



New latest Cretaceous microvertebrate fossil assemblages from the Hațeg Basin (Romania)

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Abstract

Late Cretaceous terrestrial ecosystems in southern Europe are relatively poorly known, although much progress has been made during the past decade, principally with regard to the microvertebrate components of these ecosystems. The Maastrichtian terrestrial deposits of the Hațeg Basin, at the easternmost end of the South European archipelago and well known for reptilian fossils (e.g., turtles, crocodylians, pterosaurs and dinosaurs), have been thoroughly screened during the past five years. Important microvertebrate assemblages, both quantitatively and qualitatively speaking, were found at Pui (Sînpetru Formation), Tuștea and, particularly, Vălioara (Densuș-Ciula Formation). Several new taxa are noted here for the first time for the Hațeg Basin, including gars, discoglossids, albanerpetontids, scincomorphan and anguimorphan lizards; dromaeosaurids and multituberculates are confirmed. Most of the microvertebrate remains are poorly preserved and precise systematic assignment has proved difficult. The Hațeg fauna appears to be primitive and endemic, with a Neopangean core composition, and suggests a composite palaeobiogeographic origin for the Late Cretaceous European ecosystems, confirming conclusions reached in studies of the larger vertebrates.

Introduction

Despite more than 150 years of collecting terrestrial vertebrate remains from the Late Cretaceous deposits of Europe (Buffetaut et al. 1997), Late Cretaceous assemblages have been considered to be weakly diversified (e.g. Nopcsa 1915), and have usually been overlooked in studies dealing with topics such as Late Cretaceous palaeocommunity structure, phylogeny and evolution of vertebrate taxa, faunal turnovers, palaeobiogeography or C/T extinction scenarios.

A renewed interest in these European assemblages has led to the unravelling of a much greater terrestrial vertebrate diversity than previously recognised (e.g. Astibia et al. 1990, Buffetaut et al. 1997). The increase of our knowledge is most evident at the level of the microvertebrates, a term used here to designate small-sized (< 2 cm, usually much smaller)

vertebrate remains recovered through micropalaeontological techniques (i.e. sediment bulk processing by wet screening), irrespective of whether these remains belonged to small or large animals.

Amongst the first studies on microvertebrate faunas from the European Upper Cretaceous was the one by Grigorescu et al. (1985) on an assemblage recovered from the Bărbat River valley, village of Pui (Hațeg Basin). Although the fragmentary nature of the assemblage has prevented a detailed taxonomic study, this work has shed the first light on the diversity of the Hațeg assemblage and on the great potential for microvertebrate material recovery of certain fossiliferous sites. This work has given a strong impetus for further work on the Hațeg microvertebrates, which started after 1992. A preliminary report is presented here.

We will discuss briefly some of the most representative elements (i.e., fishes, amphibians and reptiles)

of the newly discovered microvertebrate assemblages from the Hațeg Basin. Most of them will be dealt with in future, more detailed contributions, together with the multituberculate mammals. All specimen numbers refer to material housed in the collection of the Laboratory of Paleontology, Faculty of Geology and Geophysics of the University of Bucharest (FGGUB); numbers with site abbreviations refer to additional material and are provisional repository numbers at the FGGUB.

Geological setting

The Hațeg Basin (Figure 1) is a Late Cretaceous post-orogenic depression in the northwestern part of the Southern Carpathians, in Hunedoara County. To the east, north and northwest, it is surrounded by the uplifted crystalline basement of the Getic nappe, and to the south by the Danubian domain. The sedimentary cover of the basin includes patchy early Permian continental, Liassic coal-bearing continental/paralic, and Middle Jurassic to Early Cretaceous carbonate and terrigenous shelf and basinal marine deposits. The lower Late Cretaceous, up to the Campanian (possibly also Early Maastrichtian) is represented by marine clastic (sometimes flysch-type) sediments, with a regressive nearshore and littoral facies at the top, marking the onset of the end-Cretaceous Laramide compressive phase (Grigorescu 1992).

The overlying late Maastrichtian terrestrial deposits are post-Laramide molasse-type sedimentary units filling up a basin formed after the main compressive phase. It was suggested (Weishampel et al. 1991) that the upper part of the continental succession may locally include lowermost Tertiary deposits as well, notably in the Upper Member of the Densuș-Ciula Formation (see below). These deposits were grouped into two main lithostratigraphical units, indicating the presence of two distinct sedimentary troughs. Sedimentological studies point to the presence of a braided-river-dominated alluvial depositional system in the central part of the basin, corresponding to the Sînpetru Formation. In the northwestern part, the correlating Densuș-Ciula Formation was formed under slightly different conditions. The Lower Member is mostly lacustrine but strongly influenced by volcanic eruptions to the west; a volcanic overprint is also present in the fluvial/lacustrine Middle Member of the Densuș-Ciula Formation, while the Upper Mem-

ber deposits are pure epiclastic sediments (Grigorescu 1992).

Previous work on Hațeg microvertebrates

Discovery of and preliminary work on the Hațeg vertebrate assemblage (1900–1980)

The vertebrate fauna of the Hațeg Basin was discovered and intensively worked by Nopcsa as early as the end of the 19th century (see Weishampel & Reif 1984). Samples from the two main fossiliferous localities known at that time (Sînpetru, along the Sibîșel River Valley, and Vălioara; see Figure 2), each of them yielding fossils at several sites, were collected by Nopcsa himself and by a Hungarian Royal Geological Survey geologist, O. Kadič, who worked around Vălioara. These workers found no significant differences between the Sînpetru and Vălioara assemblages, both comprising primitive turtles (*Kallokibotio bajazidi*), crocodylians (*Allodaposuchus precedens*), titanosaurids (*Magyarosaurus dacus*), ornithopods (*Rhabdodon robustus*, and the primitive hadrosaur *Telmatosaurus transsylvanicus*), and the nodosaurid *Struthiosaurus transilvanicus*.

The Sibîșel Valley outcrops yielded additional vertebrates, namely pterosaur remains (cf. *Ornithocheirus*, a pteranodontid pterosaur; see Jianu et al. 1997) and a maniraptoran theropod described by Andrews (1913) as the peleciform bird *Elopteryx nopcsai* (Csiki & Grigorescu 1998). No microvertebrate remains in the sense used in the present paper were known at the time, however, although Kadič found some small theropod teeth (< 10 mm height); these were mixed up with crocodylian teeth in the MAFI collections (Csiki & Grigorescu 1998).

The first microvertebrates (1980–1990)

When prospecting and excavations were restarted in the late seventies by parties from the Faculty of Geology and Geophysics (Bucharest) and the Muzeul Civilizației Dacice și Romane (Deva), the rich Sibîșel Valley outcrops yielded the first scattered microvertebrate remains. These comprised small velociraptorine theropod and multituberculate mammal teeth (Grigorescu 1984), which were recovered through wet screening of the matrix of an extensively worked fossil site yielding mainly turtles, crocodylians and dinosaurs. No microvertebrate fossil sites were ever identified

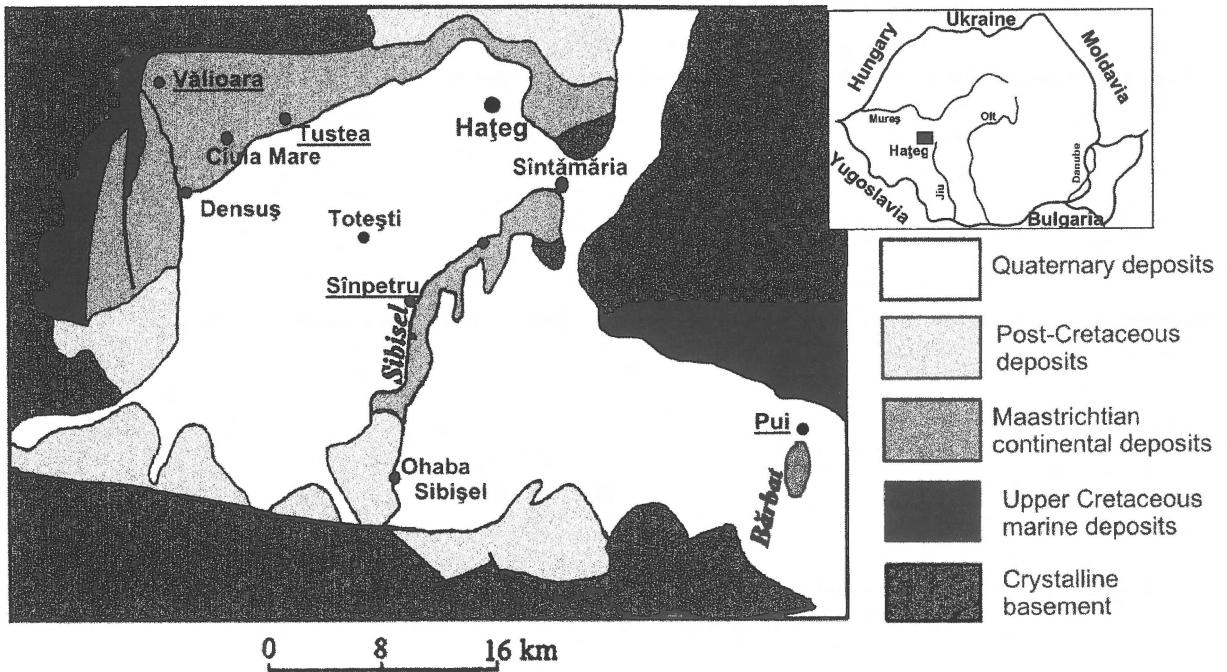


Figure 1. Position (inset) and schematic geology of the Hațeg Basin. Main fossiliferous localities are underlined.

in the Sibișel Valley, however; microvertebrate remains, mostly shed crocodylian and small theropod teeth, were found either isolated or during excavations of fossiliferous pockets with macrovertebrates.

Farther east, at Pui, the lower part of the Sînpetru Formation, which crops out in the Bărbat River valley, revealed the first microvertebrate fossil site. The spot, a fine grey-greenish silty sandstone, was excavated and sieved by a joint French-Romanian team, yielding (Grigorescu et al. 1985) chondrosteian (*Acipenseriformes*) and teleost (*Characidae*) fishes, indeterminate amphibians, turtles, crocodylians, and squamates, titanosaurid, theropod and ornithopod teeth, as well as multituberculate remains (two molars, the type specimens of *Paracimexomys ?dacus* Grigorescu & Hahn 1986 = *Barbatodon transsylvanicum* Rădulescu & Samson 1986). From Pui, two morphotypes of lower incisors were reported as additional multituberculate material. These presented a first hint at the diversity of this unique multituberculate fauna. This was further supported by the discovery in the Sibișel Valley of a multituberculate skull with complete upper dentition (Rădulescu & Samson 1997). Finally, the discovery in 1988 of the dinosaur nesting site near Tuștea in the Densuș-Ciula Formation (Grigorescu et al. 1990) revealed a new, potentially promising, microvertebrate

locality, as the nesting horizon also yielded scattered eggshells and small indeterminate bone fragments.

The period of intensive search for microvertebrates (1990–present)

Starting in 1992, our team began intensive field campaigns with the aim to identify and excavate new microvertebrate fossil localities. Although the searches proved fruitless in the Sibișel Valley area, we were successful in other parts of the Hațeg Basin (Figure 1). At Pui, three new microvertebrate fossil sites (known as FGGUB localities Pui1, 4 and 5) were identified and test sieved (~ 25 to 50 kg of sediments from each site); none of these sites was, however, as rich as that excavated in 1984.

Pui1 (P1; green-greyish, slightly variegated micaceous silty mudstones) yielded the richest and most diverse assemblage including discoglossid frogs, albanerpetontids, indeterminate (?anguimorph) lizards, multituberculates (a minute fragment of a pm4), along with eggshell fragments and freshwater gastropods. From Pui4 and Pui5 (P4, P5; both localities in red silty mudstones), only sparse amphibians (anurans and albanerpetontids) were recovered along with gastropods and eggshell fragments. It is noteworthy that P5 yielded the most diverse eggshell (three morpho-

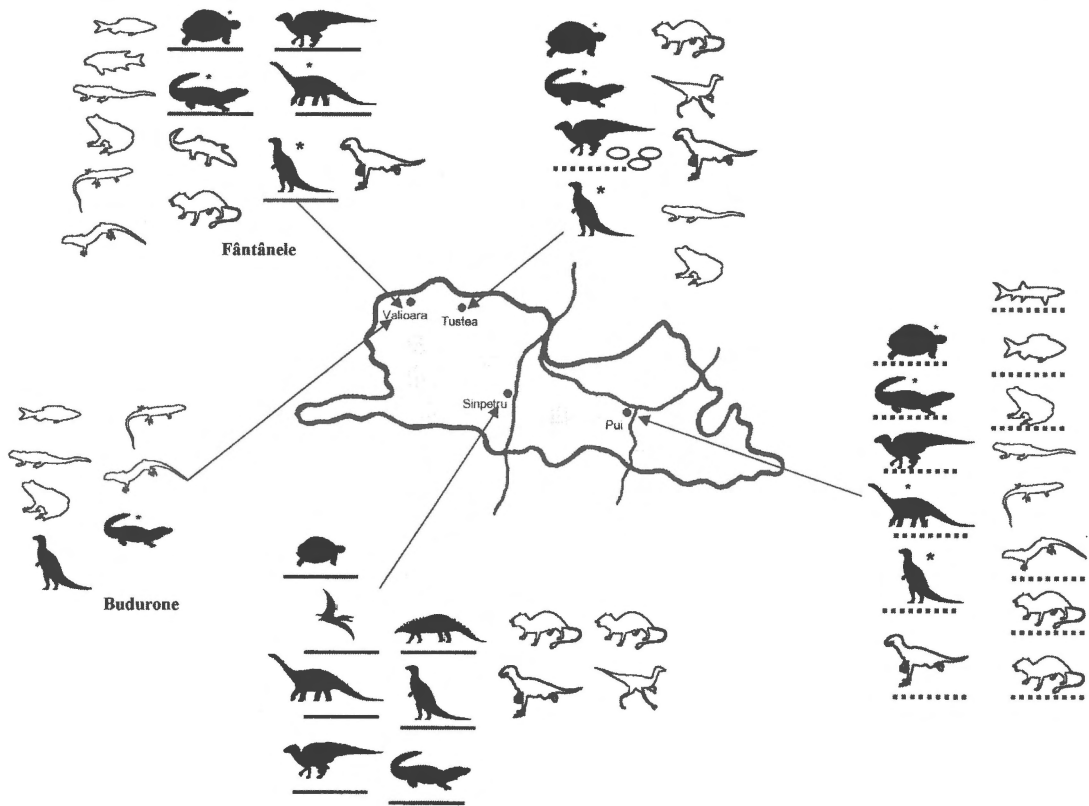


Figure 2. The evolution of our knowledge of Hațeg vertebrate assemblages, with emphasis on the microvertebrates. Fossiliferous sites and vertebrate assemblages from the Hațeg Basin – present state of the art. Outlined figures: microvertebrates. Stars: macrovertebrates recovered also from microvertebrate fossil sites. Underlined figures: vertebrates known at Nopcsa's time. Figures underlined with dots: vertebrates (including microvertebrates) known in 1990.

types) and gastropod (five taxa) assemblages. The permanently high level of the Bărbat River during the last years has prohibited any further excavations at these sites.

The most important microvertebrate fossil sites are located in the northern part of the basin, namely in the Densuș-Ciula Formation. At the Tuștea (T) nesting site, ongoing large-scale excavations have offered the possibility of wet screening of large quantities of the bright-red micaceous, egg-bearing siltstones. The recovered microvertebrates are relatively rare and poorly preserved. The relatively diverse assemblage from this site includes nevertheless indeterminate anurans, albanerpetontids, turtles, crocodylians, dromaeosaurid theropods, and multituberculates, as well as abundant – but not diverse – eggshell fragments and gastropods.

The richest microvertebrate localities are to be found in the northwestern part of the basin, around the village of Vălioara, where two sites, known as Vălioara-Fântânele (VF) and Vălioara-Budurone

(VB), have yielded the large majority of the microvertebrate remains found so far in the Hațeg Basin, revealing the most diverse assemblages as well. Both of these sites are located in the Middle Member of the Densuș-Ciula Formation. The Budurone site has produced, through screening of some 150 kg of sediments (dark, grey-bluish to blackish mudstones), an assemblage dominated by freshwater vertebrates. It includes indeterminate fish vertebrae, discoglossid frogs, albanerpetontids, two types of lizards, and rare crocodylians. The most outstanding feature of the site is the large quantity of carbonised seeds found, along with gastropods, charcoal fragments and small pyrite concretions. Fântânele is the site that has yielded the richest and most diverse (although not always well-preserved) assemblage. Some 300 kg of sediments (represented by grey-greenish, massive, compact silty mudstones, locally slightly variegated) were processed. The recovered assemblage includes fishes (*Lepidosteus* sp., and an indeterminate teleost?), dis-

coglossid frogs, albanerpetontids, various lizards (at least three types, one of which is an indeterminate scincomorph), turtles, crocodylians (*Allodaposuchus* and cf. *Doratodon*), dinosaurs (mostly small theropod, but also rare *Magyarosaurus* and *Rhabdodon* teeth), and multituberculates. Rare characeae and ostracods, freshwater gastropods and bivalves as well as eggshell fragments were also found at this site.

Several new sites were experimentally screened from autumn 1997 to spring 1998, on account of their general facies resemblance to VF and VB. Some of them (FGGUB sites VF2 and VB2) have produced interesting microvertebrate material (which has not yet been fully worked through) that may justify large-scale screening operations. The recovered assemblages include taxa found also in more thoroughly worked sites.

Fishes

Class Osteichthyes

Subclass Actinopterygii

Infraclass Neopterygii

Order Ginglymodii (Lepisosteiformes)

Family Lepisosteidae

Genus *Lepisosteus*

Lepisosteus sp.

Material: FGGUB V.400 (tooth), V.401 (2 scales).

A few fish remains, recovered from the Fântânele locality, can be assigned to a lepisosteid. The scales (FGGUB V.401: Figure 3.1) are of typical rhomboidal shape, thick and covered with ganoine. The fragmentary tooth (FGGUB V.400: Figure 3.2) exhibits a plicidentine base and pointed tip, capped with translucent enamel. Both the tooth and scales are smaller than any previously figured Cretaceous gar remains from Europe. The morphology of the tooth is indicative of the genus *Lepisosteus*; another gar taxon (*Antractosteus*) from the European Upper Cretaceous has teeth with lanceolate tip (Gayet, In: Sigé et al. 1997). Late Cretaceous European lepisosteids have been recorded from the Lower Campanian of Ventabren (Cavin et al. 1996), the Campanian of Villeveyrac (Buffetaut et al. 1996), Montsérét (Tong et al. 1993) and Champ-Garimond (Sigé et al. 1997), and from the Maastrichtian of Aude (Le Loeuff 1992) and Cruzy (L. Cavin, pers. comm.) (all France), from the Maastrichtian of Laño, Spain (Astibia et al. 1990) and from the

Late 'Senonian' (Late Campanian-Early Maastrichtian, cf. Le Loeuff 1992) of Portugal (Buffetaut et al. 1996). Most of the material (scales, teeth, cranial fragments) is listed as indeterminate lepisosteid, although both gar genera were present in Europe.

As far as their published record is concerned, *Antractosteus* seems to be restricted to the Campanian, while most Maastrichtian localities (now also Vălioara in the Hațeg Basin) have yielded remains of the genus *Lepisosteus*. Their origin was supposed to be either Pangean (Patterson 1984) or Gondwanan (Gayet, In: Sigé et al. 1997), the second hypothesis being supported by the absence of the gars in Australia, Antarctica and Europe east of Messel (Germany; Gayet, In: Sigé et al. 1997: 117). The discovery of typical gar remains in the Upper Maastrichtian of the Hațeg Basin considerably weakens the former argument and provides further support both for the Pangean origin and early evolution and radiation of the group and to the predominantly vicariant evolution of Cretaceous European faunas.

Amphibians

Infraclass Lepspondyli

Order Anura

Family Discoglossidae

Genus *Eodiscoglossus*

Eodiscoglossus sp.

Material: FGGUB V.402 (2 maxillae); V.403 (right prearticular); V.404 (right prearticular); V.405 (left prearticular); V.406 (humerus); V.407 (humerus); V.408 (humerus); V.409 (acetabular portion of ilium); V.410 (iliac shaft); V.411 (acetabular portion of ilium). Additional referred material includes P1.9 (ilium); P1.10 (parietal, radioulna, tibiofibula); P1.8 (maxilla); VF.9 (3 tibiofibulae, phalanges); VF.21 (radioulna, 3 tibiofibulae); VF.30 (10 maxillae); VF.40 (3 sacra, 2 urostyles); VF.44 (6 humeri, 8 radioulnae, 22 tibiofibulae); VF.45 (7 ilia); VF.46 (12 phalanges); VF.47 (8 prearticulars); VB.2 (2 maxillae); VB.5 (maxilla, tibiofibula); VB.7 (humerus, 2 radioulnae, femur, 7 tibiofibulae, 6 phalanges); VB.12 (prearticular, parasacral, quadratojugal, pterigoideum, ilium); VF2.3 (ilium, phalanx); VF2.5 (tibiofibula, radioulna). All specimens are fragmentary.

The maxilla fragments (FGGUB V.402; see Figure 3.3) belong to relatively small specimens, of two

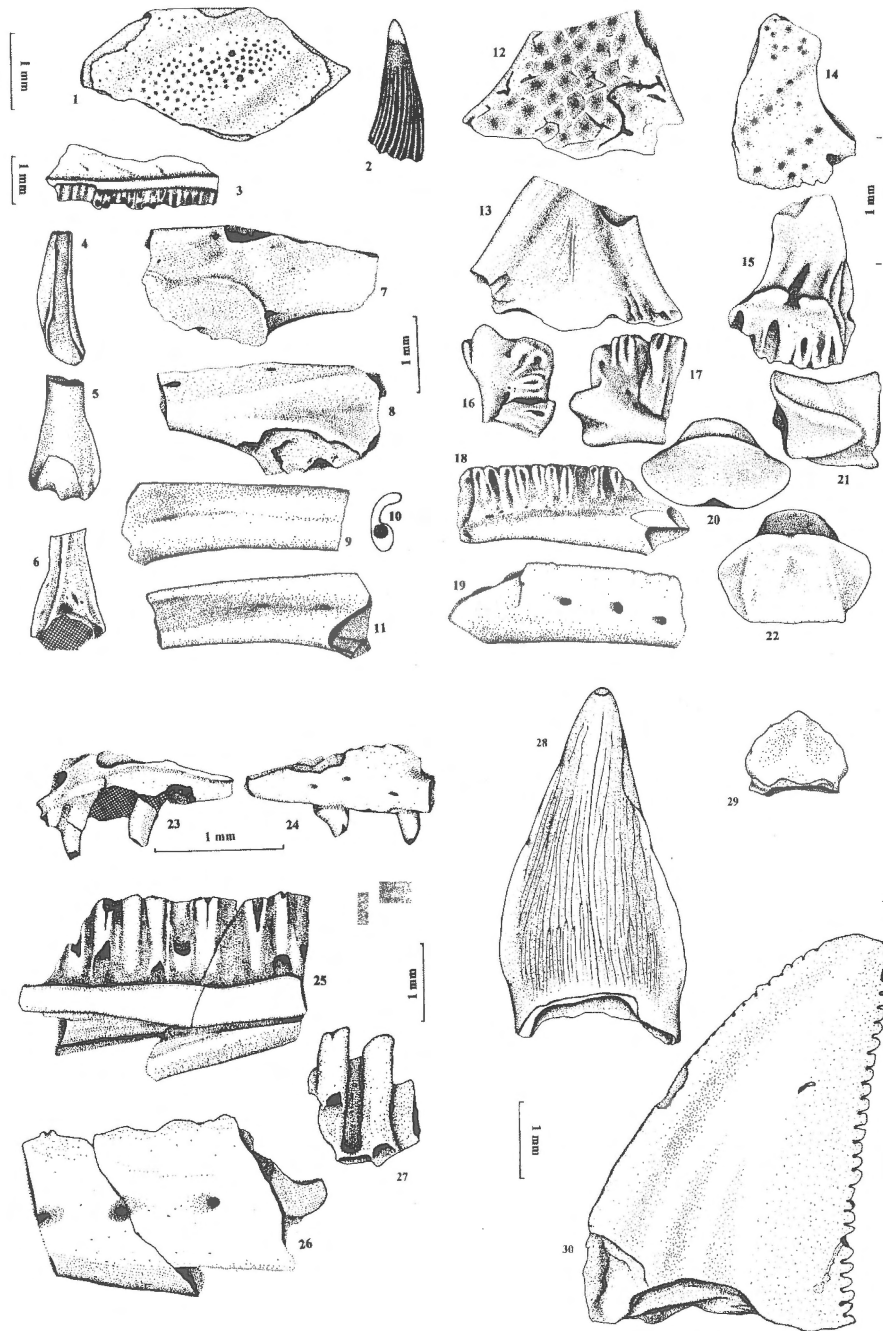


Figure 3. Microvertebrate remains from the Upper Maastrichtian of the Hațeg Basin. 1–2: *Lepisosteus* sp., scale (FGGUB V.401) and tooth (FGGUB V.400), respectively. 3–11: *Eodiscoglossus* sp., left maxilla (3: FGGUB V.402), right prearticular (4: FGGUB V.403), humerus (5–6: FGGUB 406) in caudal and cranial view, respectively; acetabular portion of right ilium (7–8: FGGUB V.409) in lateral and medial view, respectively; right iliac shaft (9–11: FGGUB V.410) in lateral, anterior, and medial view, respectively. 12–22: *Albanerpeton* sp., frontal (12–13: FGGUB V.412) in dorsal and ventral view, respectively; left premaxilla (14–15: FGGUB V.413) in lateral and medial view, respectively; symphyseal end of right dentary (16–17: FGGUB V.414) in dorsal and medial view, respectively; left dentary (18–19: FGGUB V.415) in medial and lateral view, respectively; second vertebra (20–22: FGGUB V.416) in cranial, lateral and ventral view, respectively. 23–24: indeterminate anguimorph lizard, fragmentary left maxilla (FGGUB V.419) in medial and lateral view, respectively. 25–27: indeterminate scincomorph lizard; fragmentary left dentary (25–26: FGGUB V.420) in medial and lateral view, respectively; fragmentary right dentary (27: FGGUB V.421) in medial view. 28: cf. *Allodaposuchus precedens* tooth crown. 29: cf. *Doratodon* tooth crown. 30: tooth of indeterminate dromaeosaurid theropod.

size classes. The lateral surface of the bone is smooth, provided only with small, oval or circular vascular foramina. The medial face shows a relatively deep fossa maxillaris and the base of the palatinus process in FGGUB V.402. The teeth are pleurodont, small, numerous, cylindrical and closely spaced; no tips are preserved. The bases of the teeth show medially placed replacement pits. The prearticular (FGGUB V.403; see Figure 3.4) lacks the crista mandibularis externa, while the processus coronoideus and processus paracoronoideus are indistinguishable. There is a medially projected, undivided crest, somewhat similar to the condition seen in modern Discoglossidae (Vergnaud-Granzini 1970), but unlike *Latonia*, this latter taxon having both processes well developed (Vergnaud-Granzini 1970, Vergnaud-Granzini & Wenz 1975, Roček 1994). The crista paracoronoidea is relatively high and the extremitas spatulata moderately developed. It is represented by several specimens, almost all of them fragmentary. FGGUB V.404 is an almost complete right prearticular, somewhat smaller (3.5 mm in length) than that figured by Evans et al. (1990) for *Eodiscoglossus oxoniensis* from the Middle Jurassic of England, but FGGUB V.405, a fragmentary specimen, is approximately four times larger.

The recovered humeri (FGGUB V.406; Figures 3.5–3.6) are all fragmentary and only represented by distal fragments; they lack the caput humeri, but a small fossa cubitalis ventralis is usually present (FGGUB V.407). This specimen, a relatively well-preserved distal left humerus, shows a prominent crista ventralis, unlike *Eodiscoglossus santonjae*. The crista medialis (= crista ulnaris) is better developed than the crista lateralis (crista radialis); the distal crests are less well developed in *Paradiscoglossus americanus*. Although Evans & Milner (1993) showed that the relative development of the distal crests could vary ontogenetically, it should be noted that in FGGUB V.408, a much smaller specimen (distal width = 0.8 mm), the crista medialis is also well developed. The olecranon scar is slightly laterally displaced, oval-elongated, moderate in size, like that seen in *Paradiscoglossus*, not oblique as it is in the Late Cretaceous *Scotiophryne pustulosa* (Estes 1969) or in the recent genus *Bombina*. The humerus, in overall size (distal width ~ 1.1 mm, preserved length ~ 1.8 mm in FGGUB V.407), is much smaller than the corresponding element of *Paradiscoglossus americanus* (Estes & Sanchiz 1982a) or *Scotiophryne pustulosa* (Estes 1969).

Of the ilia, only fragments are preserved (FGGUB V.409, V.410; see Figures 3.7–3.11), although a reconstruction of the acetabular region and proximal shaft is tentatively made. FGGUB V.409, a fragmentary right ilium, is one of the better preserved specimens, consisting of the proximal part with the anteriormost end, pars ascendens and descendens ilii (supracetabular and subacetabular expansions), tip of the tuber superius (dorsal tubercle) and distal part of the iliac shaft broken off. The pars ascendens seems to have been probably not as large as in *Paradiscoglossus americanus* (Estes & Sanchiz 1982a: fig. 2b). The supracetabular fossa is wide and long, although shallower than in *Paradiscoglossus*, oriented horizontally. The acetabulum is oval, elongate, with a slightly raised posterior rim. The pars descendens is small, as shown by FGGUB V.411. The tuber superius (dorsal tubercle) is prominent, crest-like, only slightly swollen in some specimens, continuous with crista dorsalis ilii (dorsal crest); a wide open angle occurs between the tuber superius and pars ascendens ilii. The crista dorsalis ilii is large and strongly medially inclined (as in the extinct *Paradiscoglossus* and *Latonia* or the extant *Discoglossus*, compare Estes & Sanchiz 1982a); laterally it is separated from the smooth, convex lateral face of the iliac shaft by a shallow longitudinal groove (Figures 3.9–3.11). The shaft is wide relative to the acetabular region as in *Paradiscoglossus americanus* and *Eodiscoglossus oxoniensis* (Evans et al. 1990), but not in *Scotiophryne pustulosa* (Estes 1969), *Eodiscoglossus santonjae* or *Enneabatrachus hechti* (Evans & Milner 1993). The morphology of the ilium, with well-developed tuber superius, strong dorsal crest and small pars descendens ilii, is strongly suggestive of a discoglossid. Their combination point to the *Discoglossus*-group (*Discoglossus*, *Paradiscoglossus*, and *Eodiscoglossus*); it is most reminiscent of *Paradiscoglossus* from the Upper Cretaceous of North America, although this latter has a more strongly developed pars ascendens ilii. Moreover, the size of the bone suggests a small discoglossid, smaller than the contemporary *Paradiscoglossus* and *Scotiophryne*, but larger than either *Eodiscoglossus oxoniensis* or *E. santonjae*.

The Discoglossidae are an ancient group of anurans, of Laurasian origin; their first representatives come from the English Middle Jurassic (Evans et al. 1990) and in Europe they are recorded continuously from this time onward, e.g. in the Upper Jurassic of England (Ensom et al. 1991) and Portugal (Evans & Milner 1991) and the Lower Cretaceous of Spain

(Vergnaud-Granzini & Wenz 1975, Estes & Sanchiz 1982b). Although frog remains are occasionally found in Late Cretaceous deposits (Le Loeuff 1992, Buffetaut et al. 1996), these represent other families, however, with the exception of Laño (Le Loeuff 1992), from where isolated discoglossid vertebrae have been recorded. Consequently, the present contribution presents the first substantial one for European Late Cretaceous discoglossids, extending the range of *Eodiscoglossus* into the latest Cretaceous. Discoglossids are known from Late Cretaceous deposits in North America (Estes 1969, Estes & Sanchiz 1982a) and Asia (Nessov 1988), showing a wide-ranging, pan-Laurasian distribution. More precise taxonomic assessment of the Hațeg anurans is not intended here, but it is possible that the remains, if proved to be diagnostic at that level, may represent (at least) yet another species of the genus *Eodiscoglossus*.

Lepospondyli incertae sedis (Allocaudata)

Family Albanerpetontidae

Genus *Albanerpeton*

Albanerpeton sp.

Material: FGGUB V.412 (frontal); V.413 (premaxilla); V.414 (symphyseal portion of right dentary); V.415 (left dentary); V.416 (second vertebra, 'axis'). Additional referred material includes P1.6 (a dentary); P4.13 (dentary, angulo-articular); T.6 (2 dentaries); VF.1 (dentary); VF.21 (angulo-articular); VF.40 (2 atlases, 2 second vertebrae); VF.46 (humerus, femur); VF.47 (3 angulo-articulars); VF.52 (9 dentaries, 2 premaxillae, maxilla; vertebrae); VF2.1 (2 dentaries, premaxilla, 2 maxilla); VF2.2 (atlas, vertebrae); VB.3 (dentary); VB.10 (maxilla); VB2.1 (dentary). All specimens are fragmentary.

The frontals are fused into a roughly triangular bone (FGGUB V.412; Figures 3.12, 3.13), that has its anterior and right posterolateral parts broken off. The dorsal surface of the bone is finely sculptured with small pits and irregular ridges. The posterior margin is distinctly trilobate, with a median and two lateral projections separating two recesses for the paired parietals. The orbital margins are markedly laterally divergent (interorbital width 0.9 mm, 2.3 mm wide along a transect 0.9 mm more posteriorly) and only slightly concave. In ventral view there is a deep fossa with a low ridge in the midline and two strong crests (0.3 mm wide each) at the ventro-lateral edges of the

bone (Estes 1981). It should be noted that the generic name *Albanerpeton* has been restricted by McGowan & Evans (1995) to forms with markedly triangular frontals having narrow, pointed apex and broad, unemarginated orbital margins (i.e. the type species *A. inexpectatum* from the Middle Miocene of France, and *A. galaktion* from the Campanian of North America). The same authors proposed the newly erected name *Celtdens* for the albanerpetontids having waisted and more rectangular frontals (see below).

The premaxillae (FGGUB V.413; Figures 3.14, 3.15) are fragmentary, the distal part of the nasal process being broken off. The outer surface is sculptured. The lateral edge is provided with a small facet for the reception of the anterior process of the maxilla. Seven tooth positions are preserved, but no complete tooth is present in any of the premaxillae. The lamina horizontalis is interrupted by a groove running dorso-ventrally.

The dentaries (FGGUB V.414, V.415; Figures 3.16–3.19) are of typical albanerpetontid morphology. The Meckelian groove is closed. The teeth are pleurodont, non-pedicellate, with slender, cylindrical shafts and slightly tricuspid, not expanded tips. The lateral surface of the bone is smooth and provided with small, oval or rounded nutrient foramina. The anteromedial, symphyseal end of the dentaries (FGGUB V.415; Figures 3.16, 3.17) shows robust processes for a strong, peg-and-socket articulation between the two halves of the mandible.

The second vertebra ('axis') is represented by several complete, well-preserved specimens. It is typical of albanerpetontids (FGGUB V.416; Figures 3.20–3.22) in being reduced and lacking a neural arch. The anterior articular surface shows two slightly defined lateral cotyles and a dorsal semicircular-shaped projection for the complex, saddle-shaped articulation with the atlas. Ventrally the anterior border is convex, largely rounded in FGGUB V.417, without the midline excavation seen in *A. cf. megacephalus* (Estes & Sanchiz 1982b: fig. 5e) or in *A. inexpectatum* (Estes 1981: fig. 4a), while a small excavation is visible there in ventral view in FGGUB V.416, but still smaller than in the above-mentioned taxa. The posterior articular surface is excavated for an amphicelous articulation with the third vertebra. It was evidently not sutured or fused to the third vertebra as it is in *A. inexpectatum* (Estes 1981), but free, as in some Early Cretaceous albanerpetontids from Teruel (Spain), referred by Estes & Sanchiz (1982b: figs 5e–g) to *Albanerpeton* (= *Cel-*

tedens) cf. *megacephalus* or as in *Celtedens ibericus* (McGowan & Evans 1995).

Genus *Celtedens*

Celtedens sp.

Material: FGGUB V.418 (frontal).

The frontal is square-shaped rather than triangular as in FGGUB V.416, a frontal above referred to as *Albanerpeton*. The anteriormost part of the medial nasal process is missing, so that it is unclear whether it had a bulbous rather than a spiky median extension. The dorsal surface of the bone is very finely sculptured with small pits and irregular ridges. The orbital margins are almost parallel (interorbital width 1 mm, width at a transect 0.9 mm and more posteriorly 1.35 mm; compare to the same dimensions in V.416) and markedly concave. In ventral view, there is a deep, flat depression without a midline ridge and with two strong crests at the ventro-lateral edges of the bone; these crests are relatively wider. The anterior (nasal) and posterior (parietal) edges are of equal width as in *Celtedens ibericus* (McGowan & Evans 1995: fig. 3) rather than slightly flaring posteriorly as in *C. megacephalus*.

Some of the cranial and postcranial remains described above as *Albanerpeton* sp. might in fact belong to this *Celtedens*-type albanerpetontid; generic differences other than those for the frontal have not yet been documented. Therefore we treat all these remains as *Albanerpeton*-like (*Albanerpeton* being the taxon more thoroughly described), bearing in mind that it may belong to *Celtedens*, a matter that will probably be solved in the future by the discovery of associated remains and further developments in understanding these intriguing lepospondyliian amphibians.

The albanerpetontids, once considered as somewhat remarkable members of the salamander family Proseriidae (Estes 1981), are now seen as representatives of their own family of uncertain phylogenetic position (Fox & Naylor 1982) or a sister-group of the crown-group Batrachia (including the Caudata and the Salientia) within the Lissamphibia (McGowan & Evans 1995). Their distribution is Laurasian; the first representatives appear in the Bajocian (Middle Jurassic) of France (Estes & Hofstetter 1976, Evans & Milner 1991). Other (usually better known) members of the family were found in the Upper Jurassic of England (Ensom et al. 1991) and Portugal (Evans & Milner 1991), as well in the Lower Cretaceous of Spain and Italy (Estes 1981, Estes & Sanchiz 1982b),

the Cretaceous of North America (Estes 1981, Fox & Naylor 1982) and the Upper Jurassic to Cretaceous of Middle Asia (Nessov 1988). Rare and isolated remains of albanerpetontids are rarely found in the European Upper Cretaceous (Laño, Spain; see Le Loeuff 1992; Cruzy, La Neuve, southern France; S. Duffaud, pers. comm.), but none of the former known occurrences are represented by such diverse skeletal material.

The European Late Cretaceous albanerpetontids were generally included in the genus *Albanerpeton*, while *Celtedens* was previously known as restricted to the Early Cretaceous (McGowan & Evans 1995); if correctly assigned, the Hațeg specimen extends the range of this taxon into the latest Cretaceous.

Subclass Diapsida

Infraclass Lepidosauromorpha

Superorder Lepidosauria

Order Squamata

Suborder Lacertilia *Infraorder Diploglossa (Anguimorpha)*

Material: FGGUB V.419 (fragmentary maxilla).

The maxilla (Figures 3.23–3.24) preserves five tooth positions. The teeth are subpleurodont (attached to the lateral parapet for about half of their height), conical and slightly recurved posteriorly. The tooth bases are slightly dilated, but without striations; the tips are monocuspid. Supradental shelf weak; there is no dental gutter.

The maxilla displays some anguimorph affinities, although more precise assignments are pending the discovery of more complete remains. It may be pointed out, however, that at least two distinct higher taxa of lizards are represented in the Upper Cretaceous of the Hațeg Basin. Both these lizard crown-groups had a pan-Laurasian distribution since the Jurassic/Cretaceous boundary (Borsuk-Bialynicka 1991), being present in Europe since the Middle Jurassic (Evans & Milner 1991).

Infraorder Leptoglossa (Scincomorpha)

Indeterminate scincomorph

Material: FGGUB V.420 (fragmentary dentary); V.421 (fragmentary dentary with teeth).

The larger, but toothless dentary (FGGUB V.420; Figures 3.25–3.26) shows ten tooth positions. The tooth implantation was apparently pleurodont, the teeth being columnar and straight-sided; all the tips are broken off. Their arrangement is not crowded. The resorption pits are slightly distal to the midline of

the root. Medially, there is a conspicuous horizontal subdental shelf, separated from the tooth row by a well-defined sulcus dentalis. The Meckelian groove is widely open posteriorly, and narrows (but still remains open) in the anterior part of the fragment; there is no sign of an intramandibular septum. On the smooth lateral surface, three alveolar foramina are preserved. Two teeth are preserved in the smaller dentary fragment (FGGUB V.421; Figure 3.27); these are pleurodont (three quarters of the tooth projecting above the lateral parapet), cylindrical and widely spaced. The crown is bicuspid, with a smaller anterior and a larger posterior cusp. Subcircular resorption pits are displaced posteromedially.

The material is too fragmentary to allow a lower-level taxonomic assignment of the specimen. The presence of the columnar, widely spaced bicuspid teeth, open Meckelian groove, well-developed subdental shelf and sulcus dentalis point to the presence of a scincomorphan lizard.

Infraclass Archosauromorpha

Superorder Archosauria

Order Crocodylia

Suborder Mesosuchia

Family Hsisosuchidae Genus *Doratodon*

Doratodon sp.

Material: FGGUB V.422 (tooth).

The tooth crown (Figure 3.29) is isoscele triangle-shaped, wider than high, latero-medially compressed with marginal carinae, convex labially and almost flat lingually. The carinae seem to have been slightly serrated, although most of the serrations are actually abraded. The tooth is highly reminiscent of some teeth recovered by Kadič from Vălioara at the beginning of the century, now housed in the MAFI collections under registration number MAFI v.12684. These teeth were separated as 'ziphodont crocodylian cf. *Doratodon*' by E. Buffetaut during a short visit in March 1979, on account of their similarity to teeth of *Doratodon charcharidens* from the Lower Campanian of Muthmannsdorf (Buffetaut 1980).

Suborder Eusuchia

Family Crocodylidae

Genus *Allodaposuchus*

cf. *Allodaposuchus precedens*

Material: FGGUB V.423 (tooth). Additional referred material includes: VF.36 (9 teeth); VF.2.4 (2 teeth); VB.10 (2 teeth); P4.12 (tooth).

These teeth (FGGUB V.423; Figure 3.28) are all, regardless of their dimensions, characterised by high, conical crowns, more convex labially than lingually. The lateral carinae (if they exist) are minute, unsertated. They are similar to, but smaller than, those usually referred to *Allodaposuchus precedens*, known from the Hațeg Basin, as well as from southern France and Spain (Astibia et al. 1990).

Order Saurischia

Suborder Theropoda family *Dromaeosauridae*

Velociraptorine indet.

Material: FGGUB R. 1580. Additional referred material includes: VF.17 (tooth); VF.25 (tooth); VF.34 (11 teeth).

The teeth referred to dromaeosaurids are mostly recurved, labio-lingually compressed fragmentary crowns (FGGUB R. 1580; Figure 3.30) that sometimes preserve the serrations on their anterior and posterior carinae. When present, the serrations display a marked size difference between the anterior and posterior denticles (i.e., the anterior denticles are half the size of the posterior ones). This difference, together with the shape of the denticles and that of the teeth, is a distinctive feature of dromaeosaurid, and more precisely velociraptorine, theropods (Currie et al. 1990), a dinosaur group shown to have been present in the Upper Cretaceous of the Hațeg Basin (Weishampel & Jianu 1996, Csiki & Grigorescu 1998). Some of the referred teeth are, however, minute and without serrated carinae; these are considered to be of juvenile velociraptorines (Norrell et al. 1994).

The Dromaeosauridae are considered as a family of typical Laurasian distribution, although they have recently been reported from the lowermost Upper Cretaceous of Sudan as well (Rauhut & Werner 1995). They were apparently widespread in Europe during the Late Cretaceous, characteristic dromaeosaurid teeth (as well as other skeletal fragments) having been recorded from Spain (Pol et al. 1992), southern France (Buffetaut et al. 1986, Le Loeuff & Buffetaut 1998) and Hațeg (Csiki & Grigorescu 1998). They are considered as typical survivors of an Early Cretaceous pan-Laurasian fauna.

Table 1. Synthetic list of microvertebrates from the Hăgeş Basin. Locality name abbreviations are the same as in the main text. Pui refers to the microvertebrate site excavated by Grigorescu et al. (1985); Sînp refers to the Sibişel Valley outcrops near Sînpetru village

Group	Localities	Material
Chondrostei		
Acipenseriformes indet.	Pui	teeth, scales
Neopterygii		
Lepisosteidae		
<i>Lepisosteus</i> sp.	VF	tooth, scales
Characidae indet.		
Indeterminate fishes	Pui	teeth
	VF	tooth vertebrae
	VB	vertebra
Anura		
Discoglossidae		
<i>Eodiscoglossus</i> sp.	VF	maxillae, parietal, prearticulars, ilia, sacra, urostyles, humeri, radioulnae, tibiofibulae, metapodials, phalanges
	VB	maxillae, prearticular, parabasale, quadratojugal, pterygoideum, ilia, humerii, radioulnae, femur, tibiofibulae, phalanges
	P1	maxillae, parietal, ilium, radioulna, tibiofibula
	VF2	ilium, radioulna, tibiofibula, phalanx
Anura indet. (?discoglossid)	VB2	tibiofibula
	T	tibiofibulae
Allocaudata		
Albanerpetontidae		
<i>Albanerpeton</i> sp.	VF2	dentaries, premaxillae, atlas
	VB2, T	dentaries
	P1	dentaries, premaxilla, frontal, angulo-articular, axis
<i>Celtdens</i> sp.	VF	frontal
Chelonia		
Cryptodira		
<i>Kallokibotion bajazidi</i>	P1, VF, T	carapace fragments
Lepidosauria		
Squamata		
Lacertilia		
Gen. et sp. indet. A (anguimorph)	P1	fragmentary maxilla
Gen. et sp. indet. B (scincomorph)	VF	fragmentary dentaries, ?teeth, vertebrae
Archosauria		
Crocodylia		
Eusuchia		
cf. <i>Allodaposuchus precedens</i>	VF, VB, T	teeth
Mesosuchia		
<i>Doratodon</i> sp.	VF	tooth
Saurischia		
Dromaeosauridae		
<i>Titanosauridae</i>	VF, Pui, T	teeth
<i>Magyarosaurus dacus</i>	VF, Pui	tooth
Ornithischia		
<i>Rhabdodon robustus</i>	VF, T, Pui	teeth
Allotheria		
Multituberculata		
? <i>Paracimexomys</i> sp. (= <i>Barbatodon transylvanicum</i>)	Pui	molar
Multituberculata indet.	VF	molar
	Pui	incisors (I ₁), P ₄
	VF	incisor (I ₁), fragmentary P ₄ , molar, premolars
	T, Sînp	incisor (I ²)
<i>Kogaionon unguereanui</i>	Sînp	fragmentary skull with teeth

Conclusions

The recent focus on the microvertebrate components of the Hațeg terrestrial fauna has resulted in the discovery of several hundred identifiable remains from microvertebrate fossil sites spread all over the continental Maastrichtian outcropping area in the basin. Taking into account the large number of specimens, both in terms of the skeletal parts and the taxonomic diversity they represent (Table 1), the results are very promising, especially since they were obtained by the processing of a relatively small amount of screen-washed matrix (650–700 kg from **all** fossiliferous sites investigated). Vălioara-Fântânele ranks probably amongst the richest microvertebrate fossil sites from the European Upper Cretaceous, and is one of the most important mammal-yielding sites as well. It should also be emphasised that, although not the focus of the present contribution, a diverse invertebrate fauna, several types of eggshells and carbonised seeds were also recovered during sediment processing.

The European Late Cretaceous continental ecosystems are relatively poorly known (e.g., Pol et al. 1992), especially if compared with North American or Asian ones. Significant progress has been made, however, during the last few years, when some thoroughly sampled new localities (Astibia et al. 1990, Pol et al. 1992, Buffetaut et al. 1996, Sigé et al. 1997) contributed to our knowledge of the composition of these ecosystems in the western part of the South European archipelago (i.e., the Franco-Iberian landmass). The newly discovered microvertebrate fossil assemblages from the Hațeg Basin, which represent somewhat isolated, eastern insular communities, for the first time offer the possibility of comparisons between the eastern and western European ecosystems (although time separation between them must be kept in mind) and, on the other hand, allow a better definition of a South European palaeofaunal province that might then be compared with better known provinces.

First, it should be emphasised that, although differences exist at low taxonomic levels between the eastern and western European palaeocommunities (for some reasons, the western ones seem to show more Gondwanan influences), at higher taxonomic levels one encounters the same groups (gars, albanerpetontids, discoglossids, scincomorphans, crocodylids, dromaeosaurids, titanosaurids, *Rhabdodon*-type ornithopods, nodosaurids) in both regions. Significant differences (in the present state of knowledge) include the absence of therian mammals and the presence of

multituberculates, the absence of certain groups of southern provenance (pleurodiran turtles, madtsoiid, aniilid and boiid snakes, abelisaurid theropods) in Hațeg, as well as specific or generic differences (probably of endemic nature) within widespread groups (e.g. *Rhabdodon*).

In general, the Late Cretaceous South European palaeobioprovince may be characterised as having been dominated by Neopangean (i.e., Middle Jurassic Pangea without central Asia; Russell 1993) relicts and endemics (acipenseriformes, lepisosteids, albanerpetontids, discoglossids, dromaeosaurids, *Rhabdodon*, nodosaurids), with other contributions from southern (Gondwanan) and Asiamerican sources during the Cretaceous. It is worth mentioning that the composition of the Hațeg community seems to be closer to this Neopangean core than to those of the Franco-Iberian ones.

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