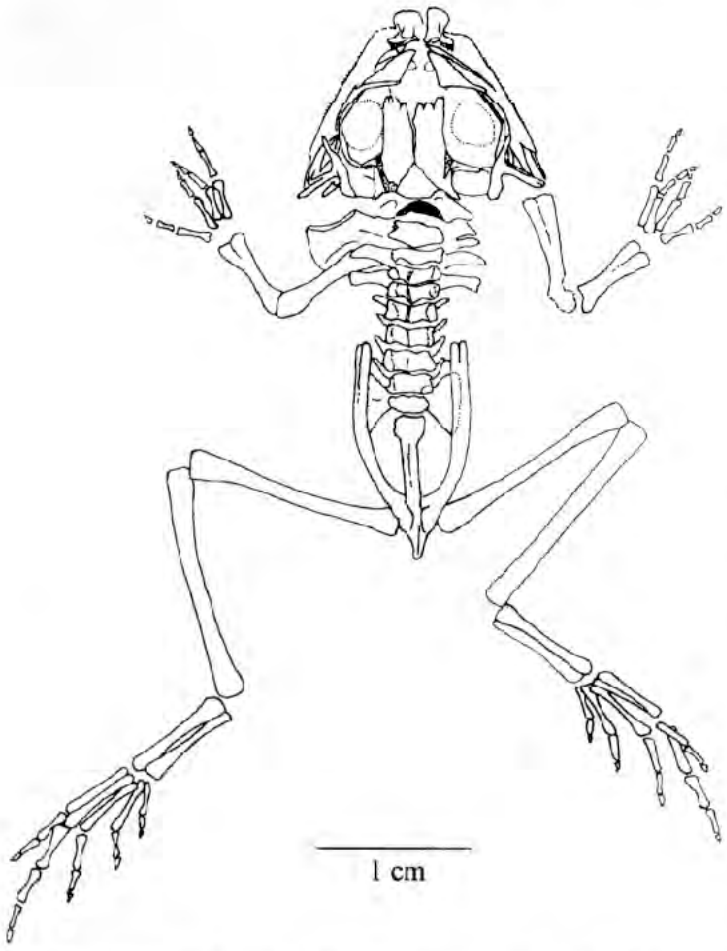

Fig. 22. A pelobatid anuran from the Eocene Green River Formation, Wyoming, that has not yet been formally described. Drawn after the original specimen.

photograph of the latex peel, his figure III.1a). This specimen is important in providing evidence for the occurrence of forms closely related to the European genus *Pelobates* in the North American Tertiary. It is also interesting from an evolutionary point of view in its retention of juvenile features in an adult.

A preliminary description is given below. It should be noted that its frontoparietal was briefly described by Roček (1988). The specimen is exposed in dorsal view, moderately compressed dorsoventrally so that the maxillae can be seen in their outer aspect, but the premaxillae are inverted so that they expose their inner surface. The dorsoventral pressure caused the frontoparietal complex to be compressed along its suture into the cavity of the braincase. However, all its constituting elements (including the slender lateral and posterolateral processes) were not damaged. The neural arches of all the vertebrae are fused with one another dorsally, and the long bones are articulated with one another in their natural position suggesting that their epiphyses were largely ossified. Together with its size, this indicates that the individual was an adult.

The premaxillae are characterized by their broad dorsal (facial) processes that extended medially to such an extent that the bones probably formed a long median suture. Short palatine processes are preserved next to each other at the ventral end of the bone, suggesting that they continued for a short distance onto the palate. Judging from the number of teeth on the exposed part of the crista dentalis of each premaxilla, there would be about eight tooth positions. Although the anterior end of each maxilla is covered by matrix, it is obvious that this part of the bone was relatively deep. Between this part of the maxilla and its zygomatico-maxillary process there is a concave margo orbitalis. The posterior process of the bone is comparatively short, and it is adjoined on the medial surface of its tip by a long and slender quadratojugal (well preserved on both sides).

Both nasals are slender and triangular in shape. Although their posterolateral process is still articulated with the facial process of the maxilla, their medial margins are widely separated. The posteromedial process of both nasals is separated from the frontoparietals, which suggests the presence of a large fontanelle above the anterior end of the sphenethmoid.

The frontoparietal consists of three parts joined to each other by sutures. The lateral elements meet in a median suture which (except for its most posterior section) is still open, so that it leaves a narrow median fontanelle between them. These lateral elements extend in a long slender process adjoining the anterior part of the otic capsule, thus forming the posterior margin of the orbit for a considerable distance. These processes are separated from the main part of the frontoparietal by a groove for the arteria orbitonasalis that entered the orbit in its posteromedial corner. In addition to this process, each lateral element of the frontoparietal extends posterolaterally in a distinct paraoccipital process. Between the posteromedial margin of the lateral parts of the frontoparietal an unpaired median element is inserted, the posterior margin of which is widely convex and forms the dorsal margin of the foramen magnum. This element prevents the median suture between the lateral parts of the frontoparietal from reaching its posterior margin. This median element is characteristic of the developing frontoparietal in larval *Pelobates* and *Eopelobates* (Roček 1981, 1988).

The alar lamella of the squamosal is narrow, pointed anteriorly (where it joins the zygomatico-maxillary process of the maxilla), and is not in contact with the lateral process of the frontoparietal, so that the dorsal surface of the otic capsule is largely exposed. The dermal bones are covered by only indistinct irregular sculpturing, which in the anterior part of the maxillae tends to be arranged in shallow horizontal grooves. Between the bones of the dorsal surface of the skull, parts of the pterygoids, prearticulars, and dentaries may be recognized, all approximately in natural position. Impressions of two outgrowths protruding from below the medial margins of the nasals can be recognized, but are difficult to identify.

The vertebral column consists of eight presacral vertebrae, the second through fourth bearing stout transverse processes. Other presacrals bear anteriorly inclined transverse processes that are of approximately the same length. The sacral processes are broadly extended antero-posteriorly, and the anterior part of them extends to the level of the mid-length of the eighth presacral. This anterior part is clearly separated on both sides from the main portion of the process and, as suggested by a bilobate impression beneath the right ilium; it was not yet fully fused to the main body of the process. Such accessory laminae may be found in other primitive Tertiary pelobatids (see Böhme *et al.* 1982) and, according to Fejérváry (1917) and Špinar (1972), they may be interpreted as dilated prezygapophyses of the sacral vertebra. The urostyle is not coalesced with the sacral vertebra, and bears no transverse processes.

Since the skeleton is exposed in its dorsal aspect, only a small part of the largely ventral shoulder girdle (a partial imprint of the left scapula) is preserved, but provides no diagnostic information.

The ilia are stout, their anterior ends (apparently completed by cartilage in the living animal) extending up to the level of the anterior margin of the seventh vertebra (although this might result from a slight anterior post-mortem shift of the pelvic girdle, as suggested by the position of the posterior tip of the urostyle). The anterior end of the iliac shafts bears a distinct longitudinal groove. Little can be said of the limbs, except that the femora are only slightly sigmoid-shaped, the tibiale and fibulare are separate from one another, and the other tarsals and carpals were cartilaginous (there seems to be an indistinct imprint of one tarsal element of the right posterior limb). There is no inner metatarsal tubercle ("spade") on the hind limb.

The principal character by which this anuran is assigned to the Pelobatidae (i.e., *Pelobates* + *Eopelobates*) is that the frontoparietal obviously develops from three elements (two lateral ones homologous with proper frontoparietals, plus a single posteromedian ossification). Many characters are paedomorphic, which means that in normal development they are present in larval or metamorphosing individuals, whereas in this anuran they persisted into the adult stage. These include: a tripartite frontoparietal not yet fused into a single composite bone, urostyle and sacral vertebra articulated and not yet fused with

one another, carpals and tarsals cartilaginous (except for the tibiale and fibulare), and the latter not yet coalesced with each other.

This specimen is significant because there is no other fossil record of an anuran closely related to the genus *Pelobates* on the North American continent since the early Oligocene (*Eopelobates grandis*).

In addition to this fossil, two other anurans have been reported from the Green River Formation. Cope (1883) mentioned a specimen consisting of the vertebral column and part of the cranium of an incompletely developed frog, and Grande (1984) illustrated an indeterminate individual with a skin impression. The taxonomic status of both anurans, as well as the repository of the first of them, is unknown.

E. Scaphiopodidae

To date, five species of *Scaphiopus* and four species of *Spea* have been described from the North American Tertiary. *Scaphiopus guthriei* (Estes 1970) is the earliest of them, recovered from the lower Eocene Wind River Formation of Fremont County, Wyoming. The holotype (Fig. 23) is a nearly complete skull associated with a fragmentary scapula. According to Estes the principal diagnostic characters are a narrow processus posterolateralis squamosi, triple emargination of the frontoparietal margins, paired frontoparietal, columella and quadrate present, and a relatively short skull. It is known only from the type locality. Estes assigned this form to *Eopelobates* on the basis of a concave skull roof, the shape of the squamosal and sphenethmoid, and the approximately subequal orbital and temporal openings. However, these characters do not enable unambiguous assignment. Moreover, the presence of paired frontoparietals and well developed columella contradict the reference of this specimen to *Eopelobates*. In addition, Estes himself pointed out the following similarities with *Scaphiopus*: relatively short skull, strongly concave posterior border of the prootic part of the oticooccipital, long narrow prootic foramen, and relatively great posterior extent of the nasals. Roček (1981) considered this form to be related to *Scaphiopus* rather than to *Eopelobates*. Recently, Henrici (1998, pers. comm.) reinvestigated this specimen and confirmed that it belongs to *Scaphiopus*. She recognized the following

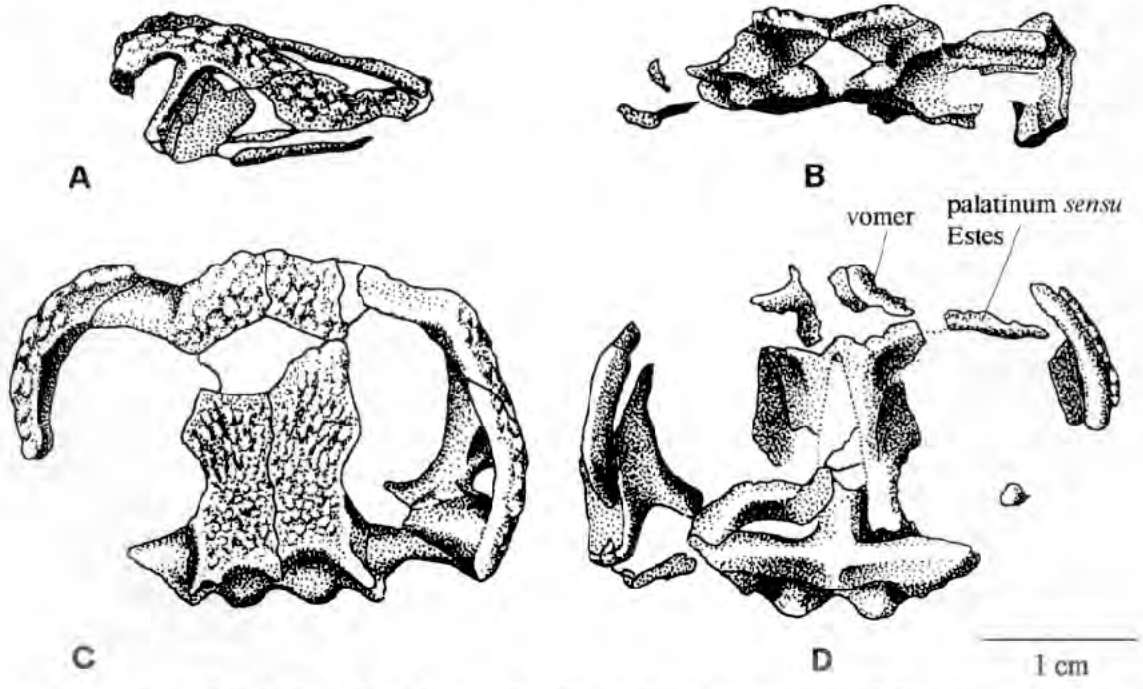

Fig. 23. Holotype of *Scaphiopus guthriei* (Estes 1970) in lateral (A), posterior (B), dorsal (C) and ventral (D) views. Redrawn from Estes (1970).

characters: a paired frontoparietal with a median suture reaching to its posterior margin, extensive nasals with a concave narial margin (preserved nearly completely on the left side), and the presence of the columella. Both maxillae are incomplete on their posterior ends so that it cannot be decided whether the quadratojugal was absent or present. The palatine is preserved on the left side, with its medial end in line with the broken lateral end of the postchoanal ramus of the vomer (Fig. 23D). However, according to Henrici, this bone (palatine sensu Estes) is divided by a crack that might be interpreted as a suture between the pars postchoanalis of the vomer (medial part) and the palatine process of the maxilla (lateral part). It should be noted that neither in *Pelobates* nor *Eopelobates* does the palatine process of the maxilla reach the vomer because the latter bone has no postchoanal process (which is, in fact, the palatine fused to it) as in *Scaphiopus* and *Spea* (Roček 1981). Henrici (1991) considered this character one of the synapomorphies for the clade including *Scaphiopus* and *Spea*. *Scaphiopus guthriei* has only been reported from the type locality.

The slightly younger *Scaphiopus skinneri* Estes 1970, which was originally described from the Leo Fitterer Ranch site west of Dickenson, Stark County, North Dakota, from the Orellan (European equivalent, Helvetian), middle Oligocene, was also reported from the early Oligocene of Saskatchewan (Holman 1968). The holotype (Fig. 24) (Estes 1970) is a nearly complete skull and vertebral column, left scapula, right coracoid, and left? thyroid ossification. It is similar to *S. holbrooki* but differs by its flattened skull. The condyle of the atlas is fused to the second vertebra, which thus is bicondylar (probably an anomalous condition according to Estes [1970]). Estes (1970) did not provide a diagnosis of *S. skinneri* and features that he discussed do not allow unambiguous definition of this species, but assignment to *Scaphiopus* seems to be without doubt. Sanchíz (1998) listed the following diagnostic characters, extracted from Estes' description: large-sized *Scaphiopus* with extensive skull ornamentation, the fontanelle between the frontoparietals absent, large rounded tympanic process of the squamosal, articulation of the squamosal with the maxilla, the pterygoid process of the maxilla present, the prootic foramen widely emarginated, anterior-posterior length of the transverse processes of the sacral vertebra at their ends equal to the length of three presacral vertebrae.

An additional three species of *Scaphiopus* are known from the Miocene. *Scaphiopus neuter* (Kluge 1966) was originally described on the basis of a nearly complete skeleton (with the exception of the distal parts of the limbs) from the lower Miocene of the Wounded Knee Area, Shannon County, South Dakota. According to the diagnosis given in the original

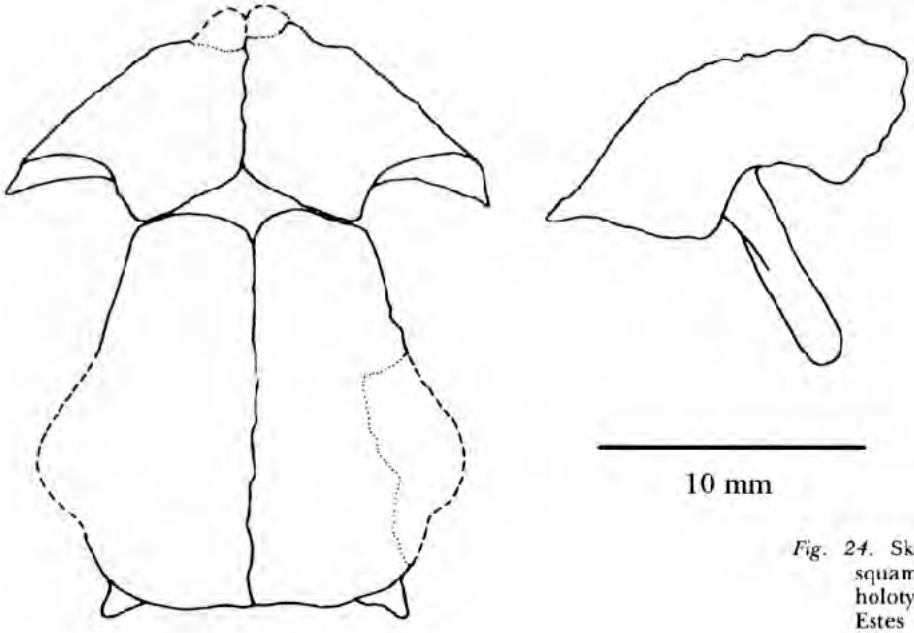

Fig. 24. Skull roof (left) and left squamosal (right) of the holotype of *Scaphiopus skinneri* Estes 1970. From Estes (1970).

description, it has nine free presacrals, the quadratojugal is absent, the sternum was probably cartilaginous, the transverse processes of vertebrae 5–9 do not appear to project strongly anteriorly (vertebra 9 may be an exception), the sacral vertebra and urostyle are fused, the maxilla and squamosal are not in contact but widely separated, the operculum is large, the frontoparietals, squamosals, maxillae and nasals are covered with slight to moderate sculpturing, there is a moderately large fontanelle between the frontoparietals (the inner borders of which are highly emarginate), the foramen prooticum is completely enclosed by bone, the processus palatinus maxillae is absent, the pterygoid process of the maxilla is absent, the tuber superius ilii is very large (however, see Fig. 25C), the postsacral webbing is very extensive, and the urostyle has two foramina for the intervertebral canals. *Scaphiopus neuter* was also reported from the early Miocene (Arikareean) in Cherry County, Nebraska (Holman 1981), and from other lower Miocene localities of North America (Kluge 1966; Holman 1968).

Scaphiopus hardeni Holman 1974 is another Miocene representative of the family. It was based on fragmentary ilia (Fig. 26), although some other bones (including maxillae, frontoparietals, and sacro-urostylar fragments) found in the type locality are supposedly associated with this taxon. It was recovered from the Clarendonian Ogalalla Formation (middle Miocene) of the Wakeeney locality in Trego County, Kansas, and published under the name *S. couchi* by Wilson (1968). Holman listed the following characters as diagnostic: snout-vent length approximately 70 mm, sphenethmoid with strong posterior median tubercle and lateral wings at right angles with respect to the longitudinal axis, and ilium similar to that of *Scaphiopus wardorum* and living *Spea holbrooki* and *Scaphiopus couchi*. *Scaphiopus hardeni* differs from the former in its smaller size and in having the pars descendens much wider anterior to the acetabulum, and from the latter two in having the tuber superius much better developed and more rugged. It is known only from the type locality.

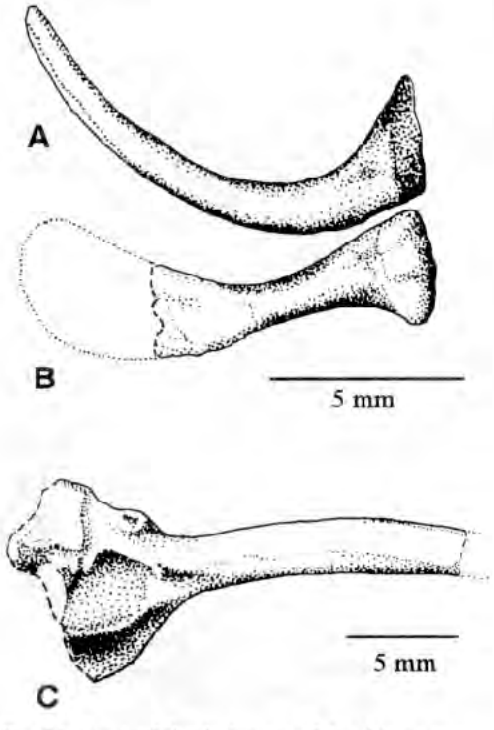

Fig. 25. Parts of the holotype of *Scaphiopus neuter* Kluge 1966. A. Left clavicle in ventral view. B. Left coracoid in ventral view. C. Right ilium in lateral view. Redrawn from Kluge (1966).

The last of the Miocene species attributable to *Scaphiopus* is *Scaphiopus wardorum* Estes and Tihen 1964. It was described on the basis of the posterior part of the left ilium (illustrated by photographs in Estes and Tihen [1964] and his figure 2 redrawn by Sanchíz [1998]), recovered from the lower part of the Valentine Formation (uppermost Miocene or lowermost Pliocene) in the Norden Bridge Quarry, Brown County, Nebraska. According to the original description, it is larger than other *Scaphiopus* (probably reaching a snout-vent length of at least 100 mm); the portion of the sub-acetabular expansion (pars descendens ossis ilii) anterior to the acetabulum is extremely narrow, the maxilla (except its lower margin) is covered by denticulate sculpture, and occasionally the denticles may be joined to form vermiculate ridges. *Scaphiopus wardorum* was also found in the Miocene (Barstovian) of the Egelhoff site (Holman 1987), in the middle Barstovian of Banner County, (Voorhies *et al.* 1987), and in the late Hemphillian of the Santee site in northern Knox County (Parmley 1992), all in Nebraska.

Material of indeterminate *Scaphiopus*, referred to as *Scaphiopus* sp. or considered indeterminate by later authors, has also been

reported from the lower Oligocene through upper Miocene (Barstovian, Hemphillian) deposits of Saskatchewan, Nebraska and Kansas (Taylor 1941a; Tihen 1960c; Holman 1968; Holman and Sullivan 1981; Parmley 1992), and from the Pliocene (Blancan) of Texas (Rogers 1976). *Scaphiopus antiquus* Taylor 1941 that was based on a fragmentary sacrum and urostyle from the Miocene (Hemphillian) of Edson Quarry, Kansas is now considered a synonym of *Scaphiopus* sp. and placed among the *nomina vana* (Sanchíz 1998).

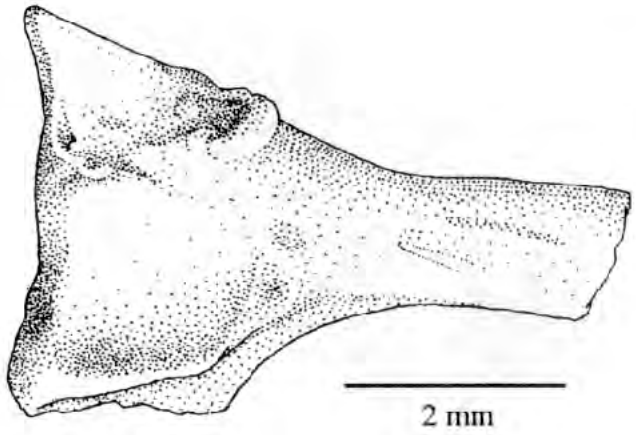

Fig. 26. Ilium of the holotype of *Scaphiopus hardeni* Holman 1974. From Holman (1974).

The earliest species attributable to the genus *Spea* appeared only in the late Miocene. *Spea studeri* (Taylor 1938) was described from the Edison Beds (middle Pliocene; upper Miocene-Hemphillian after Sanchíz [1998]) deposits of the Rhino Hill site in Logan County, Kansas, from impressions and bones of a nearly complete skeleton (Fig. 27). According to Taylor (1938) it is a medium-sized member of the genus, approaching the character of *S. bombifrons* more closely than any other living form; the spade is large, the tibiale and fibulare are fused together at the ends, the sacral diapophyses are fan-shaped, the sacrum is fused with the urostyle, and there is a broad fontanelle between the frontoparietals. This species differs from *S. bombifrons* by having different carpalia and in the atlas being very different in size. It is known only from the type locality.

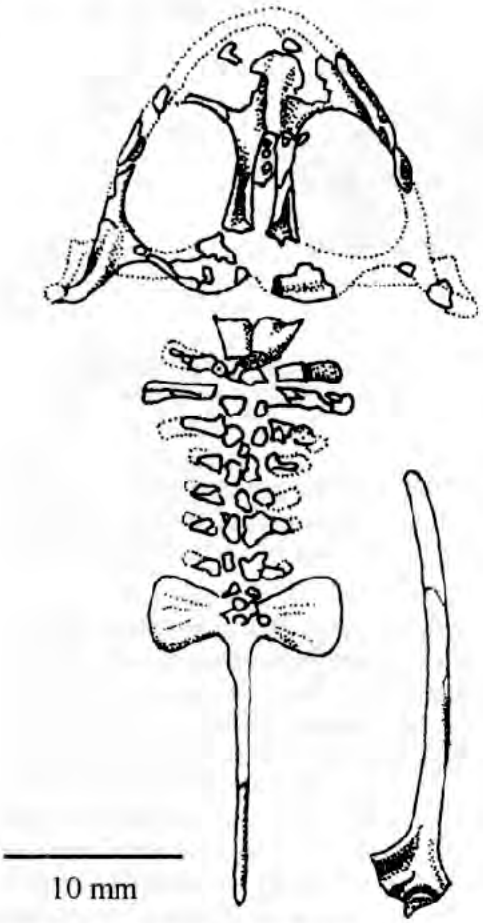

Fig. 27. Ventral view of the skeleton of the holotype of *Spea studeri* (Taylor 1938) (left) with its left ilium in lateral view (right). Redrawn after Taylor (1938).

Spea alexanderi (Zweifel 1956) was described from the lower Pliocene (?upper Miocene) Esmeralda Formation in Fish Lake Valley, Nevada, on the basis of the posterior part of the skull, the vertebral column, portions of the pectoral and pelvic girdles, and some limb bones of a three-dimensionally preserved skeleton (Fig. 28). According to the diagnosis in the original description, it is similar to *Scaphiopus* but differs in having the sacrum fused with the eighth vertebra. Since such fusion occurs comparatively often in anurans (not just in the *Scaphiopus-Spea* complex), some additional characters would be needed to provide a more reliable diagnosis. Material assigned to this taxon has also been reported from the middle Miocene (Barstovian) through Mio-Pliocene of North America (Holman 1973b; Estes and Tihen 1964).

In addition to these two extinct species, contemporary *Spea bombifrons* (Cope 1883) was recorded from the middle Miocene (Barstovian) of Nebraska (Holman 1976, 1987; Voorhies *et al.*

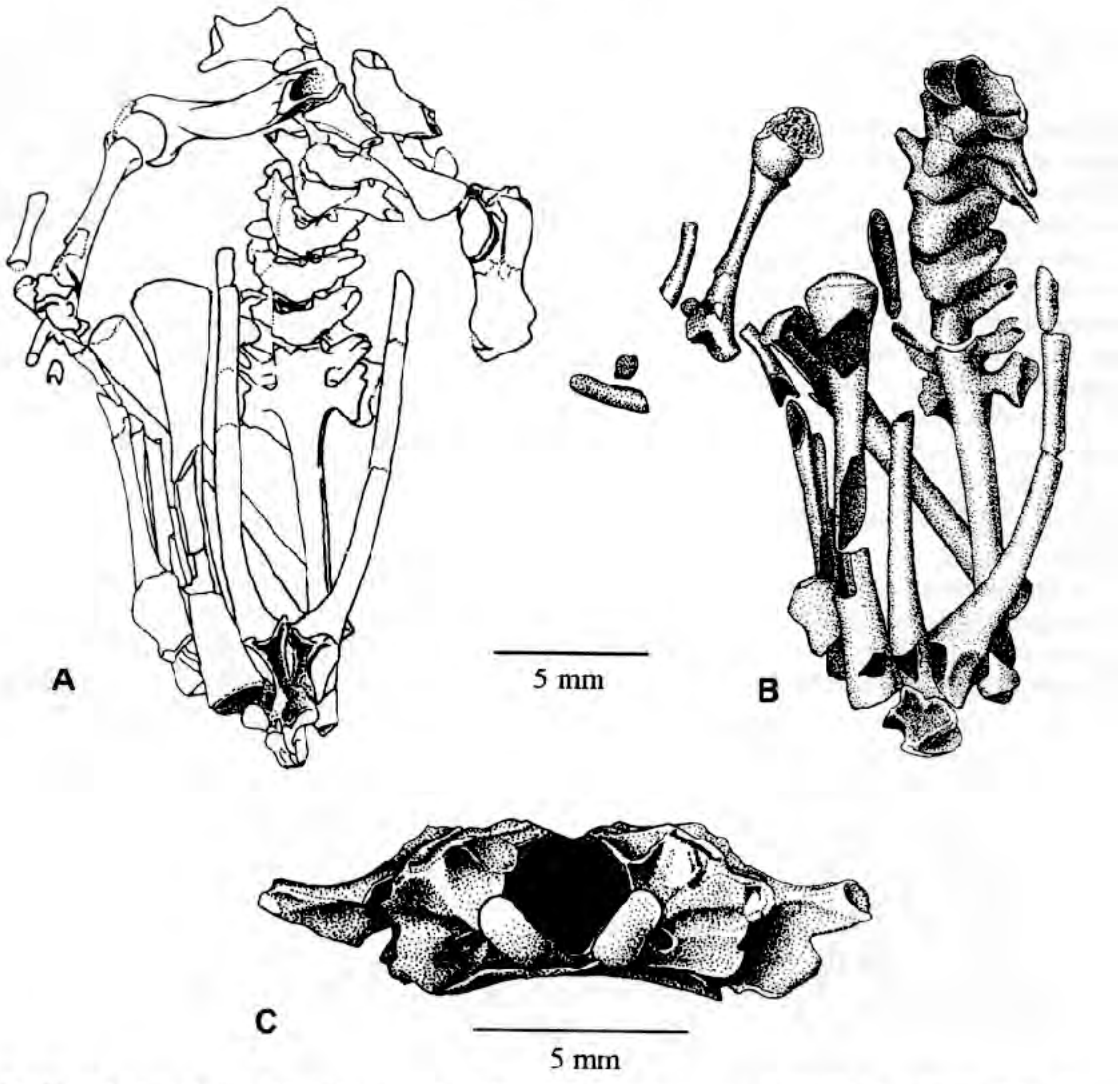

Fig. 28. Holotype of *Spea alexanderi* (Zweifel 1956). A. Postcranial skeleton in ventral view (its condition in 1956). B. Postcranial skeleton in ventral view (its condition in 1986). C. Skull in posterior view. A and C redrawn from Zweifel (1956); B is an original drawing.

1987) and from the Pliocene (Blancan) of Kansas (Holman and Schloeder 1991). Another extant species, *Spea hammondi*, was questionably reported (as *Scaphiopus* cf. *hammondi*) from the upper Pliocene Glenns Ferry Formation of the Hagerman area in Twin Falls, Owyhee and Elmore Counties, Idaho (Chantell 1970).

Some forms originally described as separate species were later re-assessed and attributed to the genus as *Spea* sp. Among such forms belongs *Neoscaphiopus noblei* from the Pliocene (Blancan) of Kansas described by Taylor (1942) on the basis of a small fragment of the sacral vertebra and urostyle. He interpreted a transverse ridge on its dorsal surface as the posterior edge of vertebra 8, although there was no trace of the line of coalescence on the ventral surface. Zweifel (1956) accepted this statement, but refused to consider *Neoscaphiopus* conspecific with *Scaphiopus* because of differences in geologic age and geographic position. The holotype (and the only) specimen was re-considered by Ritland (1955) and Tihen (1960c). It can be agreed that the type of *Neoscaphiopus noblei* represents an anomalous specimen that does not provide features worthy of specific diagnosis and, following Tihen (1960c), it can be referred to *Spea* sp.

Other named species may also be assigned to *Spea* sp. because their diagnoses do not provide sufficient information for species determination. These include *Scaphiopus*

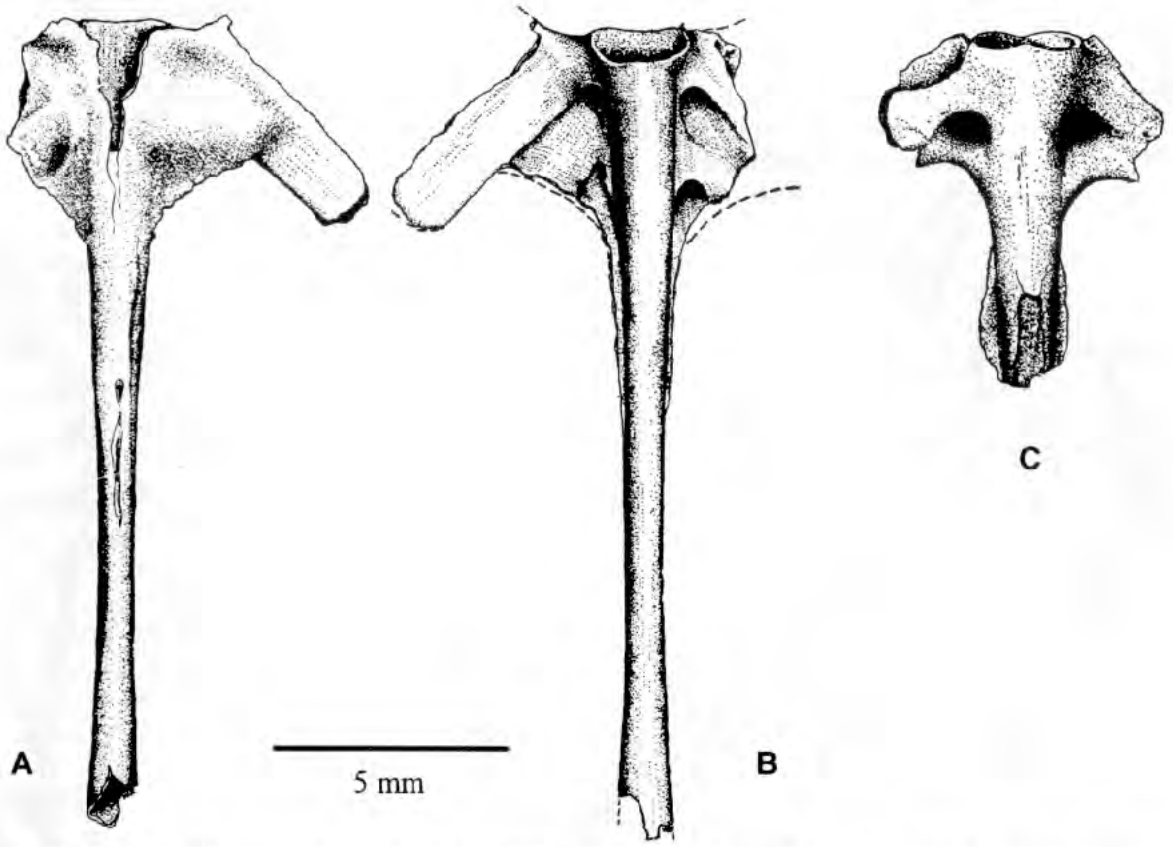

Fig. 29. Holotype of *Scaphiopus pliobatrachus* Taylor 1936, in dorsal (A) and ventral (B) views, and holotype of *S. antiquus* Taylor 1941 in ventral view (C). From Taylor (1941a).

pliobatrachus Taylor 1936 and *Scaphiopus diversus* Taylor 1942 (Fig. 29). Since some authors have not recognized *Spea* as a separate genus, some discoveries attributed to *Scaphiopus* may, in fact, represent *Spea*.

The first scaphiopodids appeared as early as the early Eocene and their fossil record is nearly continuous into the Recent, whereas pelobatids survived for only a short period of time on the North American continent (middle Eocene through early Oligocene). It may be speculated that they, in common with the pelodytids, did not succeed in competition with scaphiopodids.

F. Pelodytidae

Only two members of this family are known from the Tertiary of North America. *Tephrodytes brassicarvalis* Henrici 1994 (Fig. 30) was based on several skeletons and isolated bones from the Arikareean (late Oligocene-early Miocene) Cabbage Patch beds exposed in several localities in western Montana. It was assigned to the Pelodytidae on the basis of a fused tibiale and fibulare, and may be distinguished from other pelodytids by (1) the lightly sculptured frontoparietals contacting each other in a long median suture, leaving no fontanelle between them, (2) presence of a posterior tip of the frontoparietal, (3) lamella alaris of the squamosal with its upper, sculptured part reduced to a nubbin and its ramus paroticus present, (4) vertebral neural arches elongate, (5) sacral diapophyses widely expanded, and (6) anterior lamina of the scapula absent. It differs from *Miopelodytes* in that the lamella alaris squamosi is reduced and the sacral diapophyses are more expanded (Henrici 1994).

The only other North American Tertiary pelodytid is *Miopelodytes gilmorei* Taylor 1941b which was based on a single articulated specimen from the middle Miocene (Barstovian

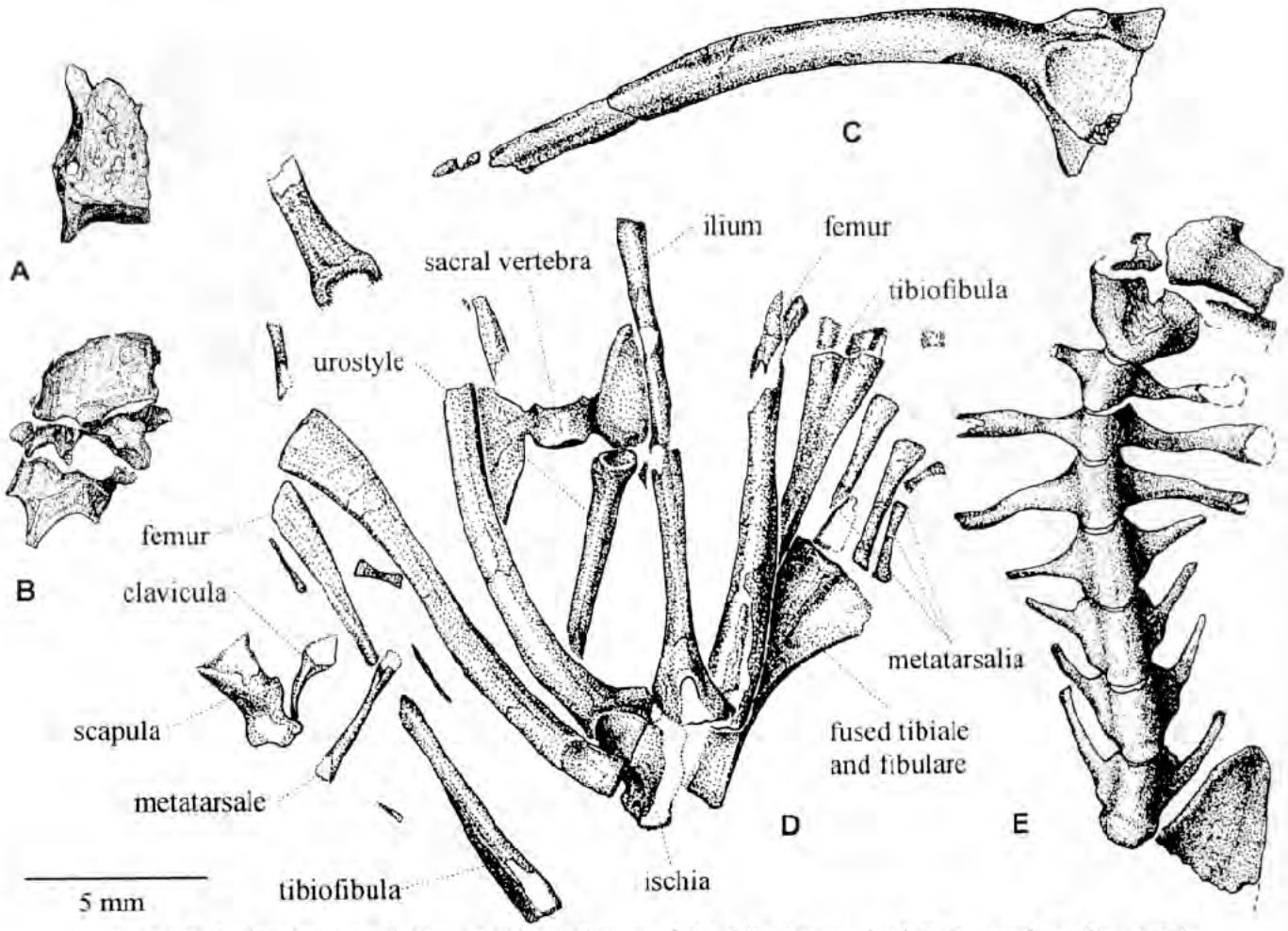

Fig. 30. Tephrodytes brassicarvalis Henrici 1994. A. Posterior half of the frontoparietal. B. Presacral vertebrae 1–3 in dorsal view. C. Left ilium in lateral view. D. Various postcranial elements. E. Vertebral column in ventral view. From Henrici (1994).

or Clarendonian) Elko Shales near Elko, Nevada (Fig. 31). Additional material, including tadpoles, has been recently collected from the type locality and is being studied by Dr. Ted Cavender (Henrici 1994). According to the original diagnosis by Taylor (1941b) it can be characterized by the absence of free ribs, eight presacral vertebrae, sacral vertebra with greatly widened diapophyses and presumably free from the urostyle, epiphyses of long bones cartilaginous, urostyle apparently composed of more than a single element, proximal tarsals (i.e., tibiale and fibulare) fused into a single bone, and the prehallux absent. It is obvious that some of these characters are of no diagnostic value. Henrici (1994) re-investigated the holotype and reported on some characters not previously known (e.g., presence of sculpturing on the dermal skull bones). Sanchíz (1998) summarized an emended diagnosis from her data, stating that the alar lamella of the squamosal is sculptured, with its posterior portion (= "otic ramus") well developed; the frontoparietal is paired, separated by a longitudinal median fontanelle, the transverse processes of the last two presacral vertebrae are directed strongly anteriorly, the sacral diapophyses are expanded but less so than in *Pelodytes*; the scapula is short, and the ischium does not extend posteriorly beyond the dorsal acetabular expansion of the ilium.

G. Leptodactylidae

A frog of the genus *Eleutherodactylus* was reported (as *Eleutherodactylus* sp.) from the upper Eocene amber of the Dominican Republic by Poinar and Cannatella (1987, 1988). Portions of the skin and the eyes were intact, but the specimen could not be determined

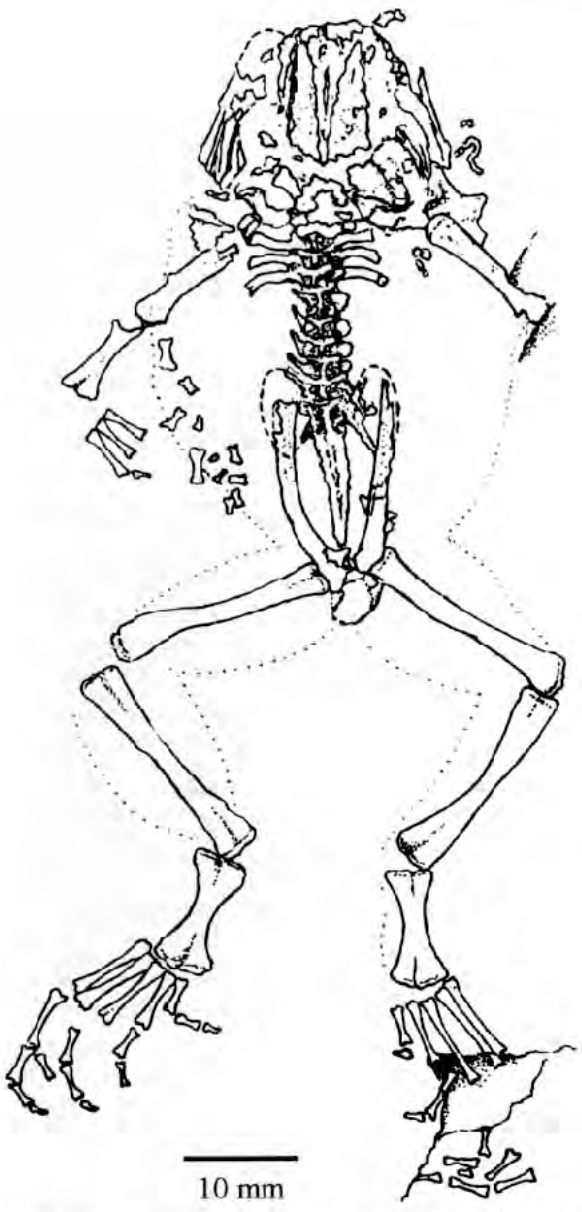

Fig. 31. Skeleton of the holotype of *Miopelodytes gilmorei* Taylor 1941 in dorsal view. From Taylor (1941b).

to species. It was also discussed by Mayer and Lazell (1988). There are several questionable remains of leptodactylids on the North American continent. Among them is a badly crushed organic impression consisting of dorsal and ventral parts described as *Eorubeta nevadensis* Hecht 1960. It was recovered from Core 8 in Member C, Sheep Pass Formation (lower Eocene) in White Pine County, Nevada. According to diagnoses given by Hecht (1960) and Lynch (1971) it may be allocated to the Leptodactylidae on the basis of a combination of the following characters: toothed maxilla, seven presacral vertebrae (Lynch recognized eight), the sacral diapophyses expanded distally and oriented at right angles to the midline, and the transverse processes of the presacral vertebrae of equal or subequal width and flattened distally, those of the posterior vertebrae being as long as the anterior ones and almost as long as the sacral transverse processes. Lynch (1971), however, concluded that *Eorubeta* does not closely resemble the skeleton of any modern frogs, including Leptodactylidae, and suggested a systematic assignment as "Family *incertae sedis*", which also was followed by Sanchíz (1998). Hecht (1960) mentioned three other frogs obtained from the same well-core as *Eorubeta*. They were never published, except for a brief note by Winfrey (1958) quoting Hecht's tentative identification of the third frog as being near *Eopelobates*.

In addition, the identity of the right ilium referred to as *Eleutherodactylus* sp. from the Thomas Farm Miocene beds of Gilchrest County, Florida cannot be justified according to Lynch (1971). It is equally likely that the fossil represents a young individual of *Acris* (*Acris barbouri* Holman 1967) that was described from the same locality (see below).

The last presumed leptodactylid is *Leptodactylus abavus* Holman 1965 from the lower Miocene of Florida. Lynch (1971) removed it from the family Leptodactylidae and placed it in the Ranidae, as *Rana abavus*. Sanchíz (1998) synonymized it with *Rana miocenica*.

Hence, it may be concluded that to date there is no clear evidence of Leptodactylidae on the North American continent.

H. Bufonidae

The earliest representative of the family Bufonidae (and, at the same time, the earliest member of the genus *Bufo*) in North America appeared in the early Miocene. It was described as *Bufo praevius* Tihen 1951 and it was originally based on iliac morphology (Fig. 32 J, K), although numerous other fragmentary elements were reported from the type

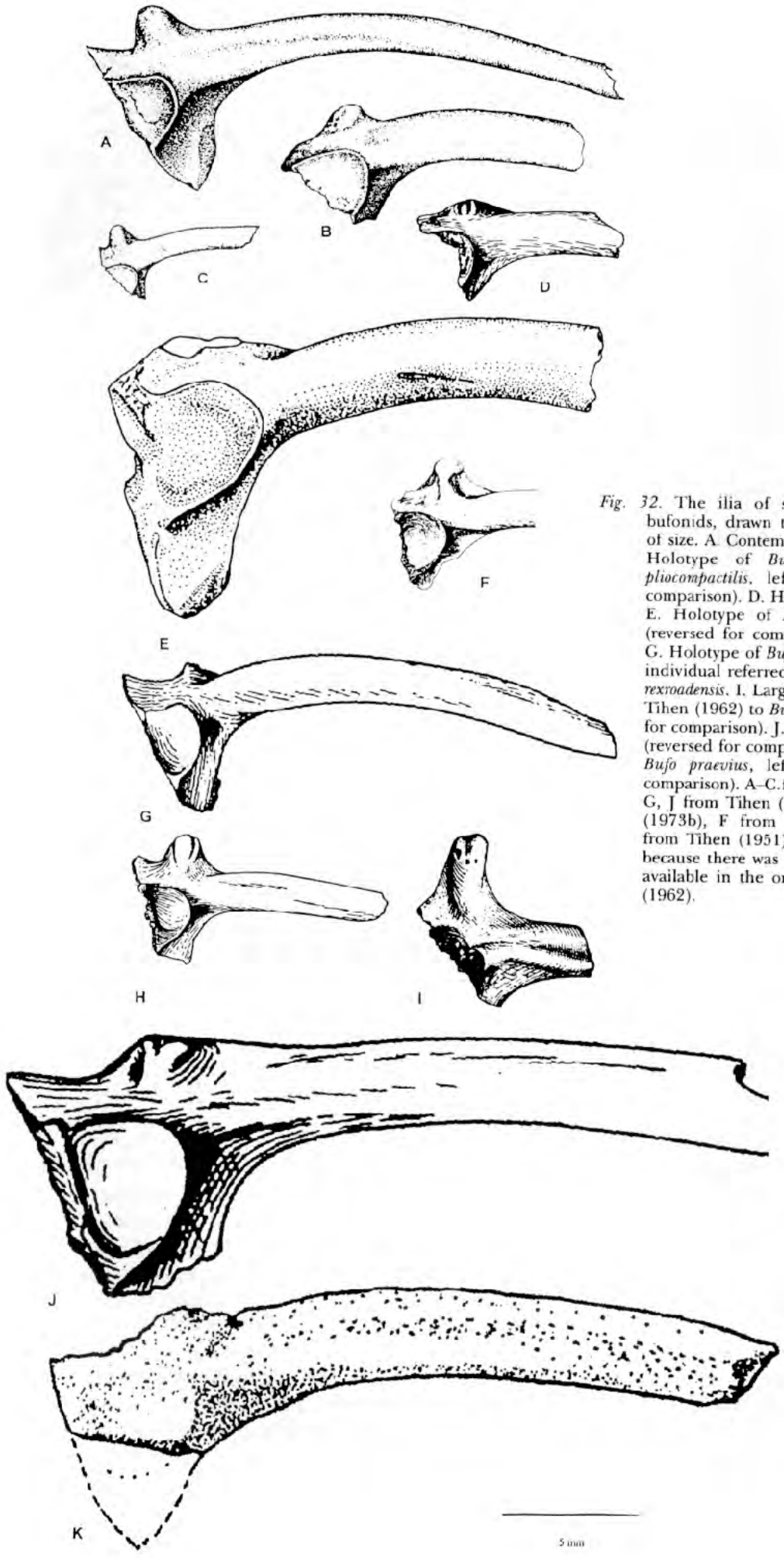

Fig. 32. The ilia of some North American bufonids, drawn to scale for comparison of size. A. Contemporary *Bufo speciosus*. B. Holotype of *Bufo holmani*. C. *Bufo pliocompactilis*, left ilium (reversed for comparison). D. Holotype of *Bufo speciosus*. E. Holotype of *Bufo kuhrei*, left ilium (reversed for comparison). F. *Bufo tiheni*. G. Holotype of *Bufo alienus*. H. Immature individual referred by Tihen (1962) to *B. rexroadensis*. I. Large individual referred by Tihen (1962) to *Bufo rexroadensis* (reversed for comparison). J. *Bufo praevius*, left ilium (reversed for comparison). K. Holotype of *Bufo praevius*, left ilium (reversed for comparison). A–C. from Parmley (1992), D, G, J from Tihen (1962), E from Holman (1973b), F from Auffenberg (1957), K from Tihen (1951). H and I not to scale because there was no information on size available in the original paper by Tihen (1962).

locality by Tihen (1951) and Holman (1967). It was found only in the lower Miocene (Hemingfordian) locality of Thomas Farm in Florida. According to Tihen (1962), its principal diagnostic characters are low tuber superius (its height being only about 20% of the length of its base) and high granular supraorbital crests oriented almost vertically and forming a sharp angle with the postorbital crests. In large, presumably old, individuals the exoccipital is fused with the frontoparietal-prootic complex, which indicates some degree of hyperostosis.

One of the North American *Bufo* that appeared nearly simultaneously in the middle Miocene (Barstovian) is *Bufo kuhrei* Holman 1973. As in numerous other bufonids, it was diagnosed on the shape of the ilium (Fig. 32E). It is known only from the Barstovian of the Norden Bridge locality in Nebraska. The main diagnostic characters are a low tuber superius and large pars descendens. Other characters given by Holman (1973b; see also Sanchíz 1998) including the large acetabular fossa and medial portion of the pars descendens bent to fuse with the corresponding part of the contralateral ilium, may be dependent on individual and ontogenetic variation. Later, Holman (1982) assigned to this species a fragment of a tibiofibula found at the same locality.

Bufo pliocompactilis Wilson 1968 is known from the middle Miocene through lower Pliocene from the mid-Hemphillian deposits of the Lemoyne Quarry in Keith County, southwestern Nebraska, and the Clarendonian of Wakeeney in Trego County, Kansas (Holman 1974; Parmley 1992). It is similar to extant *Bufo compactilis*, although the ilia can be distinguished by their small size and a particularly high, narrow tuber superius. Because of the similarity of *Bufo pliocompactilis* and *Bufo compactilis*, Sanchíz (1998) argued that the fossil species was synonymous with the extant form and designated it *nomina dubia*.

The earliest records of *Bufo suspectus* Tihen 1962 are from the middle Miocene (Barstovian), but its stratigraphic range may be extended into the upper Pliocene. It may be distinguished by the posterior margin of its tuber superius ilii being steeper than the anterior one. Since ilia of *Bufo valentinensis* Estes and Tihen 1964 are hardly distinguishable from those of *Bufo suspectus* (this fact was recognized by Estes and Tihen), *B. valentinensis* is now considered a synonym of *B. suspectus* (Sanchíz 1998). The holotype of *B. valentinensis* is known from the Miocene (Barstovian) of Norden Bridge Quarry, Nebraska (Estes and Tihen 1964), and the type of *B. suspectus* is from the Pliocene (Blancan) of Fox Canyon, Kansas (Tihen 1962). Other material referrable to this species comes from the Barstovian, Clarendonian and mid-Hemphillian Egelhoff sites (Chantell 1971; Holman 1987), Hottell Ranch (Voorhies *et al.* 1987), Kleinfelder in Saskatchewan (Holman 1970, 1973b), Norden Bridge (Holman 1973b), Railway Quarry (Tihen 1962; Estes and Tihen 1964; Holman and Sullivan 1981), Wakeeney (Wilson 1968; Chantell 1971; Holman 1974), and Lemoyne Quarry (Parmley 1992) in Nebraska, Kansas and Canada respectively.

Bufo marinus is an extant species questionably known from the Miocene of Kansas (Sanchíz 1998). Moderately younger are other representatives of *Bufo*, some of them being referrable to living species. *Bufo hibbardi* Taylor 1942 is a late Miocene toad known from Barstovian sites in Nebraska (Chantell 1971; Holman 1973a,b, 1982, 1987), and with some doubt from the mid-Hemphillian deposits of the Lemoyne Quarry in Keith County, southwestern Nebraska (Parmley 1992), and from a (late?) Hemphillian site in Kansas (Tihen 1962). Probably the same form (*Bufo* cf. *hibbardi*) was also reported from the Valentine Formation of Nebraska (Estes and Tihen, 1964). According to Tihen (1962) it can be distinguished from other species of *Bufo* by the anterior margin of its tuber superius ilii being much steeper than the posterior margin.

Bufo alienus Tihen 1962 is a late Miocene (Hemphillian, Ogallala Formation) toad found in 1884 at "Quarry E" near Long Island in Phillips County, Kansas. The holotype (and only known specimen) is the right ilium (Fig. 32G) that can be distinguished, according to Tihen, from other species of *Bufo* by its very low tuber superius, the posterior slope of which is markedly steeper than the anterior. Moreover, the tuber projects somewhat medially from the axis of the shaft.

Bufo holmani Parmley 1992 is a late Miocene (Hemphillian) member of *Bufo* described on the basis of ilia from the Devil's Nest Airstrip Locality in Knox County, northeastern Nebraska. According to Parmley, it differs from all other North American bufonid species by extremely large and robust ilia (see Fig. 32B), with the tuber superius long and smooth, the acetabulum large, and the ilial shaft compressed along its upper two-thirds but wider and ridge-like along the lower one-third. Besides the type locality, it was reported from Santee, another late Hemphillian site in Knox County, Nebraska.

Three forms associated with extant species, although sometimes with doubts, were reported as cf. *B.(americanus)* sp. from the Miocene (Hemphillian) Long Island site in Kansas (Moodie 1914) and as *Bufo* aff. *compactilis* from the Miocene (Hemphillian) of Lemoyne Quarry in Nebraska (Parmley 1992). Only the second species has an unquestionable record from the Pliocene (Blancan) of Kansas. The third is *Bufo cognatus*, which was questionably reported (as *Bufo* cf. *cognatus*) from the late Miocene (Clarendonian) of Wakeeney in Kansas (Holman 1974), and from the Hemphillian of Driftwood Creek in Nebraska and Long Island in Kansas (Tihen 1962). Its possible occurrence was also reported from the lower Pliocene (late Hemphillian) Santee Site of Nebraska by Parmley (1992). Other discoveries are from the early Blancan: Beck Ranch in Texas (Rogers 1976), Big Springs (Rogers 1984; Holman and Schloeder 1991) and Hornet's Nest (Rogers 1984; Holman and Schloeder 1991) in Nebraska.

It seems that in the Pliocene, bufonids constituted the dominant element of the North American anuran fauna (before they were accompanied by ranids in the late Pliocene). *Bufo campi* was based on a left tibiofibula from the lower Pliocene (Hemphillian) locality of Paterson Field, Arroyo de los Burros, Rincon, Chihuahua, Mexico (Brattstrom 1955a). Although the tibiofibula is generally considered a uniform element with little diagnostic value, this one is distinguished by the presence of a prominent ridge along the middle part of the bone, not known in any other Recent or fossil member of the genus. The taxon is represented only by the holotype and its taxonomic status needs to be confirmed by additional material. The possible occurrence of the extant species *Bufo speciosus* in the lower Pliocene (late Hemphillian) Santee Site of Nebraska was reported by Parmley (1992).

The following two extinct species have their fossil record limited to the middle Pliocene. *Bufo spongifrons* Tihen 1962 was based on the complete left frontoparietal, which is marked on its dorsal surface by moderately heavy cranial crests. The supraorbital and postorbital crests and, to a lesser extent, the entire dorsal surface of the frontoparietals, exhibit a light, porous, spongy texture. Associated ilia from the type locality (presumably belonging to the same taxon) have a high tuber superius, with its posterior slope steeper than the anterior. It was collected from "Quarry E" near Long Island in Phillips County, Kansas, which is of middle Pliocene (Hemphillian) age, as was the holotype ilium of *Bufo alienus*. Tihen (1962) also referred three ilia (distinct from those of *B. alienus*) to *B. spongifrons*. Whether they are actually associated with the holotype frontoparietal remains unproved.

The second of these extinct middle Pliocene species is *Bufo tiheni* Auffenberg 1957 which was originally based on a fragmentary sacral vertebra from the middle Pliocene (Hemphillian) Alachua Formation near Haile, Alachua County, Florida. Five ilia from the same locality were tentatively referred to this species although they are rather variable among themselves. According to Tihen (1962), the relatively long and somewhat depressed sacral centrum, as well as the moderate tuber superius ilii with its anterior slope decidedly steeper than the posterior are principal diagnostic characters of this species. *Bufo tiheni* is known only from the type locality.

The late Pliocene bufonids are represented by one extinct form, whereas two others may be associated with contemporary species. *Bufo rexroadensis* Tihen 1962 was based on a frontoparietal that bears heavy supraorbital and postorbital crests meeting each other at an obtuse angle. Both crests are greatly thickened at their point of juncture, but do not cover the posterior portion of the bone. Tihen (1962) associated with this frontoparietal several ilia (supposedly belonging to both immature and mature individuals) with very high

tuber superius having subequal anterior and posterior slopes, or with the anterior slope slightly steeper, as well as sacral vertebrae with short centrum and crests on their neural arches usually meeting in a broad, subangular arch. All this material comes from the Pliocene (Blancan, Rexroad Formation) Fox Canyon locality, Meade County, Kansas. In addition to the type locality, *Bufo rexroadensis* was also reported from the Pliocene Blancan localities, Beck Ranch in Texas (Rogers 1976) and Rexroad in Kansas (Tihen 1962; Gehlbach 1965; Schultze *et al.* 1985).

Bufo woodhousii is a recent species that was reported from two Pliocene Blancan localities: Beck Ranch in Texas (Rogers 1976) and Benson Locality, Cochise County, Arizona (Brattstrom 1955b; Tihen 1962; Gehlbach 1965). *Bufo alvarius* is also an extant species distributed in extreme southeastern California, southern Arizona and extreme southwestern New Mexico. Tihen (1962) tentatively referred to this species (as *Bufo* cf. *alvarius*) an anterior end of the urostyle from the Blancan of the Benson Locality of Cochise County, Arizona.

As stressed by Sanchíz (1998) numerous species of North American fossil *Bufo* were described on the basis of disarticulated material; however, at least ilia display some differences that can be considered taxonomically significant (Fig. 32). Bufonidae are known in North America since the lower Miocene (*B. praevius*). However, they became taxonomically more differentiated in the late Miocene (Hemphillian). In Europe, the earliest bufonids are also from the early Miocene and these records are already tentatively associated with contemporary taxa. It is difficult to decide whether the taxonomically diversified North American Miocene-Pliocene record reflects the true situation because many taxa are weakly based and need revision.

I. Hylidae

The Hylidae appears to be the second largest anuran group in the Tertiary of North America. Their earliest representative is *Hyla swanstoni* Holman 1968 which was based on the left ilia (Fig. 33B) originating from the early Oligocene Cypress Hills Formation in the vicinity of the north branch of Calf Creek in Saskatchewan. According to the original diagnosis, it is similar to the ilium of *H. miofloridana* Holman 1967 from the lower Miocene of Florida in its weakly developed tuber superius and in having a groove on the lateral border just anterior to the acetabulum, but differing from this species in being smaller and in having the groove shallower and with an indistinct ventral border. A few other disarticulated elements (ilium and fragmentary tibiofibulae) were recovered from the same locality.

Other representatives of *Hyla* are recorded only from the early Miocene (Hemingfordian), together with *Acris* and *Proacris*. *Acris* sp. was reported from the Arikareean of Martin Canyon, Colorado (Chantell 1965). Its later fossil record from the Barstovian (Egelhoff in Nebraska) (Holman 1987) and Clarendonian (Wakeeney in Kansas) suggests a continuous occurrence into the Recent. According to Holman (1967), the form from Egelhoff is different from *A. barbouri*, and probably belongs to a different species. *Acris barbouri* Holman 1967 was described on the basis of the right ilium (Fig. 34A) from the lower Miocene (Hemingfordian) of Thomas Farm, Gilchrest County, Florida. According to the original diagnosis it can be distinguished from *A. crepitans* and *A. gryllus* in that the tuber superius is relatively smooth

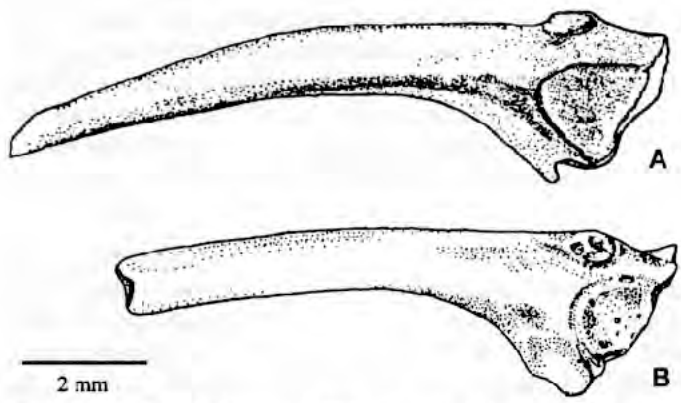

Fig. 33. Ilia of the holotypes of *Hyla miocenica* (A) and *Hyla swanstoni* (B). A from Holman (1966) and B from Holman (1968).

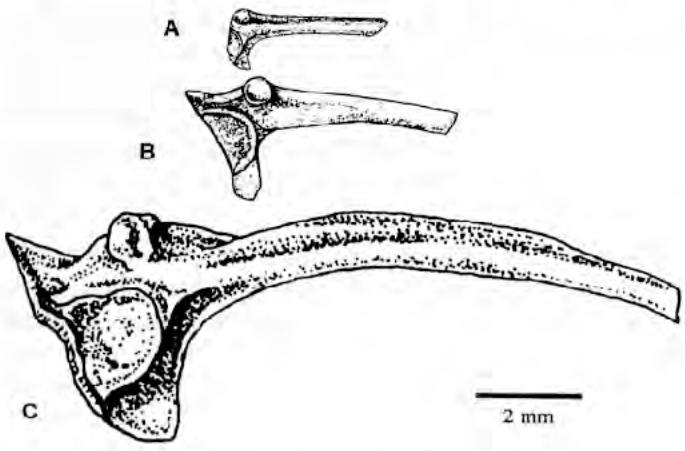

Fig. 34. Ilia of the holotypes of *Acris barbouri* (A), *Proacris mintoni* (B) and *Pseudacris nordensis* (C). A from Holman (1967), B (reversed for comparison) from Holman (1961), and C from Holman (1987).

and the pars ascendens is relatively short. During the same period, *Hyla* may be represented by *Hyla miofloridana* Holman 1967, which is based on a single left ilium from the Hemingfordian of Thomas Farm, Florida. However, as no other material than the holotype is available, and because allocation to the Hylidae is based on diagnostically weak evidence, Sanchíz (1998) listed *H. miofloridana* as *nomina dubia*.

The last species of *Hyla* that was reported from the lower Miocene (as *Hyla goini* Auffenberg 1956) is a recent species, *Hyla squirella*. *H. goini* was based on several fragmentary ilia from the Miocene (Hemingfordian) of Thomas Farm, Florida, to which Holman (1967) referred some other disarticulated material from the same locality. Since Holman could not distinguish these ilia from those of recent *Hyla squirella*, Sanchíz (1998) considered it synonymous with the latter species. It was also reported (as *H.* cf. *squirella*) from the upper Miocene-lower Pliocene (Barstovian) Valentine Formation of Norden Bridge Quarry, Nebraska (Estes and Tihen 1964; Chantell 1964).

Proacris mintoni Holman 1961 is a representative of the third hylid genus in the Hemingfordian of North America. It was described on the basis of a single isolated left ilium (Fig. 34B) found in the Thomas Farm site, Florida. No other material except for the holotype is available. Holman (1961, 1967) considered the following characters as diagnostic for the genus: large acetabulum, the pars descendens making an angle of about 90° with the iliac shaft and completely delimited dorsally by the anteroventral margin of the acetabulum, the rounded tuber superius placed anterior to the acetabulum, and a small ridge present between the tuber superius and pars ascendens. Although its morphology is clearly different from other taxa, the fact that only a single specimen is available casts some doubts on the validity of this taxon.

Several other hylids have been reported from the Barstovian, some of them tentatively assigned to extant species. *Hyla miocenica* Holman 1966 was described on the basis of a single left ilium (holotype in Fig. 33A) recovered from the middle Barstovian of Coldspring, Trinity River Pit, Texas. According to Holman, its principal distinguishing character is the shape of the tuber superius which is more oval in outline than in *H. arenicolor* and *H. squirella*, and less flattened and more protruding from the shaft than in *H. versicolor*. Assignment of a sacral vertebra from the Barstovian of Town Bluff, Texas, to *H. miocenica* by Holman (1977) is only tentative.

Pseudacris nordensis Chantell 1964 was described on the basis of a fragmentary ilium from the Barstovian Norden Bridge site of Nebraska. Later, Holman (1987) recorded a complete right ilium (Fig. 34C) from Egelhoff, also Nebraska, which he attributed to this species. According to Chantell (1964) and Holman (1987), this species can be distinguished by the following characters: (1) dorsal acetabular expansion small and narrow, posteriorly directed, and with its anterior edge straight. (2) dorsal protuberance (= tuber superius) elevated and far from the fossa, (3) ventral acetabular expansion narrow and larger than

modern species of *Pseudacris*; and (4) a longitudinal ridge on the medial surface of the ilial shaft. Sanchíz (1998) considered it similar or even synonymous with *P. clarki* and listed it as *nomina dubia*. Unidentified *Pseudacris* sp. was recorded on the basis of a fragmentary ilium from Egelhoff by Chantell (1971); Holman (1987) found another type of ilium attributable to this genus.

All other hylids are tentatively assigned to contemporary species. *Hyla versicolor* was reported (as "*Hyla* cf. *versicolor* or *Hyla chrysoscelis*") from the Norden Bridge Quarry, Nebraska (Chantell 1964, 1966). *Hyla chrysoscelis* has a continuous fossil record only since the middle Pleistocene. In this connection it is worth mentioning that the ilia of *H. chrysoscelis* and *H. versicolor* are difficult to distinguish from one another, so their taxonomic determination should be taken only as tentative.

Acris crepitans is also a contemporary species that was tentatively reported (as *A.* cf. *crepitans*) from the Barstovian localities of Egelhoff (Chantell 1971) and Norden Bridge Quarry (Estes and Tihen 1964; Chantell 1964), both in Nebraska, and from the Pliocene (Blancan) localities of Beck Ranch, Texas, and Rexroad, Kansas (Tihen 1960a; Chantell 1966; Rogers 1976). *Hyla* cf. *cinerea* was reported, as was *Hyla* cf. *gratiosa* from the Barstovian Valentine Formation of Norden Bridge Quarry, Nebraska (Estes and Tihen 1964; Chantell 1964). *Pseudacris clarki* was questionably reported (in this case as *Pseudacris* cf. *clarki*) from the Valentine Formation of the Norden Bridge Quarry (Estes and Tihen 1964; Chantell 1964). Holman (1996), considering *Pseudacris* from the middle Miocene Glad Tidings site of Nebraska, suggested that all Barstovian records reported as *Pseudacris* cf. *clarki* could possibly represent a new extinct species of *Pseudacris*.

In addition, three types of ilia that could belong to *Hyla* sp. were reported from the Miocene (Barstovian) of the Egelhoff site (Holman 1987), and several ilia of unidentifiable *Hyla*, resembling some living species, were found in the middle and upper Hemphillian of Nebraska (Parmley 1992). Two remaining Tertiary hylids are from the late Pliocene, both being also tentatively attributable to recent species. *Acris gryllus* was reported (as *Acris* cf. *gryllus*), from the Pliocene Wendell Fox site in Kansas (Tihen 1960b), and *Hyla* cf. *regilla* was reported, on the basis of the left ilium, from the upper Pliocene Glenns Ferry Formation of the Hagerman area in Twin Falls, Owyhee and Elmore Counties, Idaho, by Chantell (1970). Holman (1968) pointed out the importance of the earliest North American hylids being referrable to the contemporary genus *Hyla*. However, one should keep in mind that the iliac morphology of all North American members of the genus *Hyla* is essentially uniform, so these early species need to be revised on the basis of other elements.

J. Ranidae

Although there is unquestionable evidence that the Ranidae occurred in North America in the Miocene, their main diversification took place only in the Pliocene. The earliest record is a left ilium from the Hemingfordian locality of Thomas Farm, Florida, described as *Rana miocenica* Holman 1965. As was mentioned above (see Leptodactylidae), *Leptodactylus abavus* Holman 1965 from the same locality was placed in the family Ranidae by Lynch (1971) as *Rana abavus*. Later, Sanchíz (1998) synonymized it with *Rana miocenica*. According to Sanchíz, the material assigned to *R. miocenica* does not show enough taxonomic features to establish its differential status from other members of the *Rana (pipiens)* group. Nevertheless, this taxon seems to provide undoubted evidence of the Ranidae in the Hemingfordian of North America.

Rana johnsoni La Rivers 1953 was described on the basis of a nearly complete articulated skeleton exposed in dorsal aspect from the Miocene (Clarendonian) near Virginia City, Storey County, Nevada. No diagnosis was given and the anatomical description is vague and non-informative; however, Zweifel (1954) compared it with *R. pliocenica* and emphasized its slender ilia and noticed its overall similarity with living *R. boylei* or *R. pretiosa*. *Rana clamitans* Latreille 1801 is a recent species that was reported, as *Rana* cf. *clamitans*, from the Miocene (middle Barstovian) of the Hotell Ranch in Nebraska (Voorhies *et al.* 1987).

Although ranid ilia are difficult to identify at the species level, several of them were tentatively assigned to *Rana pipiens* (as *Rana* cf. *pipiens*), reported from the upper Miocene (Clarendonian) Wakeeney site in Kansas (Holman 1974), and from the Pliocene (mid-Hemphillian) site Lemoyne Quarry and upper Hemphillian Santee and Mailbox Prospect sites, all in Nebraska (Parmley 1992). Similarly, some ilia from the latter two localities were provisionally referred to *Rana catesbeiana* (as *Rana* cf. *catesbeiana*) (Parmley 1992). *Rana (pipiens)* sp. was reported from the upper Pliocene (Blancan) of the Beck Ranch site in Texas (Rogers 1976). Quite a large number of disarticulated bones from the upper Pliocene Glenns Ferry Formation of the Hagerman area in Twin Falls, Owyhee and Elmore Counties, Idaho, were attributed to *Rana pipiens* by Chantell (1970). Unidentifiable *Rana* was reported from the Miocene (Barstovian) of Egelhoff site (Holman 1987), and from other sites of the Miocene-Pliocene Valentine Formation of Nebraska (Estes and Tihen 1964).

Rana pliocenica Zweifel 1954 is represented by slightly disarticulated posterior parts of the skeleton including the fifth vertebra, exposed in ventral aspect from the late Miocene (Hemphillian) near Rodeo, Contra Costa County, California. According to the original diagnosis it may be characterized by a relatively deep medial groove on the ventral surface of the sacral vertebra and a relatively deep ilial shaft (Fig. 35). According to Zweifel it most closely resembles living *R. aurora* and *R. pipiens*.

All other fossil remains of *Rana* were tentatively assigned to extant species. *Rana areolata* and *Rana palustris* were reported from the upper Pliocene (Blancan) of the Beck Ranch site in Texas (Rogers 1976), *Rana sylvatica* from the Pliocene (Blancan) of Hornet's Nest, Nebraska (Rogers 1984; Holman and Schloeder 1991), and *Rana* cf. *aurora* from the upper Pliocene Glenns Ferry Formation of the Hagerman area in Twin Falls, Owyhee and Elmore Counties, Idaho, by Chantell (1970).

Some other forms were described as Ranidae, but only two of them may be considered valid species of *Rana*. *Anchylorana moorei* Taylor 1942 from the Pliocene (Blancan) locality Rexroad 3, Kansas, is characterized by the fusion of the sacral vertebra and urostyle; however, as pointed out by Holman (1963b), this is an anomaly which should not be taken as a diagnostic character. Since in other available characters this sacral vertebra corresponds to that in *Rana*, this species is considered a synonym of *Rana* sp. by Sanchíz (1998). Questionable taxa include *Rana feyae*, *Rana rexroadensis*, *Rana ephippium*, *Rana meadensis*, and *Rana valida* all having been described from the same locality on the basis of sacral vertebrae (Taylor 1942). Sanchíz (1998) reviewed this material and concluded that only two ranid forms were present, namely *R. feyae* and *R. rexroadensis*. Nevertheless, since the original descriptions are not sufficient, Sanchíz placed all mentioned forms among *nomina dubia*.

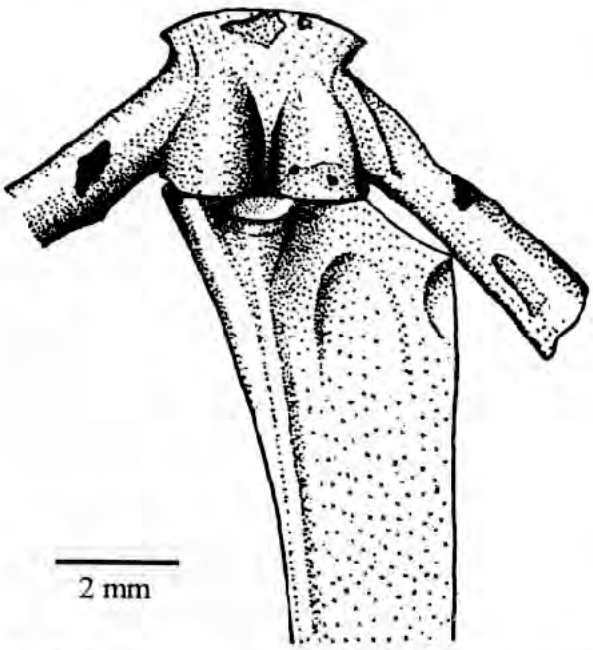

Fig. 35. Sacral vertebra and slightly disarticulated urostyle of the holotype of *Rana pliocenica*. From Zweifel (1954).

K. Microhylidae

Only one microhylid was questionably reported from the Tertiary of North America: *Gastrophryne* cf. *carolinensis* from the Miocene (Hemingfordian) of Thomas Farm, Florida (Sanchíz 1998).

L. Indeterminate Anura

Indeterminate anurans were reported from the early Eocene

Golden Valley Formation of North Dakota (Estes 1988), and from the middle Eocene Laredo Formation in Webb County, Texas (Westgate 1989).

V. TERTIARY ANURA OF AUSTRALIA

Fossil anurans from Australia were recently reviewed by Tyler (1991) and individual taxa are discussed by Sanchiz (1998). Twenty species have been recovered from eight localities, ranging from the early Eocene through the Pleistocene. The fossil record includes hylids, myobatrachids, and microhylids (but not ranids), which are also present in the modern fauna. Only a single extinct genus, the microhylid *Australobatrachus*, with two species, has been recognized. Within the Myobatrachidae, one extinct species each of the living genera *Kyarranus* and *Crinia* have been named, as well as two extinct species of *Lechriodus* (from the Lower Eocene and Miocene, and two of *Limnodynastes* (Upper Oligocene and Miocene). The living hylid species *Pelodryas caerulea* has been questionably reported from the Middle Miocene, and unnamed species of *Litoria* have been cited from other localtities. Quaternary fossils, dating back to 40 000 years ago, include exclusively species living in the same areas today.

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