



The oldest representative of a brown frog (Ranidae) from the Early Miocene of Germany

MADELAINE BÖHME

The brown frogs (*Rana temporaria*-group) are a monophyletic group in the family Ranidae, which have a scarce fossil record in Europe that begins only in the Late Pliocene. A new fossil from the Dietrichsberg locality (Germany, Thuringia) extends their stratigraphic range back to the Early Miocene, and suggests that their origin lies outside the Western Palaearctic, most probably in Asia, with subsequent immigration in the Burdigalian.

The recent European species of *Rana* are distinguished by ecological and morphological characteristics and are placed into two monophyletic groups of non-sister-group relationship (Günther 1996): the more aquatically adapted green or water frogs (Western Palaearctic green frogs, group of *Rana ridibunda*) and the brown frogs with a mainly terrestrial mode of life. Brown frogs are a group of about 20 species (8 Western Palaearctic, 10 or more Eastern Palaearctic, and 2 Caucasian species) of medium-sized Ranidae with prominent dorsolateral folds and dark facial masks. This group, with strong morphological similarities, generally known as the group of *Rana temporaria*, is restricted to the Palaearctic. Their monophyly is proven by cytogenetic investigations (Mensi *et al.* 1992; Green & Borkin 1993). Among the European species (*Rana temporaria*, *R. arvalis*, *R. dalmatina*, *R. graeca*, *R. latastei*, *R. iberica*, *R. italica*, *R. pyrenaica*), the moor frog *Rana arvalis* occupies a special position with regard to chromosome number and some osteological details. Green & Borkin (1993) placed this taxon as the sister group to all other European and East Asian brown frogs.

The fossil history of brown frogs is poorly known. The geologically oldest Asian representatives are known from the Late Miocene of Kazakhstan, locality Pavlodar – *R. cf. amurensis*, *R. cf. arvalis*, *R. (temporaria)* sp. and Japan, locality Kabuto-Iwa – *R. (temporaria)* sp. (see Sanchiz 1998). In Europe, the brown frogs have been much more common since the Pleistocene. Until now the oldest representatives of the recent species *Rana temporaria*, *R. dalmatina*, *R. arvalis*, and the extinct *Rana straussi* from Willershausen (Špinar 1980), occur in the Late Pliocene. The possible record of *Rana temporaria* in the Early Miocene of Central Europe is therefore of biogeographical importance.

Locality and stratigraphy. — The Dietrichsberg locality is situated in the northern part of the Rhön mountains, 5 km south of the town Vacha (E 10°02', N 50°47'). This area is part of the northern Rheinisch Volcanic Arc and is characterised by volcanism during the Early Miocene. The fossil bearing sediment, underlying a basaltic sheet, is an oilshale similar to those from the well known Messel locality. According to palynological data, radiometric data of basalts, and correlation with a nearby small-mammal bearing horizon, these sediments are of middle to late Burdigalian age (mammal zone MN3) approximately 19 to 20 Myr ago (M. Böhme 1993).

Among the excellently preserved vertebrate fossils (partly with soft part preservations), a small leuciscine minnow (*Palaeoleuciscus dietrichsbergensis* M. Böhme, 1993) is predominant. Apart from a second fish (*Palaeotinca egeriana* Obrhelova, 1969), the following remains are known: a discoglossid frog, a soft shell turtle (M. Böhme 1995) and a vespertilionid bat.

Suborder Neobatrachia Reig, 1958

Family Ranidae Gray, 1825

Genus *Rana* Linnaeus, 1758

The two recent European species groups of *Rana*, the *Rana ridibunda* group, and the *Rana temporaria* group can be distinguished by a set of osteological characteristics (G. Böhme 1977; Špinar 1980, for East Asian brown frogs see Nokariya 1984). In the present study only the morphology of ilium, squamosal, quadratojugal, maxilla and the frontoparietal are significant. The ilioischadic juncture, a very important feature for separation of the both groups (G. Böhme 1977), is not visible in this specimen.

Rana cf. *temporaria* Linnaeus, 1758

Fig. 1.

Description and comparisons. — The relatively small (skull/body-length 52.5 mm) frog is exposed in dorsal aspect and is completely preserved with the exception of the intermaxillary region, the right carpal region, and the distal phalanges of the left fourth toe. The fossil is covered by a thin oilshale lamina except in the pelvic region (Fig. 1B). Nevertheless, the important osteological details are well visible.

The skeleton displays typical ranid features (see Fig. 2). The frontoparietal is paired and lacks sculpture and fontanelles, the vertebral column consists of eight presacral vertebrae, and free ribs are absent. The sacral vertebra bears a narrow transverse processes and has two distal condyles. The terminal phalanges are simple and a praehallux is developed.

Based on the osteological features, the Dietrichsberg frog is clearly a member of the brown frogs. The left ilium is visible from the medial side (Fig. 1A). The dorsal crest is lower than the vexillum and runs parallel to the ventral margin of the latter. The tuber superior is markedly developed and protrudes over the dorsal crest (which is a distinguishing characteristic of *R. temporaria*; Fig. 2K) and the whole bone is mostly straight. The frontoparietal is comparatively broad; its length/width ratio is 2.0. In *R. temporaria* this value is 2.30–2.75 ($n = 7$), in *R. arvalis* 2.14–2.74 ($n = 4$), in *R. dalmatina* 2.23–2.60 ($n = 5$), and in *R. graeca* 2.12 ($n = 1$; cf. G. Böhme 1977: fig. 5b). In contrast, the frontoparietal of green frogs is much more slender, in *R. ridibunda*, 2.78–3.16 ($n = 5$) and *R. lessonae*, 2.75 ($n = 1$; cf. G. Böhme 1977: fig. 5h). The position of the parietal eminence is situated more laterally (as in *R. temporaria*, *R. dalmatina*, *R. graeca* but not in *R. arvalis*, Fig. 2D, E and G. Böhme 1977: fig. 5), and the linea medialis is longer and in its distal part it parallels the lateral margin of the frontoparietal (Fig. 2D). The quadratojugal is comparatively large, being approximately the same size as the squamosal. On the squamosal, the zygomatic process is not elongated as in green frogs (Fig. 2G–I). Furthermore, the palatine process of the maxilla is reduced and stout (Fig. 2A–C). Altogether, these features support the view that the Dietrichsberg specimen belongs to the brown frogs. In contrast, the green frogs possess a more curved ilium with a high dorsal crest (Fig. 2M), a slender frontoparietal, a medial shift of the parietal eminence (Fig. 2F), a short quadratojugal (shorter than the squamosal), an elongated and narrow palatine process of the maxilla (Fig. 2C), and a prolonged zygomatic process (Fig. 2I).

Within the Recent European brown frogs, the species *R. dalmatina*, *R. latastei*, *R. graeca*, and *R. iberica* are distinguishable from the Dietrichsberg specimen in the possession of long hind limbs. The ratio between femur + tibiofibula and skull/trunk-length is always greater than 1.0 (cf. Günther *et al.* 1996: fig. 173). In the fossil specimen, this measurement is 0.9 which corresponds to the average value of *R. temporaria*.

In contrast to *R. arvalis*, the ilium of the Dietrichsberg frog possesses a lower dorsal crest and a tuber superior that protrudes over the dorsal crest. The palatine process of the maxilla is low. On the frontoparietal the parietal eminence is situated more laterally, the prootic process is prominent and anteriorly orientated, the occipital process is better developed, and the linea medialis is more noticeable. The angle of the sacral wing (between the transverse processes) is lower in *R. arvalis* (mean 85° – min./max. 72 – 93° , $n = 3$) than in the Dietrichsberg specimen (115°). In contrast, the latter value corresponds well to *R. temporaria* which has a mean angle of 105° (min./max. 95 – 125° , $n = 6$).

The Pliocene brown frog *Rana straussi* Špinar, 1980 differs from the Dietrichsberg specimen and the recent species by a smaller skull (body/skull-ratio 4.3 to 4.8, contrary to the Dietrichsberg specimen of 3.5 like other Brown frogs). Furthermore, the zygomatic process of *R. straussi* is not reduced and is therefore of the type of the green frogs (Špinar 1980).

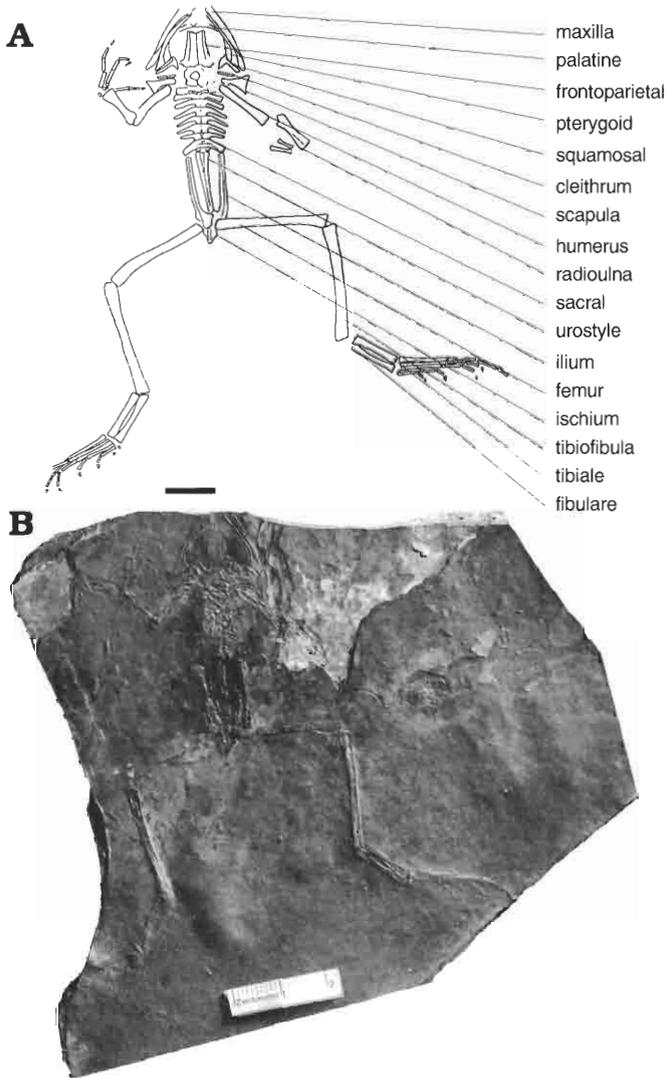


Fig. 1. *Rana cf. temporaria*. Nearly complete skeleton in oilshale (Mr. Haldenwang's collection, no number). A. Explanatory drawing (scale bar 10 mm). B. Photograph (on the right site: a young individual of *Palaeoleuciscus dietrichsbergensis*).

The morphology of the ilium, squamosal, quadratojugal, frontoparietal, maxilla, and the metric relations of the Dietrichsberg frog are similar to the Recent species *Rana temporaria*. Only a slightly broader shape of the frontoparietal differs from *R. temporaria*. Due to the overlying oilshale lamina the parietal part of the frontoparietal (the position and development of the prootic, occipital and transverse lines) is not clearly visible. For these reasons I prefer an open nomenclature and describe the Dietrichsberg frog as *Rana cf. temporaria*.

Conclusions. — The presence of *Rana cf. temporaria* in the Early Miocene (MN3, 19 to 20 Myr ago) of Central Europe considerably extends the stratigraphical range of brown frogs (Fig. 3). Mensi *et al.* (1992) suggest, based on the molecular clock-hypothesis, that the common ancestor of *R. temporaria* and *R. iberica* split from the other Western Palaeartic brown frogs in the Late Pliocene. If this is true,

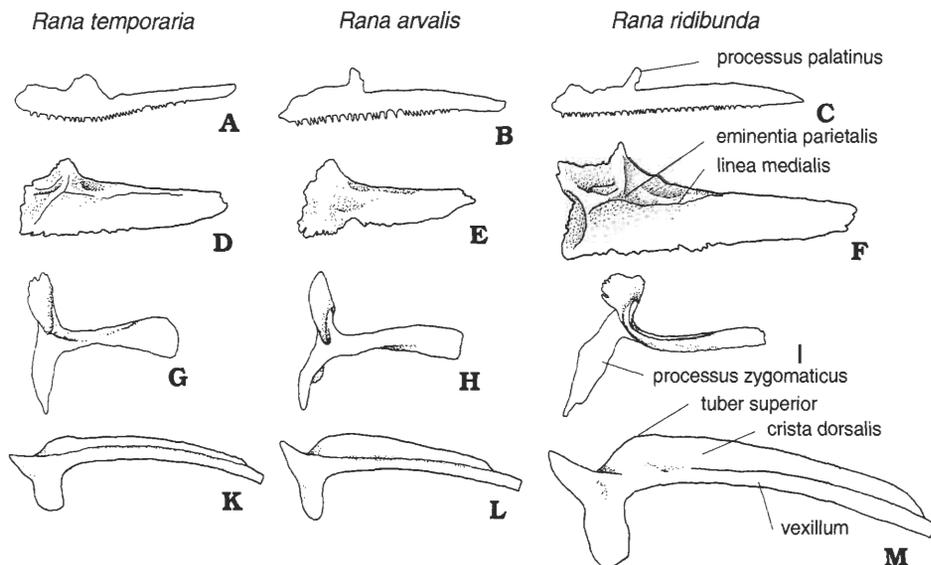


Fig. 2. Osteological features of the extant brown frogs *Rana temporaria* (BSP 1982 X 2277) and *Rana arvalis* (BSP 1982 X 2374) and the Western Palearctic Green Frog *Rana ridibunda* (BSP 1982 X 5340). A–C, maxilla; D–F, frontoparietal; G–I, squamosal; K–M, ilium. Not to scale. See Appendix for explanation of institutional abbreviations.

and the Dietrichsberg specimen is one of this common ancestor, than this main stock of Western Palearctic brown frogs is osteologically very similar to the extant *R. temporaria*. Contrary, if the Dietrichsberg specimen is a member of the extant *R. temporaria* then the first split of the main stock of Western Palearctic brown frogs must precede the Early Miocene.

The next question is, are brown frogs an autochthonous European group and if not, where is their possible center of origin. The green frogs have been known in Europe since the Late Eocene (MP17, Rage 1984). The oldest representative of a true Western Palearctic green frog (= group of *Rana ridibunda*) is documented from Lower Oligocene deposits (MP22, 32 Myr ago; Sanchiz, Schleich, & Esteban 1993). These authors interpret this group as an Asian immigrant during the Eocene/Oligocene faunal turnover ('grande coupure'). During the Oligocene and Early Miocene, the Western Palearctic green frogs are very common (personal observation) and are the only European representatives of the family Ranidae. Because this group and the Western Palearctic brown frogs were not sister groups, there is no possibility of an autochthonous evolution of brown frogs in Europe. The sister group of the Western Palearctic brown frogs are according to Green & Borkin (1993), Chinese and Japanese forms. So, the most likely interpretation is that the Western Palearctic brown frogs are Asian immigrants. Although, brown frogs are currently unknown in Oligocene and Lower Miocene deposits of Central or Western Asia, this area may be a possible centre of origin for this group.

The late Early Miocene and Middle Miocene have long been known as a time of extensive faunal interchange (cf. Van der Made 1996). Plate tectonic movements in the Arabian and Anatolian Realm at the end of the Burdigalian lead to a closure of the Tethys ocean and therefore to new landbridges and migration routes between Europe, Africa and Asia (Rögl 1998). In contrast to the Eocene/Oligocene faunal migration ('grande coupure'), this process was extended over a long time interval. The equid *Anchitherium* (from Northern America via Asia) and the anthracotheriid *Brachyodus* (from Africa) arrived earlier in Europe in the MN3 than the proboscideans of African origin or the modern cricetids of Asian origin, which first occur in Europe in the early MN4. This faunal interchange is also obvious in the lower tetrapods and fishes. At the Dietrichsberg locality *Palaeoleuciscus* occurring in MN3 is the first true leuciscine minnow (M. Böhme 1993) to appear in Central Europe, and the first barbines and cyprinine representatives arrived later during MN4 (M. Böhme unpublished). The oldest bufonids oc-

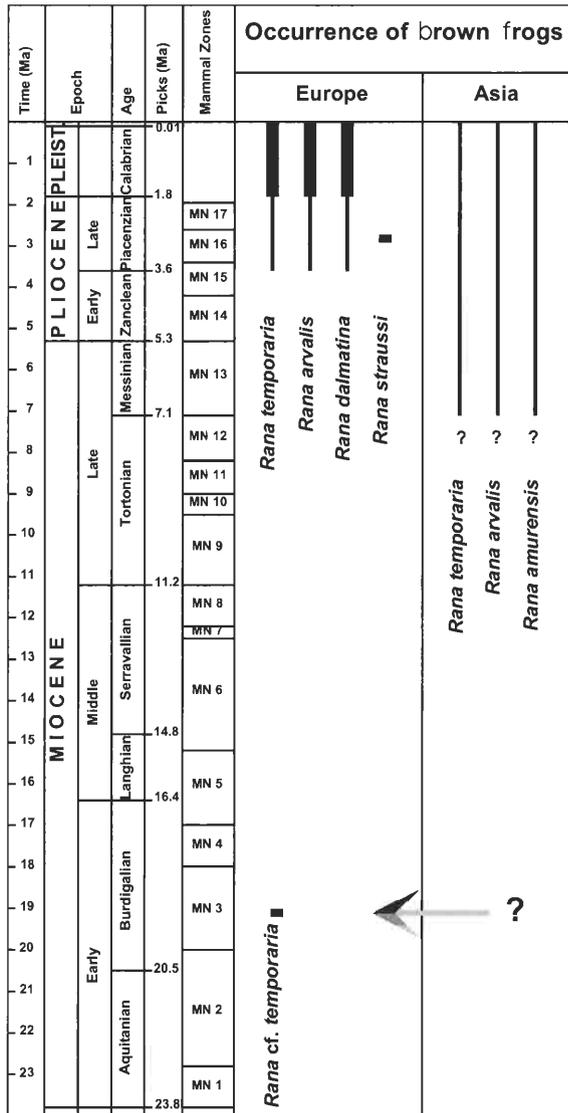


Fig. 3. Stratigraphical occurrence of brown frogs in Europe and Asia (after Sanchiz 1998). Possible migration is indicated by arrow.

cur in the early MN4 (Sanchiz 1977), the first hylids in the late MN4 (Sanchiz 1997). Within the reptiles the African migration of trionychid turtles during the Burdigalian (M. Böhme 1995), the first appearance of chamaeleonids in the early MN3 (Moody & Roček 1980), and of varanids (*Varanus sensu stricto*) at the MN3/MN4 transition (M. Böhme unpublished) are remarkable.

In this context, the first immigration of brown frogs from a possible center of origin in Western or Central Asia during the MN3 corresponds well with the biogeographical situation in the late Early Miocene. It took place in the beginning of a great change in the European herpetofauna which is characterised in a similar way to North America (Tihen 1964; Estes & Baez 1985) by immigration of modern elements, Recent genera or species groups.

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Appendix

The described original of *Rana* cf. *temporaria* is housed in the private collection of Mr. Lutz Haldenwang (address of the collector: An der Siedlung 4, 01445 Radebeul, Germany). Comparisons are made on the following osteological material (Bayerische Staatssammlung für Paläontologie und Geologie, München; BSP 1982 X – numbers): *Rana ridibunda* (1829, 2879, 4463, 4576, 5340); *Rana temporaria* (697, 2276, 2277, 2281, 2415, 2459, 4082, 5520, 5937–5940, 6122); *Rana dalmatina* (2282, 2912, 5339, 2984, 5338); *Rana arvalis arvalis* (1840, 1844, 2374, 6107, 6133).

Madelaine Böhme [m.boehme@lrz.uni-muenchen.de], Universitätsinstitut für Paläontologie und Historische Geologie München, Richard-Wagner-Straße 10, D-80333 München, Germany.