

Vertebrates from the Early Miocene lignite deposits of the opencast mine Oberdorf (Western Styrian Basin, Austria):

2. Amphibia

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(With 56 text-figures and 1 table)

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Abstract

The amphibian fauna from the Lower Miocene (MN4) sites Oberdorf O3 and O4 near Graz (Austria) is composed of *Albanerpeton inexpectatum* (Albanerpetontidae); *Chelotriton* sp., cf. *Chioglossa* sp., *Salamandra sansaniensis*, and *Triturus roehrsi* (Salamandridae); *Latonia ragei* (Discoglossidae); *Palaeobatrachus* sp. (Palaeobatrachidae); *Pelodytes* sp. (Pelodytidae); *Hyla* sp. (Hylidae); and *Rana (ridibunda)* sp. (Ranidae). While *S. sansaniensis* and green frogs are common amphibians in the European Miocene, the enigmatic *Albanerpeton inexpectatum* is a very rare taxon, registered for the first time outside its type locality. *Triturus roehrsi*, abundant in Oberdorf, is a primitive newt previously only known after a few vertebrae from the type locality. *Triturus roehrsi* can be phylogenetically adscribed to the subgenus *T. (Triturus)*, probably close to the living *T. vittatus*. The giant *Latonia ragei*, a poorly known discoglossid, seems to be the predominant species in the anuran assemblage, palaeobatrachids and ranids being quite scarce. The few *Pelodytes* remains that have been recovered probably represent an undescribed species. The presence of *Hyla* points to an arrival to Europe of this immigrant much earlier than the previously known Vallesian and Turolian records.

Key words: Anura; Caudata; Allocaudata; Amphibia, Miocene; Austria; Paleontology.

Zusammenfassung

Die Amphibienfauna aus den Fundstellen O3 und O4 des Unter-Miozäns (MN4) in der Nähe von Graz (Österreich) besteht aus: *Albanerpeton inexpectatum* (Albanerpetontidae); *Chelotriton* sp., cf. *Chioglossa* sp., *Salamandra sansaniensis* und *Triturus roehrsi* (Salamandridae); *Latonia ragei* (Discoglossidae); *Palaeobatrachus* sp. (Palaeobatrachidae); *Pelodytes* sp. (Pelodytidae); *Hyla* sp. (Hylidae); und *Rana (ridibunda)* sp. (Ranidae). Während *S. sansaniensis* und die Grünfrösche zu den häufigen Amphibien im Miozän Europas zählen, ist der rätselhafte *Albanerpeton inexpectatum* ein seltenes Taxon, das erstmals außerhalb der Typuslokalität gefunden wurde. *Triturus roehrsi*, ein primitiver Wassermolch, ist in Oberdorf häufig, vorher war er nur durch einzelne Wirbel aus der Typuslokalität bekannt. *Triturus roehrsi* kann dem Subgenus *T. (Triturus)* zugeschrieben werden und steht möglicherweise der rezenten *T. vittatus* nahe. Der riesige *Latonia ragei*, ein kaum bekannter Scheibenzüngler, scheint die vorherrschende Species unter den Froschlurchen zu sein, während Palaeobatrachidae und Ranidae ziemlich selten vorkommen. Die wenigen Reste, die von *Pelodytes* gefunden wurden, repräsentieren vielleicht eine unbeschriebene Art. *Hyla* deutet auf eine wesentlich frühere Einwanderung in Europa hin als die vorher bekannten Funde aus dem Vallesium und Turolium belegen.

Schlüsselwörter: Froschlurche; Schwanzlurche; Allocaudata; Miozän; Österreich; Paläontologie.

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Introduction

In spite of a recent increase in the paleoherpetological research, the fossil record of European amphibians remains rather poor (SANCHIZ in press), and the discovery of new sites and faunal assemblages is still highly relevant for the understanding of the phylogenetic and faunistic dynamics of this group. The layers O3 and O4 in the open-cast mine Oberdorf, in the Köflach-Voitsberg coalfield situated West of Graz (Steiermark, Austria), have yielded an important vertebrate fauna which also includes a small number of amphibians. Oberdorf O3 and O4 have been dated in the late Otnangium (chron C5Dn; DAXNER-HÖCK et al. 1998), equivalent to the earliest Aragonian in the Western European usage (Van der MADE 1998). The mammalian fauna indicates a Neogene Mammal Unit MN4, and has been dated about 17 Ma by magnetostratigraphy (DAXNER-HÖCK et al. 1998).

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Materials and methods

The fossil materials studied (1903 batrachian fragments), are deposited in the collections of the Naturhistorisches Museum Wien (NHMW), and usually all are disarticulated elements, most of them minute broken remains. Oberdorf O3+O4 is a mixed sample of both layers. The comparative material belongs to the herpetological collection of the Museo Nacional de Ciencias Naturales (Madrid, Spain; MNCN). Anatomical nomenclature follows SANCHIZ (in press) for Anura, and FRANCIS (1934) and ESTES (1981) for Allocaudata and Caudata. Complete synonymy lists can be found in ESTES (1981) and SANCHIZ (in press), for Caudata and Anura respectively, and will not be repeated here.

Systematic paleontology

Order Allocaudata FOX & NAYLOR, 1982

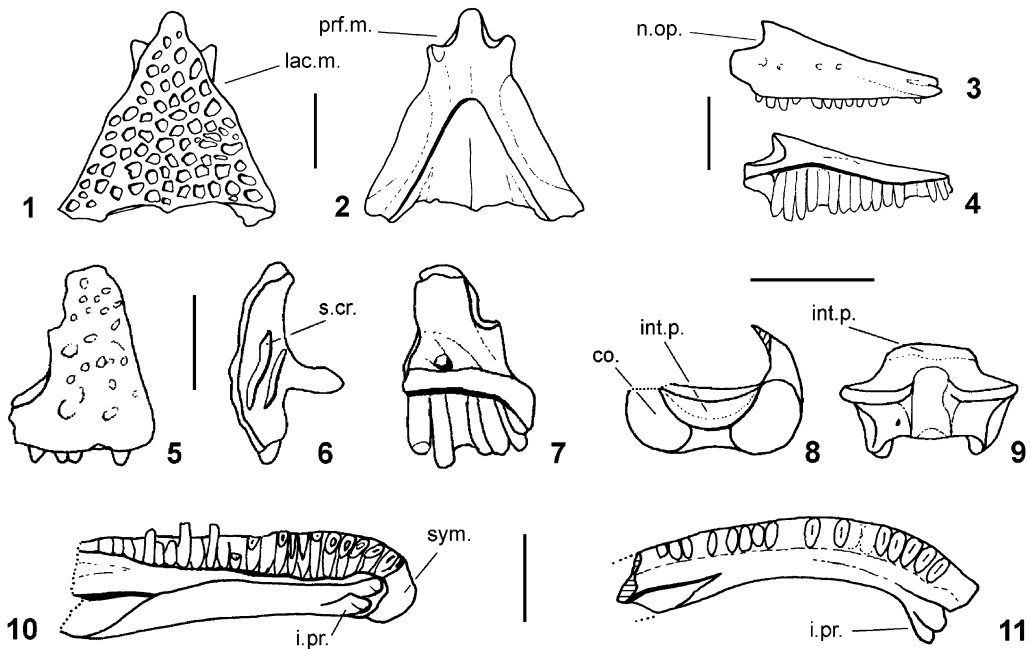
Albanerpetontidae FOX & NAYLOR, 1982

Albanerpeton ESTES & HOFFSTETTER, 1976

***Albanerpeton inexpectatum* ESTES & HOFFSTETTER, 1976**

(fig. 1–11)

M a t e r i a l: Eight premaxillae (Oberdorf O3: 1998z0015/0001/1; Oberdorf O4: 1998z0015/0002/1–7). 18 frontals (Oberdorf O3: 1998z0015/0001/2–4; Oberdorf O3+O4: 1998z0015/0003/1; Oberdorf O4: 1998z0015/0002/8–21). 6 parietals (Oberdorf O3: 1998z0015/0001/5; Oberdorf O4: 1998z0015/0002/23–27). 1 lacrymal? (Oberdorf O4: 1998z0015/0002/22). 2 undetermined skull roof fragments (Oberdorf O4: 1998z0015/0002/28–29). 2 maxillae (Oberdorf O3: 1998z0015/0001/6; Oberdorf O4: 1998z0015/0002/30). 33 dentaries (Oberdorf O3: 1998z0015/0001/



Figures 1–11: *Albanerpeton inexpectatum*. Frontal in dorsal (1) and ventral (2) views (Oberdorf O4); lac.m.: lacrymal margin; prf.m.: praefrontal margin. Left maxilla in external (3) and inner (4, reversed) views (Oberdorf O3). Right premaxilla in external (5), symphysis (6) and inner (7) views (Oberdorf O3) s.cr.: symphysis crests. Atlas in anterior (8) and ventral (9) views (Oberdorf O3). co.: cotyle. int.p.: intercotylar process. Left dentary in inner (10) and upper (11) views (Oberdorf O3). i.pr.: intersymphysary processes. sym.: symphysis. Scale equals 1 mm.

7–11; Oberdorf O3+O4: 1998z0015/0003/2–5; Oberdorf O4: 1998z0015/0002/31–54). 1 atlas (Oberdorf O3: 1998z0015/0001/12). 5 vertebrae (Oberdorf O3: 1998z0015/0001/13; Oberdorf O4: 1998z0015/0002/55–58).

Description and taxonomic assignment: All the elements recovered agree with the extremely peculiar morphology of *Albanerpeton inexpectatum*, as described from La Grive (France) by ESTES & HOFFSTETTER (1976) and ESTES (1981). Its detailed description would be unnecessary. Some small differences have been noticed between the material from La Grive and Oberdorf: the atlantal intercotyle process seem better developed in Oberdorf, as well as the inter-premaxillary symphysis, which is strengthened by two vertical crests and narrow elongated furrows. The articulation between the lower mandibles has always two accessory processes, but in a sample of 10 dentaries from Oberdorf O4, two elements presented a subequal development of the processes, while in the remaining ones the upper or lower process was slightly better developed (50%) than the other. Teeth are sometimes very weakly tricuspidate, as indicated for the type locality, but more often unicuspidate in our case, even both conditions occur in the same bone. The teeth do not have circular sections, instead they are anterior-posteriorly compressed, especially in the lower and middle parts of their height. In premaxillae, but probably also in the other tooth-bearing elements, the teeth are implanted in narrow alveo-

lar sockets. Nevertheless, the minor differences found between the specimens from Oberdorf and La Grive, pending future variability studies, do not warrant at present the supposition that a different taxon might have been living in Oberdorf.

C o m m e n t s: The albanerpetontid sample from Oberdorf is the second one studied from the European Tertiary, and in spite of being older, it clearly shows a close morphological similitude with *Albanerpeton inexpectatum*, a species previously known only from La Grive (France; MN 7+8). Albanerpetontids are an extinct enigmatic group of uncertain relationships, known from the Jurassic and Cretaceous of North America, Europe and Central Asia (ESTES 1981, FOX & NAYLOR 1982, NESSOV 1988, MCGOWAN & EVANS 1995), and appears unexpectedly also in the Miocene of La Grive, as discovered by ESTES & HOFFSTETTER (1976).

Order Caudata OPPEL, 1811

Salamandridae GRAY, 1825

Chelotriton POMEL, 1853

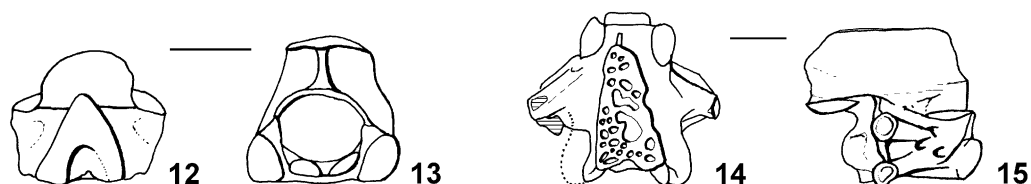
***Chelotriton* sp.**

(fig. 12–15)

M a t e r i a l: One otoccipital (Oberdorf O3: 1998z0016/0001/1). 1 atlas (Oberdorf O3: 1998z0016/0001/2). 17 precaudal vertebrae (Oberdorf O3: 1998z0016/0001/5–13; Oberdorf O3+O4: 1998z0016/0003/1; Oberdorf O3: 1998z0016/0002/1–6). 3 postsacral vertebrae (Oberdorf O4: 1998z0016/0001/7–9). 1 neurapophysis of a trunk vertebra (Oberdorf O3: 1998z0016/0001/3). 2 caudal vertebral centra (Oberdorf O3: 1998z0016/0001/4; Oberdorf O4: 1998z0016/0002/10). 1 humerus (Oberdorf O3: 1998z0016/0001/14).

D e s c r i p t i o n and taxonomic assignment: Both the otoccipital and the more complete vertebrae preserved could be clearly referred to the salamandrid "group II genera" of ESTES (1981). The neurapophyseal dermal plates, if not broken, have the shape of a broad arrow point, a characteristic of *Chelotriton*, a genus widely distributed in the European Tertiary. Nevertheless, some neural spines show a sculpture based on pits, and not a pustular pattern. According to the distinction made by ESTES (1981), the latter feature would indicate a member of the genus *Tylototriton* (including *Echinotriton*), rather than *Chelotriton* or the early Miocene *Brachycormus*. If we take into account that our material represents larval or metamorphosing specimens, as indicated by size and bone texture, the absence of well developed pustular tubercles can be merely explained as an ontogenetic bias. The presence of *Tylototriton* in Oberdorf would also be unlikely on chronological grounds, because in Europe this genus has been found only in the Lutetian (ESTES 1981). A larger sample, including full adults, as well as data on the still unknown morphology of isolated elements of *Brachycormus* and *Chelotriton ogygius* (see RŔĚK 1996), would be necessary to confirm the Oberdorf species identification as *Chelotriton paradoxus*.

C o m m e n t s: As acknowledged by ESTES (1981) and RŔĚK (1994b, 1996), the generic boundaries among *Brachycormus*, *Chelotriton*, and *Tylototriton* are difficult to delimitate, a situation made even more difficult once that neotenic evolutionary trends have been detected in the group.



Figures 12–15: *Chelotriton* sp. Atlas in dorsal (12) and anterior (13) views (Oberdorf O3). Trunk vertebrae in dorsal (14) and lateral (15) views (Oberdorf O3+O4). Scales equal 1 mm.

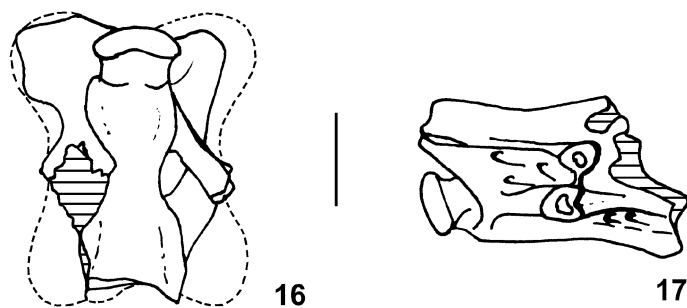
Chioglossa BOCAGE, 1864

cf. *Chioglossa* sp.
(fig. 16–17)

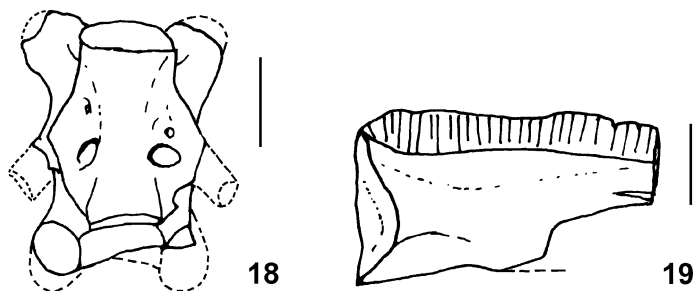
M a t e r i a l: One trunk vertebra (Oberdorf O4: 1998z0017/0002/1).

D e s c r i p t i o n and taxonomic assignment: Unfortunately only one fragmentary vertebra has been found. The condyle, more rounded than in *Salamandra* and with reduced notochordal fossa, is separated from the centrum by a clear constriction. In ventral view, the centrum shape is elongated, and its width decreases in the middle, increasing posteriorly in the cotyle region, where it shows a ventral surface posteriorly flattened. Rib-bearers of subequal size, with its bases placed in the anterior and middle half of the vertebra. Crests between centrum and ventral rib-bearers are not well developed. In spite that only a few morphological features are observable, they are sufficiently diagnostic to allow a generic assignment, following the criteria and description given by ESTES (1981). Only the absence of a developed notochordal notch in the condyle would not be like most fossil *Chioglossa* specimens, but this feature has been found to be quite variable in a sample of *C. meini* from La Grive that was available for comparison. Besides *Chioglossa*, the highest similitude would be with *Mertensiella*, but it differs in the position of the origin of the ventral rib-bearer, placed much more anterior in Oberdorf, and in *Mertensiella* having well developed ventral crests between posterior centrum and lower rib-bearers (SANCHIZ & MLYNARSKI 1979).

C o m m e n t s: This living genus, now relict in the Iberian peninsula, is known from the Miocene of La Grive (MN 7+8) and with doubt also from the German Upper Oligocene (ESTES 1981).



Figures 16–17: cf. *Chioglossa* sp. Trunk vertebrae in ventral (16) and lateral (17) views (Oberdorf O4). Scale equals 1 mm.



Figures 18–19: *Salamandra sansaniensis*. Trunk vertebra (18) in ventral view (Oberdorf O4). Right dentary (19) in inner view (Oberdorf O4). Scales equal 1 mm.

Salamandra LAURENTI, 1768

Salamandra sansaniensis LARTET, 1851

(fig. 18–19)

Material: One dentary (Oberdorf O4: 1998z0018/0002/1). 1 atlas (V1) (Oberdorf O4: 1998z0018/0002/2). 9 trunk vertebrae (Oberdorf O4: 1998z0018/0002/3–11). 1 postsacral vertebra (Oberdorf O4: 1998z0018/0002/12). 4 caudal vertebrae (Oberdorf O3+O4: 1998z/0018/0003/1; Oberdorf O4: 1998z0018/0002/13–15). 2 neural arches (Oberdorf O4: 1998z0018/0002/16–17). 1 rib (Oberdorf O4: 1998z0018/0002/18).

Description and taxonomic assignment: Identification criteria for vertebrae follow ESTES & HOFFSTETTER (1976) and SANCHIZ & MLYNARSKI (1979). The fragments recovered are badly broken, but they agree in size and morphology with *S. sansaniensis*, within the variability of the fossil sample from La Grive (ESTES & HOFFSTETTER 1976; personal observations).

Comments: This *Salamandra* species group of large sized animals is widespread in the Central European Tertiary, from late Eocene to Upper Miocene (ESTES 1981), and resembles closely the living *Salamandra infraimmaculata*, from Turkey, Lebanon, Israel and other Near East countries.

Triturus RAFINESQUE, 1815

Triturus roehrsi HERRE, 1955

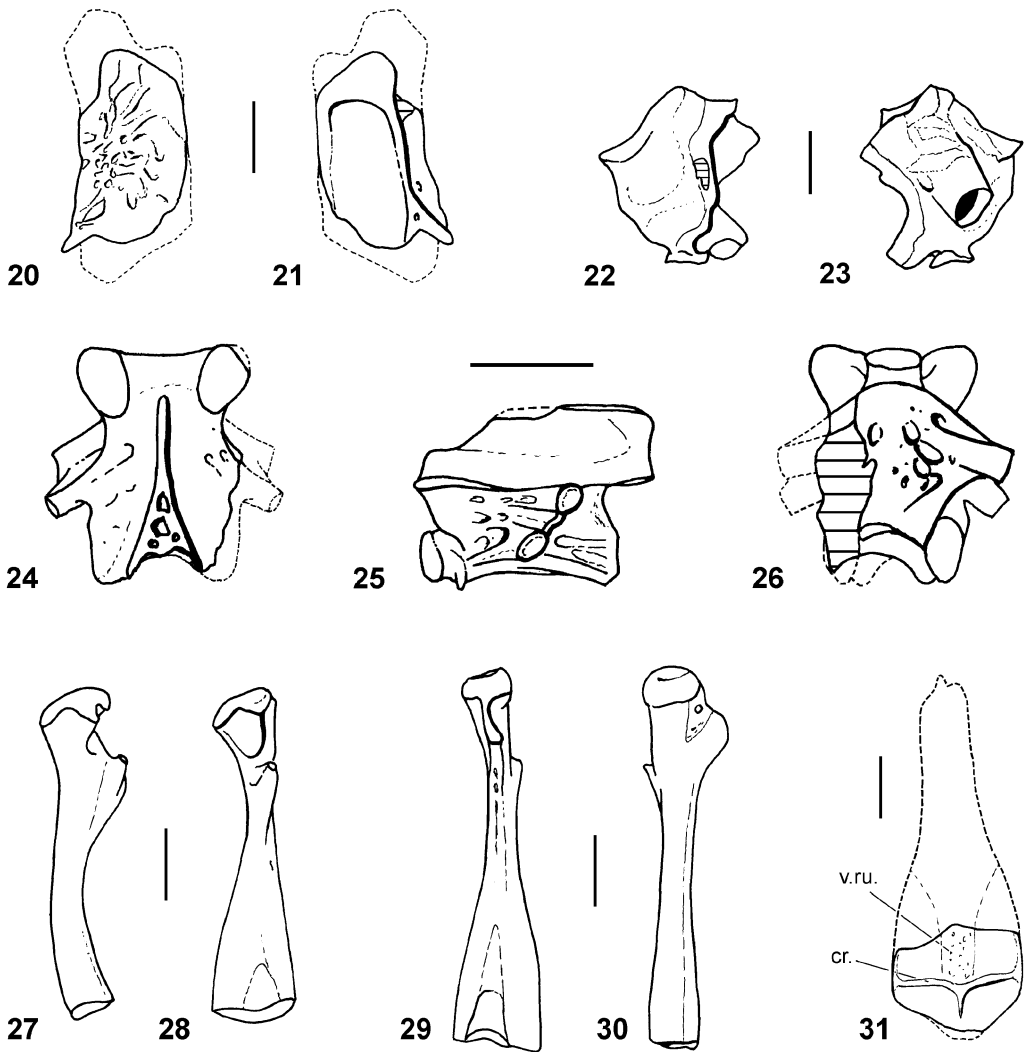
(fig. 20–31)

1955 *Triturus röhrsi*.– HERRE: 792–794, fig. 6.

1981 *Triturus rohersi*.– ESTES: 89, fig. 21 E.

The original descriptor dedicated this species to the German scientist Dr. Manfred RÖHRS, and thus the correct spelling would be *roehrsi* after the provisions of the current International Code of Zoological Nomenclature (1985, Article 32d–i).

Material: Thirty five frontals (Oberdorf O3: 1998z0019/0001/1–3; Oberdorf O4: 1998z0019/0002/1–32). 3 parietals (Oberdorf O4: 1998z0019/0002/33–35). 8 otoccipitals (Oberdorf O3: 1998z0019/0001/4–5; Oberdorf O3+O4: 1998z0019/0003/1; Oberdorf O4: 1998z0019/0002/36–40). 8 maxillae (Oberdorf O3: 1998z0019/0001/6–7; Oberdorf O4: 1998z0019/0002/41–46). 5 parasphenoids (Oberdorf O3: 1998z0019/0001/8; Oberdorf O4: 1998z0019/0002/



Figures 20–31: *Triturus roehrsi*. Left frontal in dorsal (20) and ventral (21) views (Oberdorf O4). Left otoccipital in dorsal (22) and ventral (23) views (Oberdorf O3). Trunk vertebra in dorsal (24), lateral (25) and ventral (26) views (Oberdorf O3). Left femur in lateral (27) and flexor (28) views (Oberdorf O3+O4). Left humerus in flexor (29) and lateral (30) views (Oberdorf O3+O4). Parasphenoid in ventral (31) view (Oberdorf O4). cr.: posterior crests. v.ru.: ventral rugosities. Scales equal 1 mm.

47–50). 9 dentaries (Oberdorf O4: 1998z0019/0002/51–59). 1 ceratobranchial? (Oberdorf O4: 1998z0019/0002/60). 26 atlas (Oberdorf O3: 1998z0019/0001/9–14; Oberdorf O3+O4: 1998z0019/0003/2; Oberdorf O4: 1998z0019/0002/61–79). 215 precaudal vertebrae (Oberdorf O3: 1998z0019/0001/15–63; Oberdorf O3+O4: 1998z0019/0003/3–19; Oberdorf O4: 1998z0019/0002/80–228). 50 caudal centra (Oberdorf O3: 1998z0019/0001/64–85; Oberdorf O4: 1998z0019/0002/229–256). 1 rib (Oberdorf O4: 1998z0019/0002/257). 1 scapula (Oberdorf O3: 1998z0019/0001/86). 14 ilia (Oberdorf O3: 1998z0019/0001/87–89; Oberdorf O4: 1998z0019/0002/

258–268). 95 humeri (Oberdorf O3: 1998z0019/0001/90–113; Oberdorf O3+O4: 1998z0019/0003/20–23; Oberdorf O4: 1998z0019/0002/269–335). 5 radius (Oberdorf O3: 1998z0019/0001/114–116; Oberdorf O4: 1998z0019/0002/336–337). 6 ulnae (Oberdorf O4: 1998z0019/0002/338–343). 82 femora (Oberdorf O3: 1998z0019/0001/117–143; Oberdorf O3+O4: 1998z0019/0003/24–31; Oberdorf O4: 1998z0019/0002/344–390). 5 tibiae (Oberdorf O4: 1998z0019/0002/391–395). 2 fibulae (Oberdorf O3: 1998z0019/0001/144–145).

D e s c r i p t i o n and systematic assignment. The species *Triturus roehrsi* was very briefly described by HERRE (1955) from the Miocene (MN 5 or 6) of Džvínská Nová Ves (= Neudorf, Spalte), based on a few fragmented vertebrae, and subsequently reviewed by ESTES (1981). I have been unable to study the type material of *T. roehrsi*, but the middle trunk vertebral morphology of the Oberdorf specimens agree with this species in neurapophyseal height, shape, dermal sculpture, lateral crests and transverse processes (rib-bearers). Furthermore, as will be discussed elsewhere, this species shows a combination of vertebral features very similar to the living *T. vittatus*, allowing the differentiation of *T. roehrsi* from any other of the extant *Triturus* species. The similarity with *T. vittatus*, and not with other *Triturus* species, can also be detected in several of the skull bones recovered. There are, however, clear differences between *T. roehrsi* and *T. vittatus*, in particular concerning the extent of skull sculpture and the ventral surface of the vertebral centra. The skull of *Triturus roehrsi* presents a pattern of sculpture based on deep furrows and irregular pits, much more extensive than in *T. vittatus*, in which it is much reduced or restricted to the orbital margin, or than in the other living species. The ventral aspect of the centra shows trabecular structures that connect it with the ventral rib-bearers, giving in many instances a peculiar rhomboid ("diamond") shape, more clearly visible in the most anterior vertebrae. The several parasphenoids found show well developed posterior crests in their ventral surface, unlike other species in the genus, although their attribution to *T. roehrsi* is not beyond doubt.

C o m m e n t s: Both HERRE (1955) and ESTES (1981) considered that this species was probably a member of the *T. (vulgaris)* group. If the taxonomic placement of the new Oberdorf material is correct, the morphology of this species would rather point to the large-sized *Triturus* clade (subgenus *Triturus*). A complete osteological analysis of this large and diversified living genus, never adequately done, would be necessary to ascertain the phylogenetic relationships of *T. roehrsi*. Nevertheless, if the vertebral and skull sculpture is considered primitive, all the living *T. (Triturus)* species share a considerable synapomorphic reduction on this feature. Whether *T. vittatus* and *T. roehrsi* present a sister-species relationship, or just a plesiomorphic phenetic similitude, cannot be decided at present. After the sample recovered in Oberdorf, *Triturus roehrsi* becomes the only extinct species of the genus which is not a *nomem dubium* or a *nomen vanum* (see ESTES 1981, for a list of taxa).

Salamandridae indet.

M a t e r i a l: One parasphenoid (Oberdorf O3: 1998z0020/0001/1). 1 maxilla (Oberdorf O4: 1998z0020/0002/1). 1 atlas (Oberdorf O4: 1998z0020/0002/2).

These fossils are either too damaged or can be referred to more than one taxon. However, there are no indications of any other salamandrid species in Oberdorf, different from the ones already described.

Order Anura RAFINESQUE, 1815

Discoglossidae GÜNTHER, 1858 (1845)

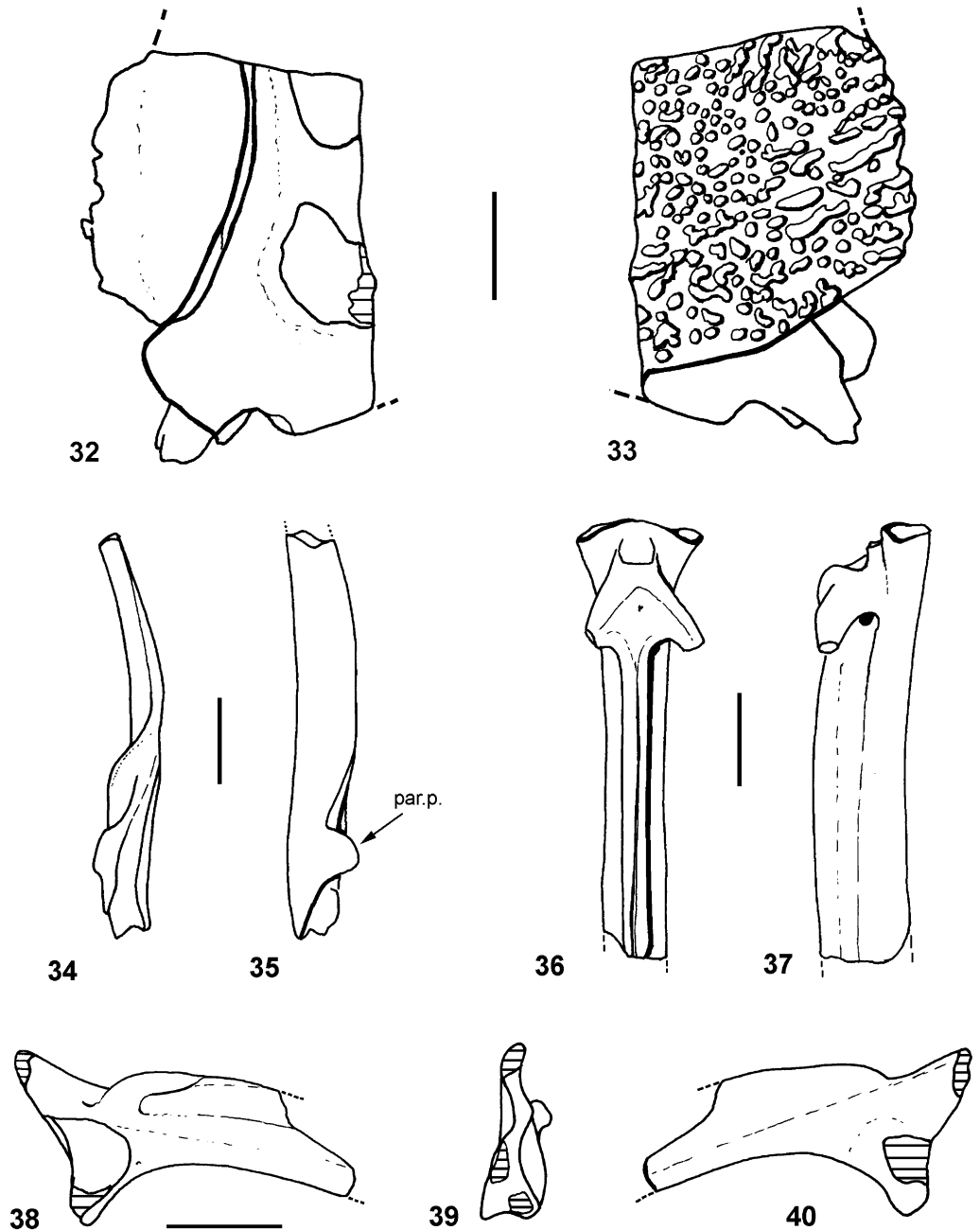
Latonia MEYER, 1843.***Latonia ragei* HOSSINI, 1993**

(fig. 32–40)

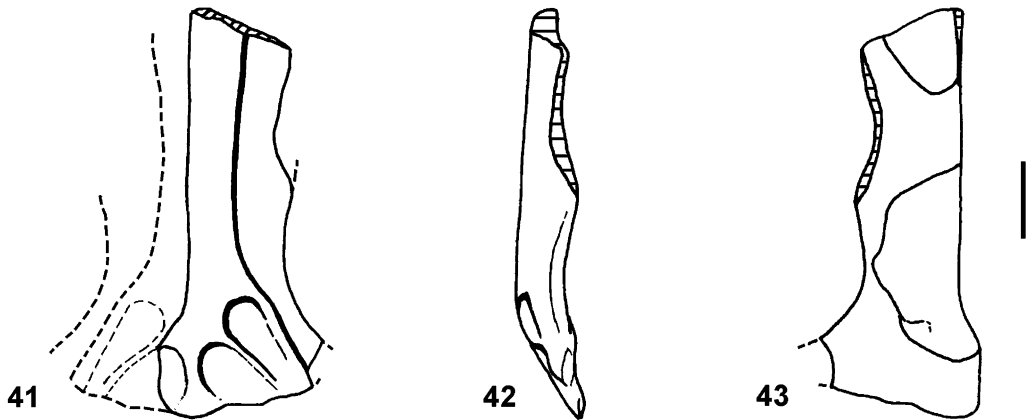
M a t e r i a l: Three premaxillae (Oberdorf O3: 1998z0021/0001/1–3). 17 maxillae (Oberdorf O3: 1998z0021/0001/4–10; Oberdorf O3+O4: 1998z0021/0003/1; Oberdorf O4: 1998z0021/0002/1–9). 1 frontoparietal (Oberdorf O3+O4: 1998z0021/0003/2). 1 frontoparietal? (Oberdorf O3: 1998z0021/0001/11). 1 squamosal? (Oberdorf O3: 1998z0021/0001/12). 4 parasphenoids (Oberdorf O3: 1998z0021/0001/13; Oberdorf O4: 1998z0021/0002/10–12). 16 mandibles (praearticular fragments) (Oberdorf O3: 1998z0021/0001/14–16; Oberdorf O3+O4: 1998z0021/0003/3–5; Oberdorf O4: 1998z0021/0002/13–22). 12 atlas (Oberdorf O3: 1998z0021/0001/17–21; Oberdorf O3+O4: 1998z0021/0003/6–7; Oberdorf O4: 1998z0021/0002/23–27). 38 vertebrae (neural arches) (Oberdorf O3: 1998z0021/0001/22–27; Oberdorf O3+O4: 1998z0021/0003/8–9; Oberdorf O4: 1998z0021/0002/28–57). 29 sacral vertebrae (Oberdorf O3: 1998z0021/0001/28–35; Oberdorf O3+O4: 1998z0021/0003/10–14; Oberdorf O4: 1998z0021/0002/58–73). 19 ribs (Oberdorf O3: 1998z0021/0001/36; Oberdorf O3+O4: 1998z0021/0003/15; Oberdorf O4: 1998z0021/0002/74–90). 40 urostyles (Oberdorf O3: 1998z0021/0001/37–39; Oberdorf O3+O4: 1998z0021/0003/16–33; Oberdorf O4: 1998z0021/0002/91–109). 15 coracoids (Oberdorf O3: 1998z0021/0001/40–43; Oberdorf O3+O4: 1998z0021/0003/34; Oberdorf O4: 1998z0021/0002/110–119). 26 scapulae (Oberdorf O3: 1998z0021/0001/44–45; Oberdorf O3+O4: 1998z0021/0003/35; Oberdorf O4: 1998z0021/0002/120–142). 8 clavicles (Oberdorf O3: 1998z0021/0001/46–47; Oberdorf O4: 1998z0021/0002/143–148). 126 ilia (Oberdorf O3: 1998z0021/0001/48–81; Oberdorf O3+O4: 1998z0021/0003/36–44; Oberdorf O4: 1998z0021/0002/149–231). 8 ischia (Oberdorf O3: 1998z0021/0001/82–86; Oberdorf O3+O4: 1998z0021/0003/45–46; Oberdorf O4: 1998z0021/0002/232). 23 humeri (Oberdorf O3: 1998z0021/0001/87–95; Oberdorf O3+O4: 1998z0021/0003/47–49; Oberdorf O4: 1998z0021/0002/233–243). Most of the less diagnostic elements (e.g. limb bones), or too fragmented remains, indicated in Anura indet., probably belong to this species, and should be considered as "*cf Latonia*".

D e s c r i p t i o n and taxonomic assignment: The remains are only broken fragments, but they clearly indicate the presence of the genus *Latonia*, extensively described by RŔĚK (1994a), with whom they agree in all observable features. The intrageneric taxonomy within *Latonia* is still not completely settled, because the differential fossilization makes difficult the necessary comparisons between taxa known after articulated (in slabs or slates) and disarticulated remains (tridimensional fragments) (RŔĚK 1994a, SANCHIZ in press). In our case, the frontoparietal has a dense sculpture based on tubercles, connected by lower ridges, very similar to the morphology of *Latonia gigantea* (see RŔĚK 1994a), but the maxilla apparently lacks any ornamentation. This combination of features indicates that the Oberdorf giant discoglossid can be referred to *Latonia ragei*, a species very similar to *L. gigantea*, recently described from the Lower Miocene of Laugnac (France; HOSSINI 1993). The frontoparietal was previously unknown for *L. ragei*.

C o m m e n t s: This species is clearly the predominant anuran form in the locality, and the size of the remains indicate that a large fraction of the sample were juveniles, even close to the early postmetamorphic stages.



Figures 32–40: *Latonia ragei*. Right fragment of frontal in ventral (32) and dorsal (33) views (Oberdorf O3+O4). Right mandible in upper (34) and inner (35) views (Oberdorf O3). par.p.: paracoronoid process. Urostyle in dorsal (36) and lateral (37) views (Oberdorf O3). Right ilium in external (38), symphysary (39) and inner (40) views (Oberdorf O3). Scale equals 2 mm.



Figures 41–43. *Palaeobatrachus* sp. Frontal fragment in dorsal (41), lateral (42) and ventral (43) views (Oberdorf O4). Scale equals 1 mm.

Palaeobatrachidae COPE, 1865

Palaeobatrachus TSCHUDI, 1838

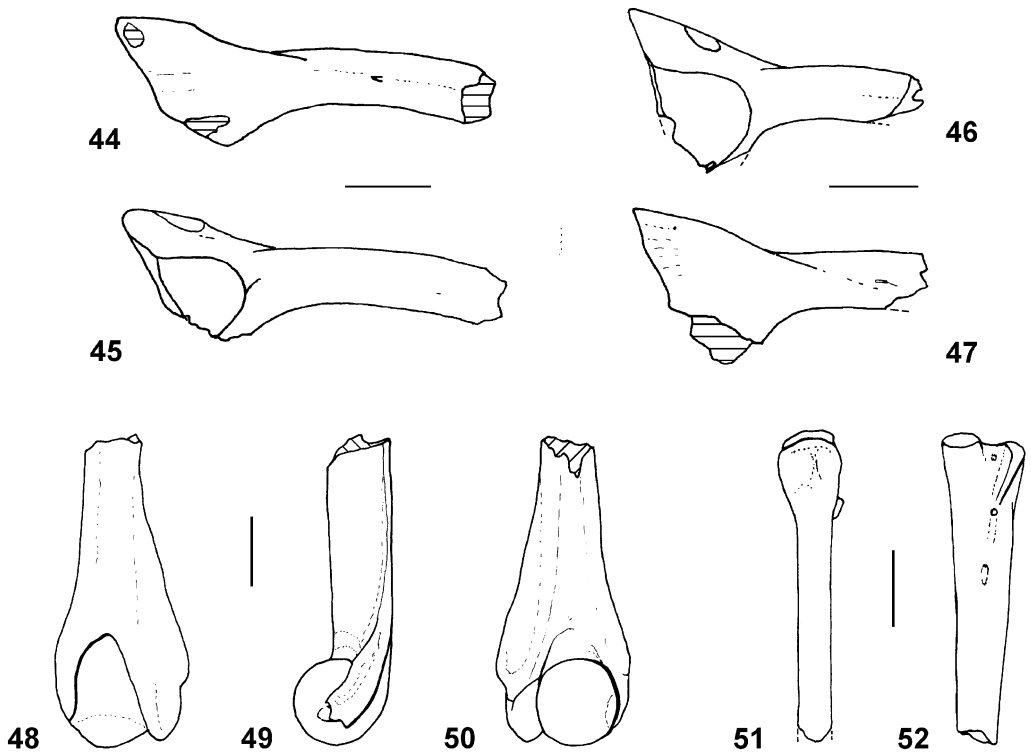
***Palaeobatrachus* sp.**

(fig. 41–43)

M a t e r i a l: Eleven minute frontoparietal fragments (Oberdorf O4: 1998z0022/0002/1–11). 3 humeri (Oberdorf O3: 1998z0022/0001/1; Oberdorf O3+O4: 1998z0022/0003/1; Oberdorf O4: 1998z0022/0002/12).

D e s c r i p t i o n and taxonomic assignment: The humeral fragments show the characteristic palaeobatrachid morphology in the absence of fossa cubitus ventralis and in having an articulating surface with the radioulna that does not cover all the eminentia capitata ball. The several minute fragments of frontoparietal that have been found indicate that this element was a single elongated bone having a flat and narrow unsculptured dorsal surface, slightly narrowing in the middle, and presented a small anterior parietal foramen. This frontoparietal morphology differs from *Albionbatrachus* and *Messelobatrachus* in the absence of dorsal ornamentation, and from *Pliobatrachus* in lacking any dorsal longitudinal crest. The available material does not allow any specific taxonomic placement within the complex genus *Palaeobatrachus* (SANCHIZ in press).

C o m m e n t s: Palaeobatrachids in general, with perhaps the partial exception of *Pliobatrachus*, are considered fully aquatic animals, similar to living pipids (e.g. *Xenopus*) in their way of life. Abundance of *Palaeobatrachus* and the discoglossine *Latonia* show an inverse relationship in the anuran assemblages of the European Miocene, being either of them predominant and the other scarce or absent.



Figures 44–52: *Pelodytes* sp. Right ilium in inner (44, reversed) and external (45) views (Oberdorf O4). Right ilium in external (46) and inner (47, reversed) views (Oberdorf O3). Left humerus in dorsal (48), lateral (49) and ventral (50) views (Oberdorf 3+4). Urostyle in dorsal (51) and lateral (52) views (Oberdorf O4). Scales equal 1 mm.

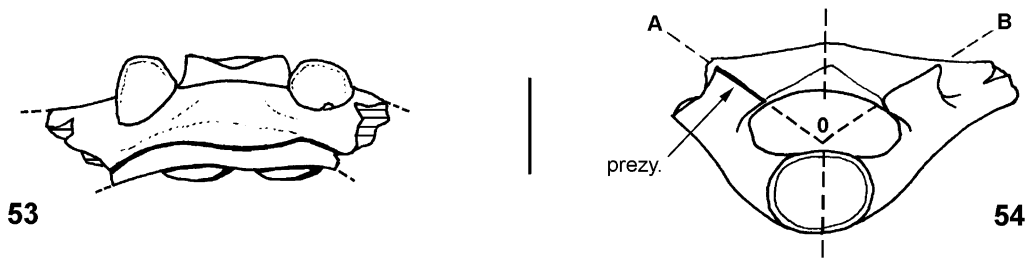
Pelodytidae BONAPARTE, 1850

Pelodytes BONAPARTE, 1838

***Pelodytes* sp.**
(fig. 44–52)

M a t e r i a l: Two neural arches (Oberdorf O3: 1998z0023/0001/1; Oberdorf O4: 1998z0023/0002/1). 1 centra (Oberdorf O4: 1998z0023/0002/2). 1 sacrum (Oberdorf O4: 1998z0023/0002/3). 1 urostyle (Oberdorf O4: 1998z0023/0002/4). 18 ilia (Oberdorf O3: 1998z0023/0001/7–14; Oberdorf O4: 1998z0023/0002/9–18). 11 humeri (Oberdorf O3: 1998z0023/0001/2–6; Oberdorf O3+O4: 1998z0023/0003/1–3; Oberdorf O4: 1998z0023/0002/5–7). 2 radioulnae (Oberdorf O3+O4: 1998z0023/0003/4; Oberdorf O4: 1998z0023/0002/8). 1 femur (Oberdorf O4: 1998z0023/0002/19). 5 tibiale-fibulare (Oberdorf O3: 1998z0023/0001/15–16; Oberdorf O4: 1998z0023/0002/20–22).

D e s c r i p t i o n and taxonomic assignment: Even as incomplete fragments, the morphology of most elements is quite characteristic for *Pelodytes* among fossil and living European



Figures 53–54: *Hyla* sp. Sacrum in dorsal (53) and anterior (54) views (Oberdorf O4). prezy.: prezygapophysis. The angle between the prezygapophyseal articular facets is indicated by the segments 0A and 0B. Scale equals 1 mm.

anurans (e.g. BÖHME 1977, RAGE 1974, SANCHIZ in press), and the generic attribution can be done with confidence. Within *Pelodytes*, the ilia from Oberdorf seem slightly different from *P. punctatus* and the fossil *P. arevacus*, and to a lesser degree from *P. caucasicus*, in having a small incipient tuber superior. This structure is nevertheless variable in Oberdorf, from only just a well defined area for insertion, to a clear distinct tubercle. The single urostyle that has been found does not present any osseous hypochordal process, but to the contrary, the only available sacral centrum does clearly incorporate an hypochordal notch, suggesting either an extreme variability or a cartilage nature for the process. In the few comparable structures, the Oberdorf material cannot be directly referred to the Miocene Iberian *P. arevacus*, nor to any living species, and perhaps represents a different species, but more numerous and informative elements are necessary to ascertain this possibility.

C o m m e n t s: Pelodytids are a rare group, present in the North American Tertiary, but with only the genus *Pelodytes* in Europe, where two western (one still unnamed) and one Caucasian living species can be found. Only one fossil species (*Pelodytes arevacus*) has been described, recovered from several Spanish Miocene sites (MN 2–9) and phylogenetically placed in the western lineage (SANCHIZ in press). The European western and eastern lineages should have diverged by the Lower Miocene, according to the fossil record and to the available DNA sequence differences (García-París, pers. comm.), being thus relevant for paleofaunistics a future assignment of the central European Miocene *Pelodytes* to either of these evolutionary lines.

Hylidae GRAY, 1825 (1815)

Hyla LAURENTI, 1768

***Hyla* sp.**
(fig. 53–54)

M a t e r i a l: One sacral fragment (Oberdorf O4: 1998z0024/0002/1). 1 scapula (Oberdorf O4: 1998z0024/0002/2).

D e s c r i p t i o n and taxonomic assignment: Both elements morphologically agree with living European *Hyla*. The scapula is an elongated bone, having well separated pars acromialis and processus glenoidalis, a middle nearly cylindrical cross section, and no

crista anterior, differing in this way from any other European genera. The procoelic sacrum has not preserved the transverse processes, but it presents an anterior cotyle, circular in shape, a short neural arch (in relation to interzygapophyseal width), and two separated posterior condyles, a set of features that allows its differentiation from juvenile *Bufo*, with the only other similar sacral morphology in the European fauna. The length of the sacral neural arch in the Oberdorf specimen is somewhat intermediate between living *Hyla meridionalis* and *H. arborea*, but the orientation of the prezygapophyses closely agrees with *H. meridionalis* (angle between both articular facets about 116°), while *H. arborea* shows clearly steeper facets, with angles about 90° .

C o m m e n t s: The genus *Hyla*, of American origin, is considered in Europe as an asiatic immigrant (SANCHIZ & RŔĚK 1996), with earliest records in the Vallesian and Turolian (see SANCHIZ in press, for a list of localities). The record from Oberdorf documents its presence in Europe at a much earlier age.

Ranidae GRAY, 1825

Rana LINNAEUS, 1758

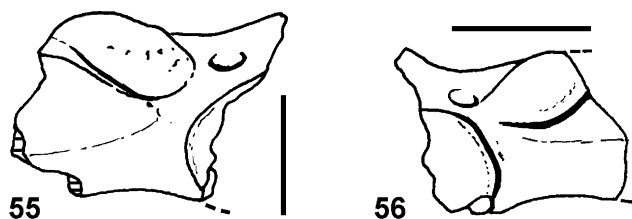
Rana (ridibunda) sp.

(fig. 55–56)

M a t e r i a l: Two vertebral centra (Oberdorf O3: 1998z0025/0001/1–2). 1 sacral centrum (Oberdorf O3+O4: 1998z0025/0003/1). 1 coracoid (Oberdorf O3: 1998z0025/0001/3). 4 ilia (Oberdorf O3: 1998z0025/0001/5; Oberdorf O4: 1998z0025/0002/1–3). 1 humerus (Oberdorf O3: 1998z0025/0001/4).

D e s c r i p t i o n and taxonomic assignment: Vertebral centra can be recognized as *Rana* because they show a slight medial and vertical notch in the condyle. The same notch is present in the diplasicoelous sacral centrum. The peculiar tuber superior of the ilium, as discussed by SANCHIZ et al. (1993), indicates the presence of green (or water) frogs in the locality, but the material does not allow any attribution to species within the *Rana (ridibunda)* species group. Other bones are too fragmented to be diagnostic within *Rana*.

C o m m e n t s: Most of the material recovered in Oberdorf probably belongs to post-metamorphic froglets. The subgenus *Pelophylax* of the large genus *Rana*, that includes the European water frogs, is considered in Europe an asiatic immigrant with an arrival datum associated to the Terminal Eocene Event (SANCHIZ et al. 1993).



Figures 55–56: *Rana (ridibunda)* sp. Left ilium in lateral external (55) view (Oberdorf O3). Right ilium in lateral external (56) view (Oberdorf O4). Scales equal 1 mm.

Anura indet.

M a t e r i a l: Twenty nine premaxillae (Oberdorf O3: 1998z0026/0001/1–7; Oberdorf O4: 1998z0026/0002/1–22). 161 maxillar fragments (Oberdorf O3: 1998z0026/0001/8–33; Oberdorf O3+O4: 1998z0026/0003/1; Oberdorf O4: 1998z0026/0002/23–156). 9 frontoparietals, mostly tadpoles (Oberdorf O3: 1998z0026/0001/34; Oberdorf O4: 1998z0026/0002/157–164). 1 prooticum (Oberdorf O3: 1998z0026/0001/35). 71 mandibles (Oberdorf O3: 1998z0026/0001/36–51; Oberdorf O3+O4: 1998z0026/0003/2–3; Oberdorf O4: 1998z0026/0002/165–217). 1 atlas (Oberdorf O4: 1998z0026/0002/218). 4 neural arches (Oberdorf O3: 1998z0026/0001/52–55). 158 vertebral centra (Oberdorf O3: 1998z0026/0001/56–82; Oberdorf O3+O4: 1998z0026/0003/4–7; Oberdorf O4: 1998z0026/0002/219–345). 19 urostyles (Oberdorf O3: 1998z0026/0001/83; Oberdorf O4: 1998z0026/0002/346–363). 1 clavicle (Oberdorf O3+O4: 1998z0026/0003/8). 2 scapulae (Oberdorf O3: 1998z0026/0001/84–85). 1 cleithrum (Oberdorf O3: 1998z0026/0001/86). 27 ilia (Oberdorf O4: 1998z0026/0002/364–390). 1 ischium (Oberdorf O4: 1998z0026/0002/391). 23 humeri (Oberdorf O3: 1998z0026/0001/87–91; Oberdorf O4: 1998z0026/0002/392–409). 91 radioulnae (Oberdorf O3: 1998z0026/0001/92–107; Oberdorf O3+O4: 1998z0026/0003/9–28; Oberdorf O4: 1998z0026/0002/410–464). 66 femora (Oberdorf O3: 1998z0026/0001/108–126; Oberdorf O4: 1998z0026/0002/465–511). 83 tibiofibulae (Oberdorf O3: 1998z0026/0001/127–142; Oberdorf O3+O4: 1998z0026/0003/29; Oberdorf O4: 1998z0026/0002/512–577). 5 tibiale-fibulare (Oberdorf O4: 1998z0026/0002/578–582).

C o m m e n t s: As indicated above, the majority of this material is referable to *Latonia ragei*, but these elements are not diagnostic enough to exclude their hypothetical attribution to other anurans. Nevertheless, there are no positive indications that any other anuran species, different from those already described, might be present in the samples.

Final Remarks

The faunistic lists provided by ESTES (1981), RŔĚK (1994b) and SANCHIZ (in press) clearly indicate that the Oligocene and early Miocene batrachian faunas are poorly known in Europe, not yet informative enough for detailed paleofaunistic or biostratigraphical comparisons. However, most of the known Miocene genera have been recovered in Oberdorf, with only the remarkable exception of pelobatid toads (*Eopelobates* and *Pelobates*). Their absence is probably merely due to a taphocenotic bias, as both genera are known to be present in Central Europe at this time (SANCHIZ in press).

Differences in species composition and abundance between the Oberdorf sites O3 and O4 are probably not significant. An approximation to the χ^2 test using Oberdorf O3 and O4 mean taxa frequencies as the expected distribution, and allowing for absences, would clearly indicate that neither of the sites statistically differ at the 95% confidence level. The absence of several taxa in Oberdorf O3, present in Oberdorf O4, makes their faunal lists *de facto* different (table 1), but this is probably only a result of the sampling process.

The materials recovered, both in Oberdorf O3 and O4, frequently (not always) represent juvenile or metamorphosing specimens, as deduced by size comparisons with their living closest relatives. Many of the fossils are badly preserved and broken, but it is not known if they have been the result of predation. No clear macroscopic digestion marks have been found in our sample, but scanning microscopy observations should be undertaken in order to check the absence of characteristic bone alterations, resembling those described for indigestible food remains of recent mammals and prey birds (e.g. FERNÁNDEZ-JALVO 1992; DENYS et al. 1995).

Table 1: Minimum number of individuals (MNI) and total number of fossils identified to genus (TFI) recovered in Oberdorf O3 and O4.

SPECIES	SITE O3	SITE O3+O4	SITE O4
<i>Albanerpeton inexpectatum</i>	3 (7.69 %)	3 (9.68 %)	14 (14.43 %)
<i>Salamandra sansaniensis</i>	0 (0.00 %)	1 (3.23 %)	1 (1.03 %)
cf. <i>Chioglossa</i> sp.	0 (0.00 %)	0 (0.0 %)	1 (1.03 %)
<i>Triturus roehrsi</i>	9 (23.09 %)	3 (9.68 %)	21 (21.65 %)
<i>Chelotriton</i> sp.	1 (2.56 %)	1 (3.23 %)	1 (1.03 %)
<i>Latonia ragei</i>	20 (51.28 %)	18 (58.06 %)	44 (45.36 %)
<i>Palaeobatrachus</i> sp.	1 (2.56 %)	1 (3.23 %)	6 (6.19 %)
<i>Pelodytes</i> sp.	4 (10.26 %)	3 (9.68 %)	6 (6.19 %)
<i>Hyla</i> sp.	0 (0.00 %)	0 (0.00 %)	1 (1.03 %)
<i>Rana</i> sp.	1 (2.56 %)	1 (3.23 %)	2 (2.06 %)
NFI	289	94	764
MNI	39 (100 %)	31 (100 %)	97 (100 %)

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