

## Terrestrial ecosystems on the Mesozoic peri-Adriatic carbonate platforms: the vertebrate evidence

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**Abstract.** The remains of Mesozoic carbonate platforms outcrop along the margins of the Adriatic Sea and the mountain chains surrounding them in Italy, Slovenia and Croatia. Despite the fact that the platforms were far from continents, abundant evidence of terrestrial vertebrates was recently found, mainly in the Norian, Lower Jurassic and Cretaceous, and is here reviewed. The presence of populations of large terrestrial vertebrates (mainly dinosaurs) on these carbonate platforms, and in particular the discovery of late Hauterivian-early Barremian sauropods and late Santonian hadrosaurids, has important paleoecological and paleogeographical implications.

**Key words.** Peri-Adriatic carbonate platforms. Mesozoic Tethysian paleogeography. Mesozoic terrestrial vertebrates. Paleichnology. Reptilia. Dinosauria. Theropoda. Sauropoda. Ornithopoda. Hadrosauridae.

### Introduction

Mesozoic carbonate platforms outcrop as thick sequences of carbonates, more or less disrupted and piled up by the Alpine orogeny, along the margins of the Adriatic Sea in Italy, Slovenia and Croatia. During the Norian these platforms were not clearly differentiated and the whole region was part of a wide pericontinental carbonate platform along the northern margin of western Paleotethys, far away from the continent (see Marcoux *et al.*, 1993). During Early Jurassic times the Trento Platform was identified in N Italy, surrounded to E and W by deep marine basins. The Cretaceous platforms are represented by the Adriatic-Dinaric Platform (= Karst Platform of Masse *et al.*, 1993), now outcropping along the eastern margin of the sea, included in the Dinarids and ending northward into the Karst and Julian Prealps, Latium-Abruzzi-Campania Platform (= Apennine Carbonate Platform, Masse *et al.*, 1993) included in the northern part of southern Apennines, and Apulia Platform, partly included in the Southern Apennines and partly constituting the undeformed peninsula of Puglia. They are usually reported in literature as "intraoceanic" platforms, placed during the Cretaceous between African and Laurasian/Eurasian continents and surrounded by deep sea basins (see for example Masse *et al.*, 1993). It was noted by Dalla Vecchia (1997b, 1998b) that these platforms were in some cases connected with other carbonate platforms and, possibly, sometimes

by them to the African (Early Cretaceous) or Laurasian (Triassic-Early Jurassic) continent, but were at best very far (hundreds of kilometres) from "land", considering it in the "orthodox" way, i.e. a wide area of silicoclastic fluvial/lacustrine sedimentation or non-deposition. The vertebrate faunas found on them (mainly the Cretaceous ones) are thus the very singular case of faunas living on carbonate platforms separated from a continental area. All other carbonate platforms bearing traces of large terrestrial inhabitants were pericontinental and the vertebrate evidence was found near the continent-platform transition (e.g. the Lower Cretaceous of the Gulf Coastal Plain in North America).

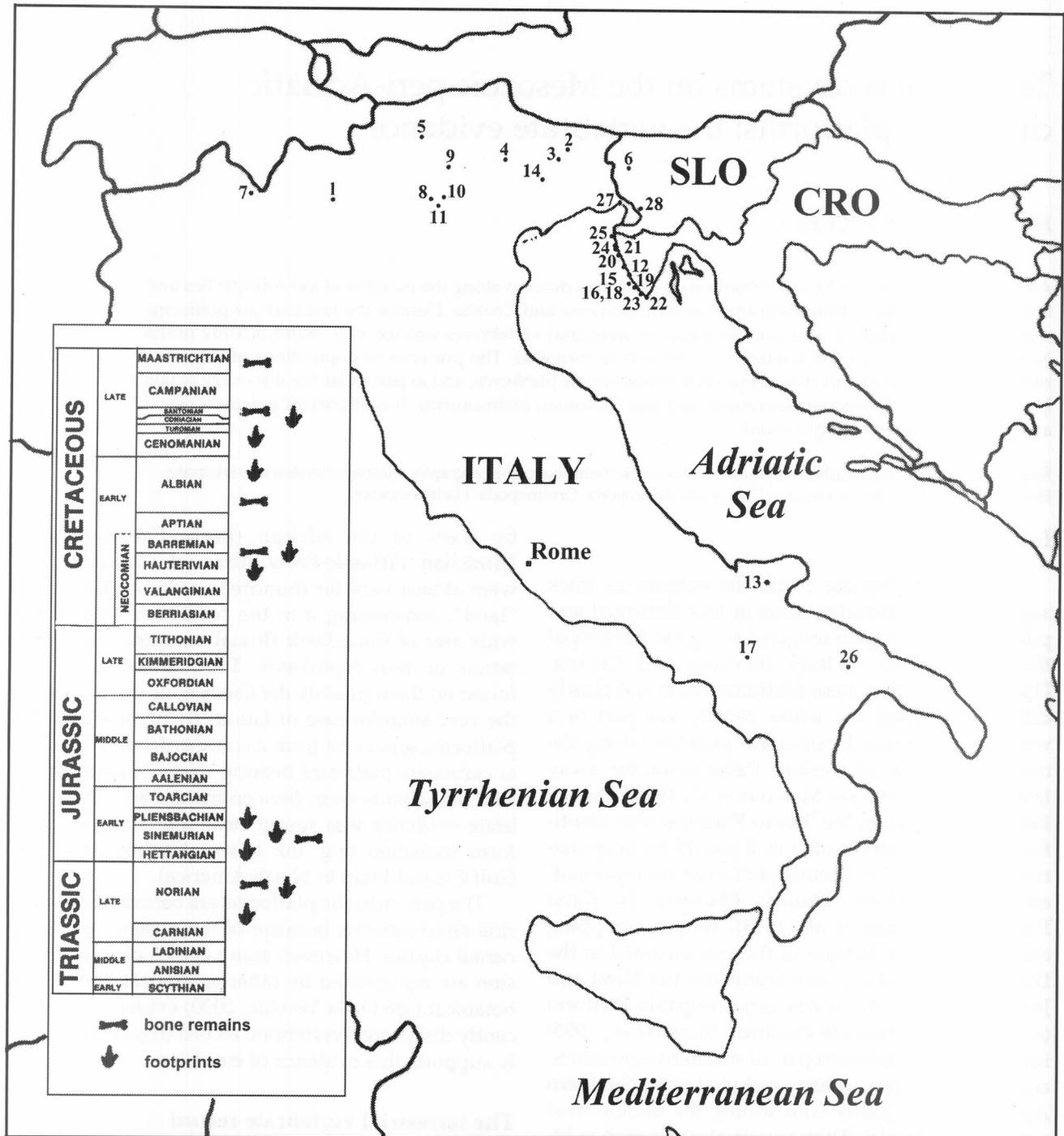
The peri-Adriatic platforms are considered as marine environments because of the absence of continental clastics. However, many events of local emersion are represented by other geological and paleobotanical (see Dalla Vecchia, 2000) evidence. The recently discovered vertebrate record (figure 1) strongly supports this evidence of emersion.

### The terrestrial vertebrate record

#### *Late Triassic (Norian)*

Skeletons of early pterosaurs (*Eudimorphodon*, *Peteinosaurus* and *Preondactylus*), the prolacertiform *Langobardisaurus*, the diapsids *incertae sedis* *Drepanosaurus* and *Megalancosaurus* and the sphenodont *Diphydontosaurus* are found in middle Norian (Alaunian) rocks derived from sediments deposited in anoxic intraplatform basins of N Italy (Lombardy and Friuli regions). Larger reptiles are represented by the aetosaur *Aetosaurus* and the phytosaur

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**Figure 1.** Location of the outcrops of the Mesozoic peri-Adriatic carbonate platforms with terrestrial vertebrate evidence. 1) Lombardy (Cene, Zogno etc.), Norian bone remains, 2) Carnic Pre-Alps (Preone, Forchiar Creek, etc.), Norian bone remains, 3) Carnic Pre-Alps (Andreis, Claut, Cimolais), Norian footprints, 4) E Dolomites (M. Pelmetto, etc.), early Norian footprints, 5) W Dolomites, Norian footprints, 6) W Slovenia, Norian footprints, 7) Saltrio, Early Jurassic bone remains, 8) Lavini di Marco and environs, Early Jurassic footprints, 9) Becco di Filadonna, Early Jurassic footprints, 10) Mt. Pasubio, Early Jurassic footprints, 11) Mts Lessini, Early Jurassic footprints, 12) Cisterna, Hauterivian footprints, 13) near S. Marco in Lamis (Gargano), late Hauterivian - early Barremian footprints, 14) Cansiglio Plateau, late Hauterivian - early Barremian footprints, 15) Valle/Bale, late Hauterivian - early Barremian bone remains, 16) Brioni Archipelago, late Barremian footprints, 17) Pietraroia, early Albian bone remains, 18) Brioni Archipelago, late Albian footprints, 19) Punesella, late Albian footprints, 20) Solaris site, late Albian footprints, 21) Quietto/Mirna river mouth, late Albian footprints, 22) Fenoliga islet, late Cenomanian footprints, 23) Grakalovac, late Cenomanian footprints, 24) Carigador, late Cenomanian footprints, 25) S. Lorenzo di Daila, late Cenomanian footprints, 26) Altamura, late Coniacian-early Santonian footprints, 27) Villaggio del Pescatore, late Santonian bone remains, 28) Kozina, Maastrichtian bone remains.

*Mystriosuchus*. Many sites with dinosaurian and "chirotheroid" footprints in the Dolomites and Carnic Pre-Alps of N Italy, and in W Slovenia (see Dalla Vecchia, 1997a, Dalla Vecchia and Mietto, 1998) confirm the common presence of terrestrial vertebrates on the platform. The site of Mt. Pelmetto (Eastern Dolomites) is stratigraphically placed near the passage between Carnian and Norian, the others are probably higher in the stratigraphic column. The dinosaur ichnological record is represented mainly by tridactyl footprints with a length from 10 up to 35 cm.

#### Early Jurassic

Abundant dinosaur ichnologic evidence was found in the Trento Platform of NE Italy. Large to small theropod, large to small ornithopod and sauropod footprints are reported from the Hettangian-Sinemurian site of the Lavini di Marco (Leonardi and Mietto, 2001). There are at least other three sites with footprints in the Trento Province (M. Avanzini, pers. comm.). Large tridactyl footprints are found in the Pliensbachian of the Lessini Mts. (Mietto and Roghi, 1993).

Remains of a large theropod the size of an adult *Allosaurus*, were found in Lombardy in 1996. They were preserved in limestone formed in an open marine setting (a ramp between a carbonate platform and a deep basin) and they have a middle Sinemurian age. Both humeri (about 35 cm long), a complete manual digit and another partial manual digit with the corresponding metacarpal, a partial furcula, a tooth and the proximal part of a fibula are among the preserved bones (C. Dal Sasso, pers. comm.).

#### Hauterivian

A site with two large tridactyl footprints and many possible sauropod prints is present in SW Istria (Croatia, Adriatic-Dinaric Platform) (Dalla Vecchia *et al.*, 2000); dinoturbation could be common (Dalla Vecchia *et al.*, 2000).

#### Late Hauterivian-Early Barremian

Footprints of a sauropod and a large theropod are reported from the Adriatic-Dinaric Platform of NE Italy (Dalla Vecchia and Venturini, 1995; Dalla Vecchia, 1999a). A site rich in dinosaur bones is present in SW Istria. Here sauropods seem to be differentiated into non-titanosaurid Titanosauriformes, the diplodocimorph *Histriasaurus* and, possibly, a camarasaurid (Dalla Vecchia, 1998a). Very small to very large individuals are represented. Theropods are testified by the unguis of a minute individual and a

tooth of a mid-size one (Dalla Vecchia, 1998b). A partial caudal vertebra suggests the possible presence of large theropods too. Early Barremian dinoturbation is reported in SW Istria (Dini *et al.*, 1998). A site with tridactyl footprints ranging in length from 15 up to 40 cm was discovered in the Gargano Promontory (Puglia, S Italy, Apulia Platform) (Gianolla *et al.*, 2000).

#### Late Barremian

Footprints of large theropods are present in a site on the Main Brioni Island and probably also on the nearby Vanga Island, SW Istria (Dalla Vecchia *et al.*, 1993; Dalla Vecchia and Tarlao, 1995; Dalla Vecchia, 1998b).

#### Early Albian

The small juvenile theropod *Scipionyx samniticus* (Dal Sasso and Signore, 1998) was found in the Pietraroaia site (Latium-Abruzzi-Campania Platform, S Italy) together with the amphibian *Celtesaurus* (also found in Spain), the rhynchocephalian *Derasmosaurus*, the lacertilians *Costasaurus* and *Chometokadmon*, and small crocodiles (Barbera and Macuglia, 1988).

#### Late Albian

Dinosaur footprints are common in W Istria. Mid-size bipedal individuals, probably mainly theropods, are represented in five sites (seven levels), the Solaris one with more than 500 footprints and tracks (Dalla Vecchia and Tarlao, 2000). The track of a relatively large ornithopod (footprint length = 28 cm) is found in the Main Brioni Island (Dalla Vecchia, 1997a), where rare large theropod prints are signalled too (Bachofen-Echt, 1925) but are not preserved *in situ* anymore. An abundant sauropodan (titanosaur) ichnological record is found in the Solaris site (Dalla Vecchia, 1994; Dalla Vecchia and Tarlao, 2000) where only small individuals (pedal print length = 24-51 cm) are represented. Rare footprints of large, probably non-dinosaurian, unidentified reptiles were found in the Solaris site (Dalla Vecchia and Tarlao, 2000).

#### Late Cenomanian

Three sites with footprints of mid-size bipedal dinosaurs were discovered in Istria (see Dalla Vecchia, 1997a, 1997b, 1998b; Dalla Vecchia *et al.*, 2001). Tracks of small sauropods (pedal prints never longer than 40 cm) are found in the Fenoliga islet (Leghissa and Leonardi, 1990) and Carigador (Dalla Vecchia *et al.*, 2001) sites of western Istria.

### Late Coniacian/early Santonian

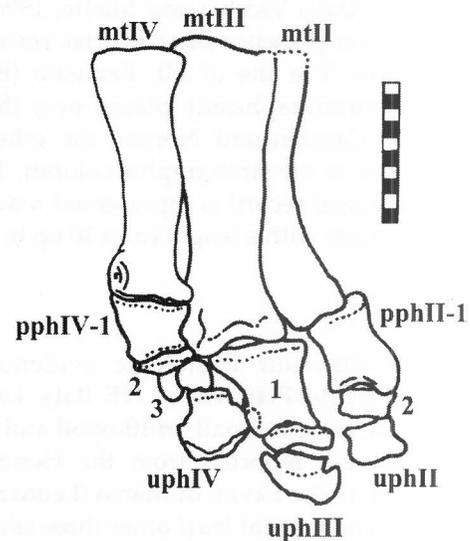
A quarry bed with hundreds of footprints was discovered in May 1999 in the Calcare di Altamura near Altamura (Puglia, Apulia Platform). Most of the footprints appear to belong to small quadrupedal trackmakers, probably ankylosaurians or odd dwarf sauropods (pers. obs.).

### Late Santonian

Dinosaurs and crocodylians have been recently excavated in the Karst of NE Italy (Adriatic-Dinaric Platform). The remains were collected in different levels inside a 8 m-thick lens of black limestone. At least 12 specimens belong to dinosaurs and seven of them can be identified as hadrosaurians: the complete articulated skeleton with the State Collections number 57021 (known with the nickname "Antonio" figures 2 and 3) about 4.5 metres long, partial forelimbs with articulated elements (57022), an isolated pubis (57023), a partial skeleton with a complete, but strongly crushed, skull and most of the lower jaw (57026), the distal segment of the caudal vertebral column (57028), a partial skeleton with limb elements, ribs, ossified tendons and the pelvic girdle (57247), some sparse bones among them probable manual phalanges and a cervical rib (57256). All the specimens are deposited at the Museo Civico di Storia Naturale of Trieste. Specimens belong to individuals of grossly the same size and the degree of ossification and fusion of skeletal elements suggests that they were not immature.

When I was charged by the Italian Ministry of Cultural Goods and Activities to do a preliminary study of the specimens (Dalla Vecchia, 1999b) only the proximal part of the tail, part of the pelvis, the hind limbs, the forelimbs and part of the pectoral girdle were visible of the complete specimen 57021, which was preserved in blocks separately prepared. The preparation of the skull, trunk and the whole tail was completed in late autumn 2000. The complete skeleton was presented to the public on December 14th 2000. Most of the following characters have been observed in that occasion.

The belonging to Hadrosauridae *sensu* Weishampel and Horner (1990) and Weishampel *et al.* (1993) is indicated by presence of several apomorphies of this clade (e.g. absence of the surangular foramen, elevation of the dorsal process of maxilla, miniaturized maxillary teeth, reduction of the carpus, loss of manual digit I, and presence of a large antitrochanter on the ilium. Some characters of 57021 and 57026 are found also in *Telmatosaurus* (Nopcsa) and most of them are considered primitive (see Weishampel *et al.*, 1993): the shape of the humerus



**Figure 2.** Specimen 57021. Right foot in dorsal view. Abbreviations: mtII-IV= metatarsal II-IV; pphI-IV = pedal phalanges of digit I-IV; uph II-IV= ungual phalanges of digits II-IV. Scale bar = 10 cm.

and its non-angular deltopectoral crest, the shape of the transversely wide distal condyle of the quadrate, the relatively narrow shape of the rostrum, the low number of maxillary tooth positions, the relative elongation of the skull and its shape (no crests or gryposaur arching of the nasals), the strong denticulation of the oral margin of the premaxilla and pre-dentary, the shape of the proximal caudal centra and corresponding neural spines (figure 3).

The postcranial skeleton of hadrosaurid genera is very conservative, much more so than in most other dinosaur groups (Weishampel and Horner, 1990). Despite this, the complete skeleton 57021 has some characters in the postcrania which are unknown or unusual in other hadrosaurids. These characters concern the shape of the neural spine of the posterior dorsal and proximal caudal (figure 3) vertebrae, the shape of transverse processes of the proximal caudal vertebrae (figure 3), the shape of haemapophyses ("booted"), the distal position of the first chevron, the low profile of the distal tail, the absence of manual digit V, the distally expanded preacetabular process of the ilium, the very long ischium, a femur decidedly short (compared to tibia, metatarsal III and humerus), a short phalangeal part of the foot relative to the length of metatarsus and with an unusual phalangeal formula (figure 2), the relative size of metatarsals (with metatarsal II shorter than III and IV, condition similar to that of some theropods like *Struthiomimus* and *Bogorovia*; the pes of the Adriatic hadrosaurs probably left asymmetrical footprints; see figure 2).

Therefore, the preliminary study supports some affinity between the small hadrosaurid represented by 57021 and 57026 (and by all other specimens if we assume the presence of only one taxon in the sample) and *Telmatosaurus*, but suggests that it is a new taxon. Some of the above cited characters, however, cannot be checked on *Telmatosaurus* and the relationships of the latter with the Adriatic hadrosaurids could be even closer. In fact, the characters concerning chevrons, pelvis and limb bones ratios and proportions in *Telmatosaurus* are unknown because no chevrons, pelvis and articulate limbs or even partial limbs were ever found (Weishampel *et al.*, 1993; pers. obs.). It is probable that the new hadrosaurid and not other hadrosaurids should be taken as model for the skeletal reconstruction of the limbs of *Telmatosaurus*. To confirm the taxonomic separation from the Transylvanian hadrosaurid, specimens 57021 and 57026 present respectively a distally expanded scapular blade like that of *Camptosaurus* (another primitive feature) and dentary teeth which are not sensibly larger than the maxillary teeth, are mesiodistally narrow and with a strong central carina. A detailed description of the new taxon and cladistic analysis of its relationships are needed.

The primitive *Telmatosaurus* from the Maastrichtian of Transylvania, of a size similar to 57021 (length ~5 m; small size is considered an apomorphy of *Telmatosaurus* by Weishampel *et al.*, 1993) and an estimated weight of 500 kg (which is at most 10% of an average adult of other hadrosaurid species according to Weishampel *et al.*, 1993; however, according to Weishampel and Horner, 1990, p. 534, the average adult body weight of a hadrosaurid is 3,000 kg) is considered one of the smallest hadrosaurid dinosaurs and an insular dwarf (Weishampel *et al.*, 1991; 1993). The apomorphies in the postcranial skeleton of the Karst hadrosaurids are probably due to their insular habitat. On islands animals evolve faster than on continents and often develop "aberrant" characters. Noteworthy, the femur is shorter than tibia, and metatarsals are elongated relatively to femoral length, which, together with the foot structure, could be a cursorial adaptation.

Theropod dinosaurs (57030) might be present in the site, possibly represented by an arcotometatarsalian metatarsal.

### Campanian/Maastrichtian

A paleokarst fissure with reptilian teeth and fragments of bone was discovered by G. Rimoli and A. Tarlao near Kozina (Karst, SW Slovenia, Adriatic-Dinaric Carbonate Platform) on spring 1999. Debeljak *et al.* (1999) dated the site to the early Campanian-late Maastrichtian (but its age is most

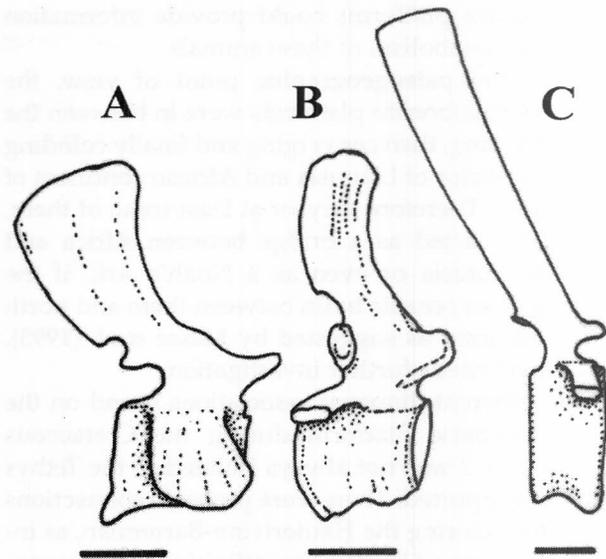


Figure 3. Proximal caudal vertebrae of some hadrosaurids. A, specimen 57021, 4th or 5th caudal vertebra in slightly dorsal view (actually the transverse process is perpendicular to the neural arch); B, *Telmatosaurus transylvanicus* (Nopcsa), caudal to the 4th and in lateroanterior view (after Weishampel *et al.*, 1993); C, "*Kritosaurus*" *incurvimanus* Parks, 5th caudal vertebra (after Parks, 1920, redrawn). Scale bar = 5 cm.

probably late Maastrichtian) and identified hadrosaur, indeterminate non-hadrosaurid ornithomimid, theropod and crocodile teeth.

### Conclusions

While it could be hypothetically argued that in some cases the bone remains were transported from a far continent into the carbonate platform by marine currents, footprints are obviously autochthonous and suggest that the carbonate platforms were emergent and inhabited by large vertebrates. This fact has many potential implications to be investigated in the future.

The emergent parts of the platforms had to sustain the populations of large vertebrates with food and fresh water. Geologists were not able to identify wide emerging portions, the suggested emerged parts being of relatively limited extension (e.g. Maticcec *et al.*, 1996). However, this could be due to the scarcity of adequate outcrops and limited search for the evidence of emersions. In this case, the terrestrial vertebrates are the only evidence of extensive emersions and this might dramatically change the previous local paleogeographic and paleoenvironmental reconstructions based on the geological data alone. Alternatively, the emergent portions of the carbonate platforms might have been of limited extent as suggested by the geological record, but the space and food requirements of the animals living on them were low enough to allow them to live on those relatively small islands, lacking a well developed fluvial system. Therefore, the study of the dinosaurs of

the carbonate platforms could provide information about the metabolism of these animals.

From the paleogeographic point of view, the Cretaceous carbonate platforms were in between the firstly dividing, then converging and finally colliding European sector of Laurasia and African continent of Gondwana. Therefore they, or at least some of them, could have acted as a bridge between Africa and Laurasia/Eurasia or even as a Noah's Ark, if the opening of an oceanic basin between them and north Africa occurred as suggested by Masse *et al.* (1993). This aspect needs further investigation.

The different dinosaur associations found on the Adriatic-Dinaric Platform during the Cretaceous suggest that it was not always isolated in the Tethys as usually reported. There were probable connections with Africa during the Hauterivian-Barremian, as indicated by some Gondwanan affinities of the sauropod fauna (Dalla Vecchia, 1998a). The platform was probably isolated during Albian-Cenomanian times (Dalla Vecchia and Tarlao, 2000; Dalla Vecchia *et al.*, 2001). The presence of late Santonian hadrosaurs suggests a possible connection with the southern Asiatic margin of Eurasia during the early Senonian, caused by the subduction of the northern margin of the Tethys (see in this sense fig. 17B-C in Head, 1998; Camoin *et al.*, 1993; Philip *et al.*, 1993). In fact, according to the present state of knowledge of the paleogeographic distribution and phylogenetic relationships of the hadrosaurids, they originated in Asia (e.g. Weishampel, 1990; Laurent *et al.*, 1997; Norman, 1998; Head and Kobayashi, 1999) or, less probably, North America (Head, 1998). These dinosaurs were relatively frequent in Asia during the Turonian-Santonian interval (see also Ryan, 1997, and Norman and Kurzanov, 1997); their remains are not found in Africa and they are unknown in Europe in the Cenomanian-upper Campanian. I hypothesize that the descendants of the Santonian hadrosaurids living on the Adriatic-Dinaric carbonate platform could have migrated to the Transylvanian Hateg basin. This occurred through the Austroalpine block, which during Campanian-Maastrichtian times was beginning to collide with the part of the Adria microplate containing the Adriatic-Dinaric carbonate platform.

Finally, the presence of levels with evidence of terrestrial vertebrates (together with palynomorphs, charophytes and fresh water ostracods and molluscs) intercalated with marine carbonates that contain bivalves, calcareous algae and foraminifers, is very important for biostratigraphic correlations between terrestrial and marine sections.

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