

# The impact of dinosaur palaeoichnology in palaeoenvironmental and palaeogeographic reconstructions: the case of the Periadriatic carbonate platforms

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**ABSTRACT** – Knowledge of dinosaur footprints has greatly changed how scientists reconstruct the palaeoenvironment and palaeogeography of the Mesozoic carbonate platforms of the Periadriatic area (Italy, Slovenia and Croatia). Geologists considered those carbonate platforms as shallow marine, intraoceanic banks (i.e., surrounded by the Tethys Ocean) during Cretaceous times. The discovery in the last 20 years of dinosaur fossils, mainly footprints, in many places and at different stratigraphic levels has demonstrated that the “shallow seas” were repeatedly or continuously populated by large terrestrial animals. Thus, the reconstructions of those carbonate platforms as a sort of Mesozoic “Bahamas Banks” was incorrect. The new record allows also testing for congruence with palaeoenvironmental and palaeogeographic reconstructions. Areas where dinosaur fossils have been found are always considered as “shallow marine” in those reconstructions, very far away from continental areas during the Late Triassic and earliest Jurassic and surrounded by deep marine basins during Late Jurassic and Cretaceous times. The results of this research are a first step toward the understanding of those dinosaurs living “at the border”, but are obviously preliminary and subject to confirmation or confutation with increased fossil sampling. The ichnological sample and the palaeogeographic reconstructions can also stimulate some reflections about the biology of the extinct dinosaurian clades and give some suggestions for the development of future research.

**Key words:** *Periadriatic carbonate platforms, Dinosauria, dinosaur palaeoichnology, Tethyan palaeogeography*

## INTRODUCTION AND GEOLOGICAL FRAME-WORK

The Periadriatic region is the portion of southern Europe surrounding the present-day Adriatic Sea, a northern branch of the larger Mediterranean Sea. This NNW-SSE elongated region is for the most part included in the territory of the Italian, Slovenian and Croatian Republics (fig. 1). Considering its geological history, most of the Italian peninsula belongs to this region.

Twenty-one years ago one of the fathers of the 20th century palaeoichnology, Giuseppe Leonardi, wrote: “We would expect to find a chapter dedicated to the Italian dinosaurs in an Italian book on dinosaurs. Unfortunately this chapter cannot exist because those reptiles “snubbed” Italy, or better the seas and islands that occurred during Mesozoic times in the place of the present-day Italian Peninsula. Dinosaurs were typically terrestrial animals and the Italian region at that time was covered by an epicontinental sea along the margin of the Tethys ocean....” (Leonardi, 1984, p.197; my translation from Italian).

According to the geological knowledge of the time Leonardi was right. The non-palinspastic maps of facies distribution in the Periadriatic area during the interval from the Norian to the Late Cretaceous (fig. 2) show only marine environments, i.e. carbonate platforms and deep basins,

with no continental clastic deposition. The stratigraphic sections of key palaeogeographic units of the Periadriatic region (e.g., Apulia, Friuli-Istria, Dalmatia, Dinarids; see Zappateria, 1990) also show the total prevalence of marine facies. Before the last decade of the 20th century, the geological literature reported only local and short-lasting emersions in the hypothetical form of small islands, indicated mainly by bauxite levels (e.g., in the Tithonian of Istria; Turonian of Campania and Apulia, S Italy), which were merely considered ephemeral oddities in a prevailing marine landscape.

According to the reconstructions made by geologists, during latest Triassic times the region was a wide carbonate platform with dominating peritidal facies, dissected by some deeper anoxic basins and bordered to the east by pelagic basins. Parts of the wide platform collapsed in Liassic times and the slope to basinal facies spread; three separate carbonate platforms occurred during the Late Jurassic-Late Cretaceous interval, surrounded by pelagic basins: the Adriatic-Dinaric Carbonate Platform (ADCP), the Apulian Carbonate Platform (APUCP) and the Apennine Carbonate Platform (APECP; i.e. the Latium-Abruzzi-Campania Platform) (fig. 2). The ADCP was the northern termination of a much larger carbonate platform that in the moments of maximum extent (e.g., Late Jurassic) included, at the opposite extremity, parts of the present day Turkey (fig. 3) (Dercourt et al., 1993; 2000).



**Figure 1** – Dinosaur sites discovered to date in Italy, Slovenia and Croatia. A site with skeletal remains in northern Slovenia and two track sites in Tuscany (Italy) do not pertain to the Periadriatic domain. The question mark indicates sites where the presence of dinosaur footprints is doubtful, or the site of provenance is not precisely known (e.g., the Late Jurassic footprint-bearing boulders of Apulia, see text).

Two main kinds of carbonate platforms can be distinguished: intraoceanic and pericontinental. Intraoceanic platforms are shallow marine banks surrounded by deep marine basins with no connection to an emergent land. The

term “intraoceanic” is somewhat incorrect, as often those carbonate platforms did not develop on oceanic crust, but on stressed and sunk continental crust. Pericontinental platforms border the margin of an emergent land with marginal

siliciclastic deposition. A classic example of the latter is the platform surrounding the North American continent in the Gulf of Mexico area during Albian-Cenomanian times. Dinosaur footprints are found in the shallow marine carbonates, but only close to their transition to the continental clastics (Pittmann, 1989). Dinosaurs moved into the carbonate platform, but only for a short range.

The Cretaceous Periadriatic carbonate platforms are considered as intraoceanic (e.g., Eberli et al., 1993; Dercourt et al., 1993; 2000) and thus it was assumed that large terrestrial animals such as dinosaurs never reached or lived on these areas. However, despite this apparently unfavourable palaeoenvironmental situation, dinosaur fossils have been discovered in Croatia, Slovenia, and northern, central and southern Italy during the last 20 years (fig. 1). The sample includes footprints, bones and even a feather. The record covers the interval Late Triassic-Maastrichtian, with a large gap in the Middle Jurassic (fig. 1).

#### *Terminology*

As in other papers (e.g., Dalla Vecchia & Tarlao, 2000; Dalla Vecchia et al., 2001; 2002), I conventionally consider as “small bipedal dinosaur footprints” those with length less than 15 cm, “medium-sized” those with length between 15 and 25 cm, “large-sized” those with length more than 25 cm.

The reference for absolute dating is the time scale by Gradstein & Ogg (2004).

## THE DINOSAUR RECORD IN THE PERIADRIATIC REGION

#### *Late Triassic*

Late Triassic dinosaur footprints have been discovered in northern Italy and western Slovenia. Mietto (1988) attributed to small theropods, a “basal ornithischian” and possibly a prosauropod some trackways and isolated footprints found in a block fallen from Mount Pelmetto in the eastern Dolomites. Chirotheroid footprints are present as well in other blocks of the same rock fall (Mietto & Dalla Vecchia, 2000). Mietto (1991) described a couple of large theropod footprints (*Eubrontes*) in the Tre Cime di Lavaredo, also in the Dolomites. A medium-sized tridactyl footprint is reported from the Puez Plateau, Western Dolomites (Leonardi & Avanzini, 1994). Ten or eleven boulders with footprints are reported from the Carnian Pre-Alps of Friuli (NE Italy), with medium to large-sized theropod and/or basal saurischian footprints, as well as possible sauropodomorph and chirotheroid tracks (Dalla Vecchia & Mietto, 1998; Dalla Vecchia, 2002b).

All of these specimens come from the Dolomia Principale (Hauptdolomit) Formation which is latest Carnian-Rhaetian in age; specimens from Mount Pelmetto are probably Late Carnian in age (Mietto, 1988).

A trackway of a bipedal animal occurs in the Norian-Rhaetian tidal dolostone of western Slovenia and is possi-

bly referable to a sauropodomorph (Dalla Vecchia, 1997a).

#### *Early Jurassic*

The entire Liassic palaeoichnological record comes from a relatively small area of northern Italy, belonging to the shallow marine Trento Platform (figs 1, 2).

The Lavini di Marco track site (Rovereto, Trento Province), with 7 footprint-bearing levels dating to the Late Hettangian-Early Sinemurian, is one of the largest in Europe. More than 70 dinosaur trackways and 280 isolated footprints have been identified (Piubelli et al., 2005), but many further specimens were not included in the study. A high ichnological diversity is represented, with footprints and tracks belonging to small to large theropods (*Kayentapus*, *Grallator*, *Anchisauripus*, *Eubrontes*), sauropodomorphs (*Lavinipes*, *Parabrontopodus*?), basal ornithischians (*Anomoepus*), possibly large ornithischians, and non-dinosaurian tetrapods (lizard-like reptiles, possible therapsids) (Leonardi & Mietto, 2000; Avanzini et al., 2001a, 2003; Piubelli et al., 2005; Nicosia et al., 2005).

Other smaller Late Hettangian-Early Sinemurian track sites have been discovered at Chizzola (medium to large theropod footprints, *Eubrontes*; Leonardi, 2000), Pizzo di Levico (Avanzini & Tommasoni, 2002), Mount Pasubio and northern Mounts Lessini (theropod and sauropodomorph footprints; Leonardi, 2000; Nicosia et al., 2005).

Early Sinemurian footprints belonging to sauropodomorphs and large theropods (*Eubrontes*) have been reported at the Becco di Filadonna near Trento (Avanzini, 1997; Nicosia et al., 2005).

The Bella Lasta site of the Mounts Lessini (Verona Province) is younger (late Sinemurian) and preserves large theropod (*Kayentapus*) and sauropodomorph footprints (Mietto et al., 2000).

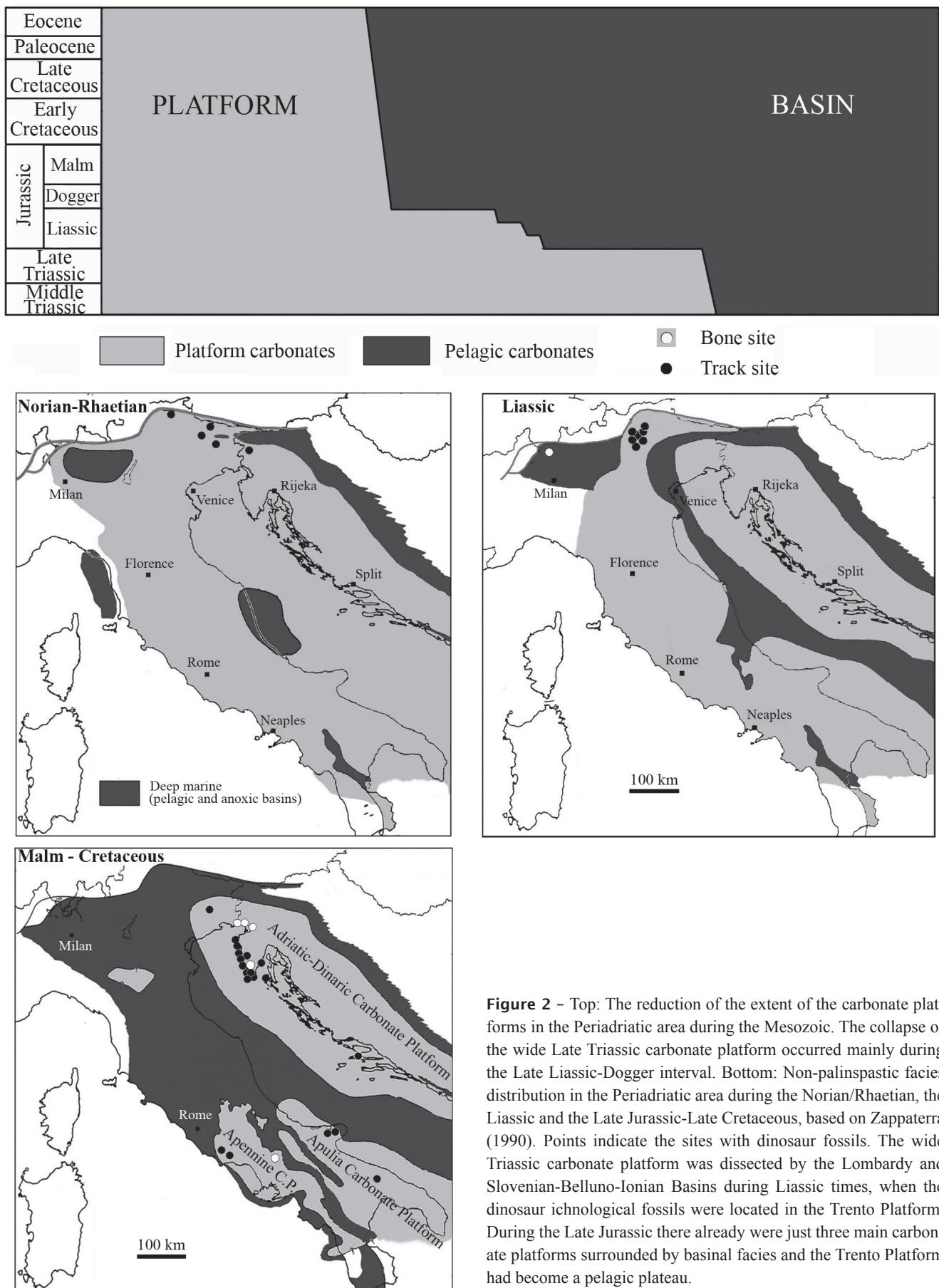
The Marocche di Drò site, Sarca Valley (Trento Province), is the youngest, being Pliensbachian in age (Avanzini et al., 1999; 2001b). It has yielded small sauropodomorph and basal thyreophoran footprints (Piubelli et al., 2005). The nearby Mt Anglone site (limit Sinemurian-Pliensbachian) is rich in theropod footprints of various sizes and possible fossils of bipedal ornithischians also occurs (Avanzini, 2007).

Finally, the partial skeleton of an 8-m-long theropod was found in the Sinemurian limestone of Saltrio, Lombardy (NW Italy) (Dal Sasso, 2001; Nicosia et al., 2005).

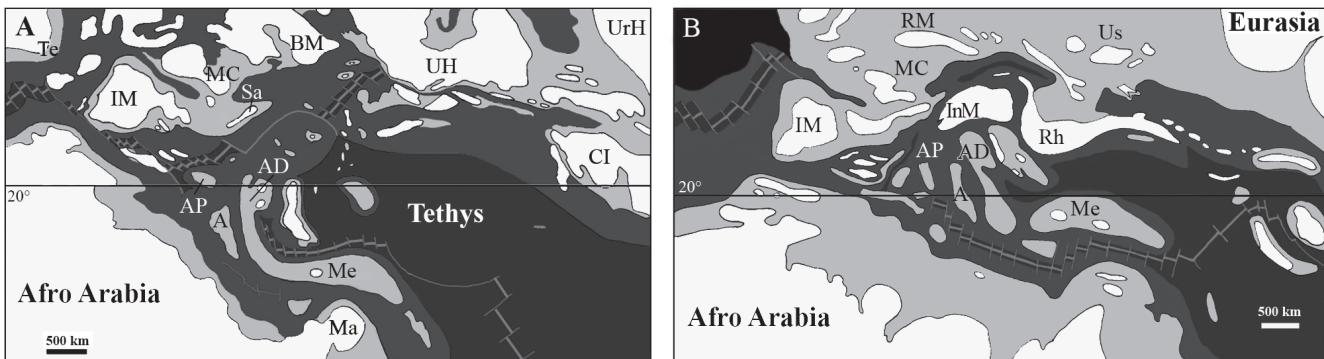
#### *Late Jurassic*

Track sites have been reported from the Upper Jurassic of Istria (Croatia; ADCP) and Apulia (southern Italy; APUCP). The Istrian sample is represented by approximately one thousand footprints and 23 narrow-gauged trackways attributed to sauropods and preserved in Late Tithonian limestone at the Kirmenjak/Chirmegnacco quarry (Mezga et al., 2003; 2007a). The pedal print lengths range from 23-52 cm.

The Apulian sample is made up of 40 tridactyl and



**Figure 2** – Top: The reduction of the extent of the carbonate platforms in the Periadriatic area during the Mesozoic. The collapse of the wide Late Triassic carbonate platform occurred mainly during the Late Liassic-Dogger interval. Bottom: Non-palinspastic facies distribution in the Periadriatic area during the Norian/Rhaetian, the Liassic and the Late Jurassic-Late Cretaceous, based on Zappaterra (1990). Points indicate the sites with dinosaur fossils. The wide Triassic carbonate platform was dissected by the Lombardy and Slovenian-Belluno-Ionian Basins during Liassic times, when the dinosaur ichnological fossils were located in the Trento Platform. During the Late Jurassic there already were just three main carbonate platforms surrounded by basinal facies and the Trento Platform had become a pelagic plateau.



**Figure 3** – Simplified palaeogeographic maps of the western Tethys. A) Early Tithonian; B) Late Cenomanian. White indicates “emergent land” (including volcanic islands), light grey “shallow marine” (carbonate platforms and terrigenous shelf), dark grey “deep marine” (including the pelagic environments on continental crust where the carbonate oozes of the Maiolica and the Chalk/Craie deposited) and darker grey “ocean basins”. Acronyms: A = Apulia Platform, AD = Adriatic-Dinaric Platform, AP = Apennine Platform, BM = Bohemian Massif, IM = Iberian Massif, InM = Insubrian Massif, Ma = Mardin (Turkey), Me = Menderes (Turkey), MC = Massif Centrale, RM = Rhenish Massif, Sa = Sardinia, Te = Terranova, UH = Ukrainian High, UrH = Uralian High. A is redrawn and modified from Thierry (2000), B is redrawn and modified from Philip & Floquet (2000).

tetradactyl footprints attributed to medium-sized theropods, occurring in three boulders used to build a pier at Mattinata (Foggia Province) (Nicosia et al., 2005; Conti et al., 2005). These boulders originated from an unknown quarry on the Gargano Promontory, which supposedly mined Upper Jurassic limestone (Nicosia et al., 2005; Conti et al., 2005).

#### *Early Cretaceous – Berriasian to Barremian (145.5-125 mya)*

The part of the Periadriatic region with the richest Cretaceous dinosaur fossil record is without a doubt the upper Adriatic area, in particular the Karst and the coast of the Istrian peninsula (ADCP), where several track sites, three sites with skeletal remains and one with a feather have been discovered (fig. 4).

The oldest dinosaur record reported in the Cretaceous of the Periadriatic region consists of some depressions exposed as vertical cross-sections in the wall of the Fantasia Quarry in Istria, interpreted as sauropod footprints by Lockley et al. (1994) and Berriasian in age. However, this interpretation has been criticized (Dalla Vecchia, 2005).

Hauterivian sauropod and large theropod footprints, as well as some dinoturbated horizons, occur in Istria at Cisterna and Cape Gustinija localities (Dalla Vecchia et al., 2000). A large theropod footprint and a sauropod manual print are preserved in a limestone block from the Sarone Quarry, Cansiglio Plateau (north-eastern Italy; ADCP), Late Hauterivian-Early Barremian in age (Dalla Vecchia & Venturini, 1995; Dalla Vecchia, 1999). Probable sauropod dinoturbation occurs in the Lower Barremian of Barbariga, southern Istria (Dini et al., 1998).

Eight short trackways and several individual footprints (6 pairs and 19 isolated) of large theropods have been reported from the Late Barremian Pogledalo site on the Main Brioni Island (southern Istria), and similar footprints pos-

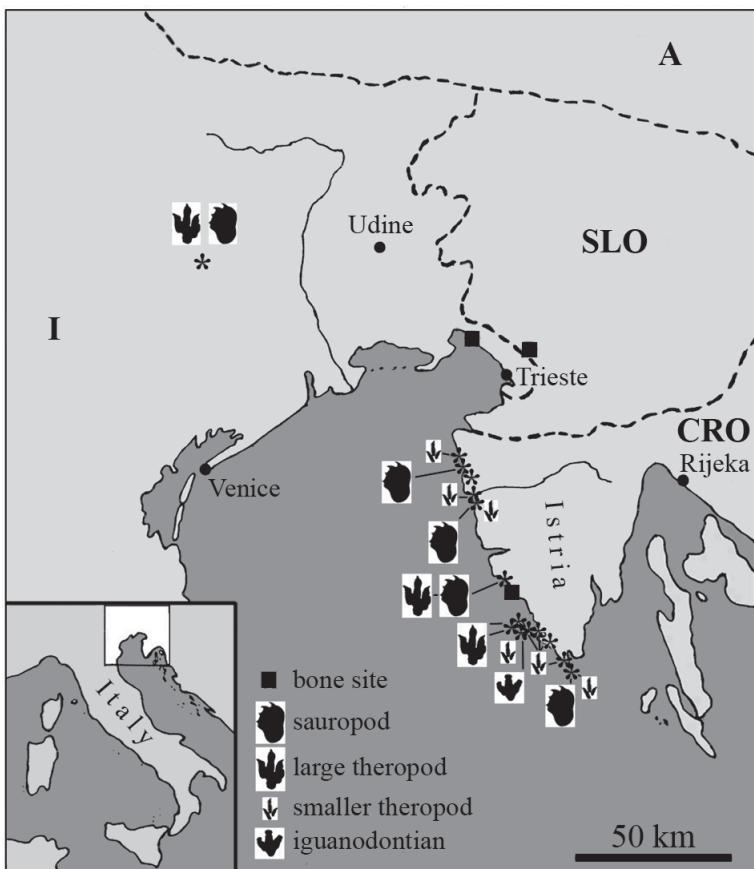
sibly occur on nearby Vanga island (Dalla Vecchia, 1998b; Dalla Vecchia et al., 1993; 2002). Finally, a site rich in dinosaur bones of Late Hauterivian-Early Barremian age crops out at the bottom of the Adriatic sea at Colone/Colonne locality near Bale/Valle, southern Istria (Dalla Vecchia, 1998a; 2005). This site has yielded remains of sauropods and much rarer fossils of small and large-bodied theropods.

Only one site has been found to date in the APUCP. More than 60 tridactyl footprints, 15 to 42 cm in length, often forming short trackways, were reported in the boulders of a quarry near Borgo Celano (Gargano Promontory, Apulia region). They occur in three different footprint-bearing levels dating to the Late Hauterivian-Early Barremian (Gianolla et al., 2000; Bosellini, 2002; Nicosia et al., 2005). They are attributed to middle to large-size theropods and to “Iguanodontian ornithopods” by Bosellini (2002, p. 217), but only to theropods by Nicosia et al. (2005). Large footprints are by far the most common (pers. obs.). Sub-circular prints with a diameter of 25 to 40 cm are also found (Nicosia et al., 2005).

#### *“Middle” Cretaceous – Aptian to Cenomanian (125-93.5 mya)*

Aptian dinosaur fossils are rare. Some possible bowl-shaped dinosaur footprints are exposed as vertical cross-section in the middle Aptian limestone of the Mt. Bernadia, Julian Pre-Alps (Udine Province, North-eastern Italy) (Dalla Vecchia & Venturini, 1996). A second Aptian track site, with over 40 footprints belonging to a relatively small quadrupedal trackmaker and possibly to theropods, was recently reported from the Aurunci Mountains close to the town of Esperia (Frosinone Province, southern Italy), belonging to the APEC.

The Albian ichnological record comes from the Upper Albian of Istria. Some tridactyl footprints, probably impressed by theropods, were preserved at the Mirna/Quieto

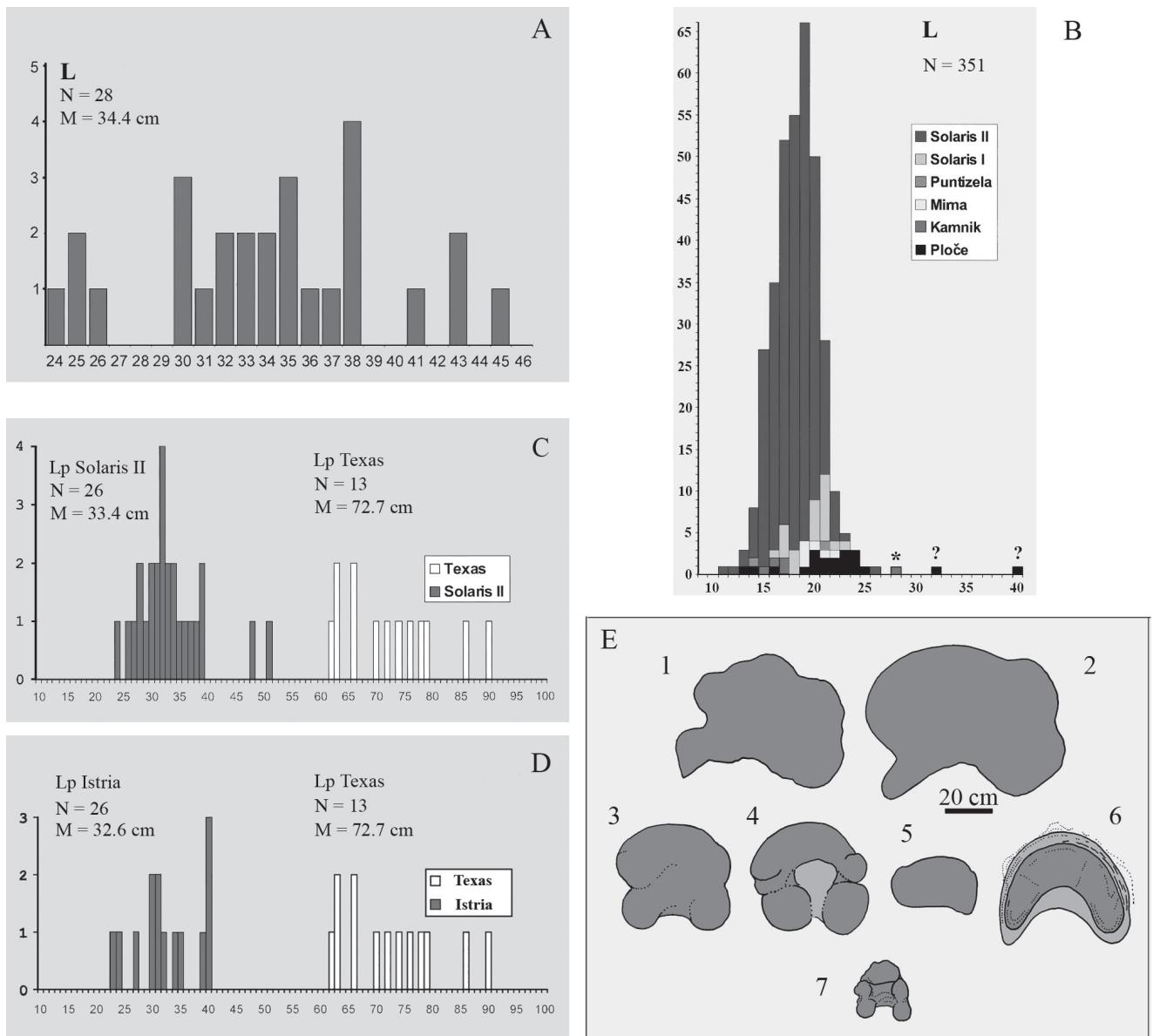


**Figure 4** – Cretaceous dinosaur sites in the upper part of the ADCP (Cansiglio Plateau, Italian and Slovenian Karst, Istrian Peninsula).

river mouth (Dalla Vecchia et al., 1993). The nearby site of the Solaris naturist camp ground near Črvar/Cervera is much larger and rich in footprints. There are 45 trackways and over 300 isolated footprints referred to medium-sized theropods, and at least two sauropod trackways and more than 65 isolated sauropod footprints belonging to *Titanosaurimanus nana* (Dalla Vecchia & Tarlao, 2000). Maximum sauropodan pedal length is 51 cm, but the average length is 30-35 cm; the largest manual print is only 24.5 cm wide. Two trackways of a small and a medium-sized theropod occur in two different levels at the southern Puntizela/Puntesella locality (Dalla Vecchia & Tarlao, 2000). Fourteen trackways, three pairs and 8 single footprints of small to medium-sized, tridactyl track makers, possibly all theropods, are found on two different footprint-bearing layers at Ploče site of the Main Brioni Island (Dalla Vecchia et al., 2002). Bachofen-Echt (1925a,b) reported about the presence of large tridactyl footprints in this site, which unfortunately cannot be located at this time. Some very weathered large tridactyl footprints are deposited in a building on the island, and could come from the Ploče site, although their exact provenance is unknown (Dalla Vecchia et al., 2002). Four trackways left by a medium-sized, tridactyl trackmaker, most probably a theropod, occur in the nearby Kamik site (Dalla Vecchia et al., 2002). The trackway of a medium-sized (pes print = 28 cm), probably iguanodontian ornithopod is also preserved on a bed just below that with the theropod footprints (Dalla Vecchia et al., 2002).

Finally, two tridactyl, possibly theropod, footprints about 20 cm long and some rounded traces are reported from the Zlatne Stijene locality near Pula/Pola (Mezga et al., 2007b).

Five Late Cenomanian track sites occur in Istria. The Lovrečica/S. Lorenzo di Daila site preserves five short trackways, seven incomplete trackways, three pairs and four single footprints of small to medium-sized theropods (Dalla Vecchia et al., 2001). The Karigador/Carigador (Ladin Gaj) site has two trackways and 8 footprints referred to small sauropods (Dalla Vecchia et al., 2001). Recently, a further narrow-gauged trackway of a small sauropod (pes print = 33 cm) has been discovered in a nearby site (Mezga, Tunis et al., 2006). The Grakalovac site exposes two trackways, a pair and a single tridactyl footprint, referred to medium-sized theropods (Dalla Vecchia et al., 2001). Some probable footprints are visible in cross-section on the cliff wall (Dalla Vecchia & Venturini, 1996). Rounded to quadrangular, shallow depressions on the footprint-bearing surface, as well on other bed surfaces of the site, could be the footprints of a small sauropod (Dalla Vecchia et al., 2001; Dalla Vecchia, 2005). The Fenoliga Islet site has a long trackway of a relatively small sauropod (Gogala & Pavlovec, 1978; 1984; Tišlar et al., 1983; Leghissa & Leonardi, 1990; Mezga & Bajrektarević, 1999; Dalla Vecchia et al., 2001). Three other trackways and five groups of footprints were attributed to small sauropods by Mezga & Bajrektarević (1999). Three



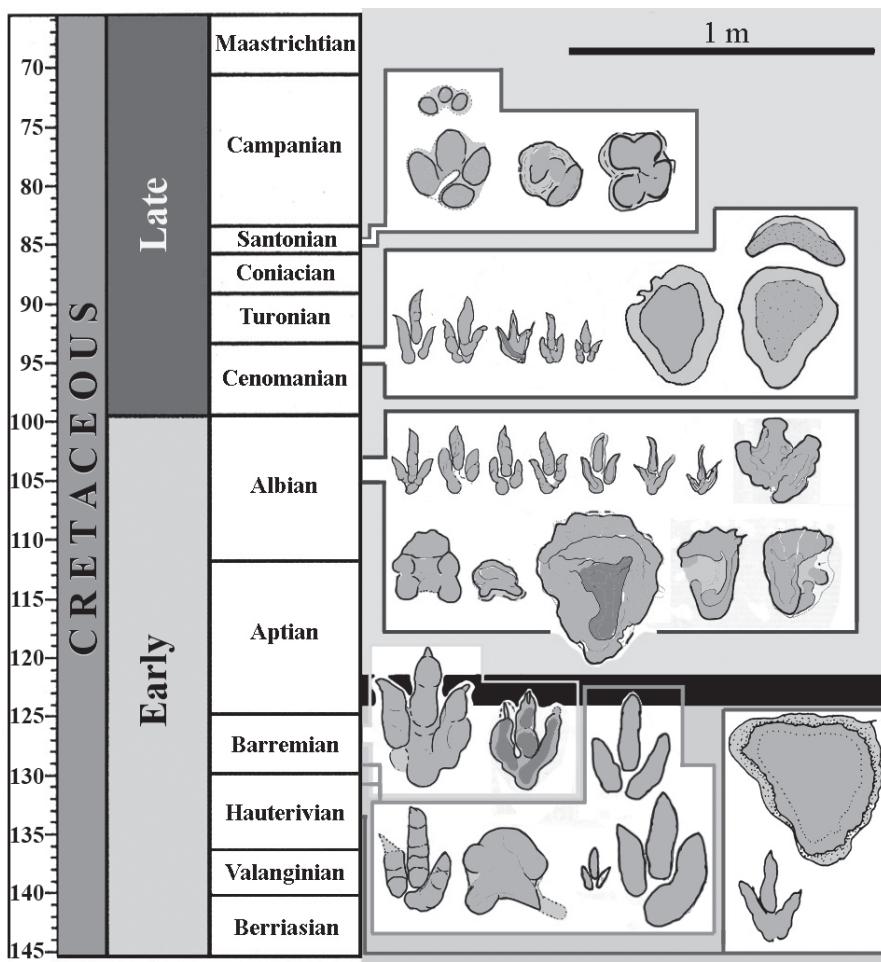
**Figure 5** – Large Hauterivian-Barremian and smaller Albion-Cenomanian dinosaurs in the northern part of the ADCP. A) Theropod footprint length distribution in the Late Barremian Pogledalo site of the Main Brioni Island (modified from Dalla Vecchia et al., 2002). B) Sample of tridactyl footprints from the Upper Albion of Istria (modified from Dalla Vecchia & Tarlao, 2000). C) Comparison of a sample of sauropod pedal prints from the Upper Albion of Istria and a sample from the Albian pericontinental platform of Texas (modified from Dalla Vecchia & Tarlao, 2000). D) Comparison of a sample of sauropod pedal prints from the Upper Cenomanian of Istria and a sample from the Albian pericontinental platform of Texas (based on data in Mezga & Bajraktarević, 1999, and Dalla Vecchia et al., 2001). E) Comparison of a sample of sauropod manus prints from pericontinental platforms and continental settings (1-6) with the largest Albian manual print of Istria (7) (modified from Dalla Vecchia & Tarlao, 2000).

trackways impressed most probably by medium-size theropods also occur (Dalla Vecchia et al., 2001). Footprints are possibly present in the Unie Island of northern Dalmatia (Dalla Vecchia et al., 2001).

An Early Cenomanian track site is reported from the APECP. It occurs in a quarry near Sezze (Latina Province), in the Lepini Mountains south of Rome, opened into the inner platform carbonates. Footprints of small-sized sauropods

and medium-sized bipedal dinosaurs (probably theropods) have been identified (Dalla Vecchia et al., 2005).

The only other dinosaur fossil from the APECP is the skeleton of the famous *Scipionyx samniticus* (Leonardi & Teruzzi, 1993; Leonardi & Avanzini, 1994; Dal Sasso & Signore, 1998), a small, juvenile theropod which comes from the Lower Albion limestone of Pietrarroia (Benevento, Campania Region).



**Figure 6** – The change in size of dinosaur footprints occurring between the Late Barremian and the Late Albian in the Periadriatic Carbonate Platforms. The black band corresponds to the Early Aptian opening of the oceanic basin between the platforms and the Afro Arabian continent according to Masse et al. (1993).

#### Late Cretaceous – Turonian to Maastrichtian (93.5–65.5 mya)

Mauko & Florjančić (2003) report the presence of several footprints referred to small to medium-sized bipedal dinosaurs in the Upper Turonian-Coniacian limestone near the Pozara promontory of south-eastern Istria. Some resemble the scratches produced in quarrying the limestone, which are common along the Istrian coast (see Dalla Vecchia et al., 2002 for a discussion about such marks). Therefore, their identity as actual footprints is debatable.

Some footprints in Upper Turonian-Lower Coniacian limestone near Stari Grad, Hvar/Lesina Island of central Dalmatia were identified as those of a sauropod (Mezga, Meyer et al., 2006). Pedal print length ranges from 29–60 cm and one reaches 92 cm, but they are all weathered and possibly underprints, and thus their size could be exaggerated.

Additional dinosaur fossils in the ADCP are represented by bones and teeth. Hadrosauroid remains have been extracted in the Upper Campanian-Maastrichtian site of the Villaggio del Pescatore, Italian Karst, Trieste Province (Bazzatti & Calligaris, 1995; Dalla Vecchia, 2001; Arbulla et al., 2006). This site was once dated to the Late Santonian, but the presence of the foraminifer *Murciella cuvillieri* just below the dinosaur-bearing beds (Palci, 2003; S. Venturini, pers.

comm.) indicates a younger age. Bone fragments as well as teeth of hadrosauroids, an indeterminate ornithischian and small theropods were found in the Upper Campanian-Maastrichtian of the Slovenian Karst (Debeljak et al., 1999; 2002). Finally, a small feather was found in the Tomaj limestone of the Lipica Formation (Early Campanian) of the Slovenian Karst (Buffetaut et al., 2002).

Two track sites occur in the Apulia platform. The main one is that of the ECOSPI quarry (former De Lucia quarry) in the Pontrelli locality near Altamura (Murge, Bari Province). A further site is located in an abandoned quarry south of Altamura (Iannone, 2003). The main site is a wide quarry bed literally covered with footprints and is one of the richest track sites in Europe, with an estimated presence of 30.000 footprints (Nicosia et al., 2000a). A single tridactyl footprint is tentatively referred to a theropod and one trackway “might pertain to a very small sauropod” (Nicosia et al., 2000a: p. 235). All other examined trackways belong to relatively small quadrupedal ornithischians (Nicosia et al., 2000a), and some of them with tetradactyl footprints are tentatively referred to ankylosaurians (Dal Sasso, 2001). A single trackway and a few isolated footprints are the type material of *Apulosauripus federicianus*, whose track maker was identified as a medium-sized hadrosaurid (the pedal print is

25 cm long) moving quadrupedally (Nicosia et al., 2000b), although this is debatable. The age is “Santonian, excluding the earliest part of this stage” according to Iannone (2003: p. 11).

The second site preserves only a few, yet undescribed footprints of possible Santonian age (Iannone, 2003).

## PALAEOENVIRONMENTAL IMPLICATIONS

While a carcass can float and be deposited far from the place where the animal lived, footprints are indisputable fossils of an animal living in a specific place. Therefore, they are important palaeoenvironmental markers. In this case, they have revealed that the Periadriatic carbonate platforms, usually considered as shallow marine banks of Bahamian type (e.g., Eberli et al., 1993; Bosellini, 2002), were populated by large terrestrial animals, and thus were at least partly emergent. To support populations of large animals like sauropods and other vegetarian dinosaurs with food and fresh water, the emergent part of the platform could not be limited to small islands. The presence of dinosaur fossils in several horizons of the Upper Triassic-Maastrichtian section suggests a continuous, or at least repeated and long-lasting, emergence of the platform (e.g., Dalla Vecchia et al., 1993; Dalla Vecchia & Mietto, 1998; Dalla Vecchia, 1994a,b; 1995; 2002a, b). In order to support this abundance of dinosaurs, those emergent lands could not merely be ephemeral bridges connecting the platforms to far continental areas. Instead, they had to be wide and stably emergent land, like the present-day Yucatan peninsula of Central America, which is the emergent part of a carbonate platform.

Dinosaur footprints have been found in stratigraphic sections where the sedimentation is only marine; for example, in the Upper Cenomanian of Istria they occur in sections dominated by rudist shell debris and rudist mounds (Dalla Vecchia et al., 2001). This suggests that we do not yet fully understand the palaeoenvironmental meaning of those stratigraphic sections.

Based on the association of the dinosaur fossils and inner platform facies in restricted intervals of the Istrian portion of the ADCP (i.e., the Upper Hauterivian-Lower Barremian), it was predicted that dinosaur fossils would be discovered in similar depositional environments on other coeval parts of the platform (Dalla Vecchia et al., 1993; Dalla Vecchia, 1994b) and in the other Periadriatic platforms (Dalla Vecchia & Venturini, 1995). A few years later this prediction was borne out when dinosaur footprints were found in the Cansiglio Plateau and in the Gargano Promontory.

Only after the discovery of the dinosaur fossils, huge stratigraphic gaps and other geological markers of the emersion of the platforms were looked at by geologists in order to explain the presence of large terrestrial animals in geological settings previously universally considered as marine. Among this geological record there is the evidence of repeated subaerial exposure in the Calcare di Altamura at ECOSPI quarry (Iannone, 2003).

the Trento Platform (e.g., Avanzini & Frisia, 1996; Avanzini et al., 2000), the absence of the Upper Campanian and Lower Maastrichtian in some sections of the Karst (e.g., Jurkovšek et al., 1996; Otoničar, 2007), the absence of the Kimmeridgian-Lower Tithonian, Lower Albian and Upper Campanian-Maastrichtian in Istria as well as, locally, that of the Upper Barremian-Lower Albian and the whole Campanian-Maastrichtian (e.g., Matičec et al., 1996; Velić et al., 2000), the absence of the Upper Albian-middle Cenomanian *partim* and Upper Cenomanian-Lower Turonian (extending locally to the lowermost Santonian) in the Apennine platform (e.g., Chioccini et al., 1989), the absence of the Turonian, Lower Campanian and Lower Maastrichtian in the Apulian platform (e.g., Luperto Sanni & Borgomano, 1989) and the repeated, local, subaerial exposures in the Santonian portion of the Calcare di Altamura at ECOSPI quarry (Iannone, 2003).

Also the presence of terrestrial plants in the Norian of Friuli, Lombardy, Campania and Latium, Lower Sinemurian of Lombardy, Pliensbachian of Veneto and Trentino, Liassic of Abruzzi, Dogger of Latium, Barremian, Coniacian-Santonian and Maastrichtian of Friuli Venezia Giulia, Lower Aptian, Lower and Upper Albian of Campania, boundary Cenomanian-Turonian of Veneto, Cenomanian-Senonian of Apulia (Dalla Vecchia, 2000a, *cum biblio*), as well as Lower Campanian of the Slovenian Karst (Dobruskina et al., 1999), support the new view of the Periadriatic Carbonate Platforms as emergent areas.

## PALAEOGEOGRAPHIC IMPLICATIONS

The Periadriatic dinosaur record has also begun to be used as a tool for supporting or rejecting previous palaeogeographic reconstructions.

The Late Norian palaeogeographic/palaeoenvironmental maps by Marcoux et al. (1993) and Gaetani et al. (2000) and the Rhaetian map by Yilmaz et al. (1996) are not in agreement with the presence of Late Triassic dinosaur footprints in the Carnian Pre-Alps, as well as in the Dolomites, because according to these reconstructions the shallow marine facies extended for hundreds of kilometers around the zones with the footprints (Dalla Vecchia, 2002b).

According to Piubelli et al. (2005) the presence of the widely distributed ichnogenus *Kayentapus* points to a connection of the Trento Platform with the continental Pangea during Hettangian-Sinemurian times. On the other hand, Piubelli et al. (2005) and Nicosia et al. (2005) consider the small size of the Pliensbachian footprints as indicative of the insular condition of those dinosaurs, due to the Late Liassic dismembering of the wide Late Triassic-Sinemurian peri-continental platform and the isolation of the Trento Platform.

The Cretaceous dinosaur record on the ADCP was tested against the palaeoenvironmental and palaeogeographic reconstructions of the Tethyan region of Dercourt et al. (1993, 2000). The Periadriatic platforms are reported in

those maps as intraoceanic banks in between the large Afro Arabian continent to the south and the Laurasian/Eurasian lands to the north, separated from the first and from each other by deep sea basins, at least since Toarcian times (fig. 3). It has been observed that the dinosaur record during the Hauterivian-Barremian interval is not in agreement with those palaeogeographic reconstructions (e.g., Dalla Vecchia, 1997b; 2000b; 2001; 2002a; 2005). A connection of the ADCP with the Afro Arabian continent during the Hauterivian-Barremian was hypothesized on the base of the dinosaur skeleton remains from Bale/Valle (Istria) belonging to taxa with a Gondwanan affinity (*Histriasaurus*), as well as to the coeval sauropod associations in Europe and North America dominated by basal titanosauriformes (Dalla Vecchia, 1998a; 2002a; 2005). Large-sized sauropods and theropods occur in the sample. The Hauterivian-Barremian footprints record the dominant presence of large predators that most likely could not live on an isolated bank. A most probable connection with the Afro Arabian continent is suggested also by the distribution of some benthic foraminifers (Cherchi & Schroeder, 1973), and because a northern connection with European lands was prevented by the presence of the Ligurian-Piedmont ocean. It was supposed that the relatively deep epicontinental sea along the northern African margin reported in the Early Tithonian map by Thierry (2000) was not so deep, at last locally, and allowed a stable connection between the Afro Arabian continent and the Adriatic-Dinaric Platform through the Apulian Platform (Dalla Vecchia, 2000b; 2002a; 2005). After the discovery of similar, large, tridactyl footprints in the Hauterivian-Barremian of the Apulian Platform, this hypothesis was advanced also by the geologist Bosellini (2002), who proposed a basically similar palaeogeographic reconstruction supported by an analysis of the geology of the eastern Mediterranean.

Based mainly on footprint size in the Cretaceous sample from the ADCP, a change between the Hauterivian-Barremian and the post-Barremian record (late Albian to Maastrichtian) has been observed (Dalla Vecchia & Tarlao, 2000; Dalla Vecchia et al., 2001; Dalla Vecchia, 1998b, 2002a; 2003a, b; 2005; Mezga, Tunis et al., 2006). The large theropod footprints disappear, or become very rare, in the post-Barremian units (figs. 5-6). Albian and Cenomanian sauropod footprints are smaller than the Hauterivian-Barremian ones as well as those that the large sauropods represented by body remains would produce. They are also much smaller than those occurring in coeval continental settings (Dalla Vecchia & Tarlao, 2000; Dalla Vecchia, 2005; fig. 5). Late Campanian-Maastrichtian skeletal remains also belong to relatively small dinosaurs (Dalla Vecchia, 2001; Debeljak et al., 2002). The sample from the Late Hauterivian-Early Barremian and Santonian tracksites of the APUCP, as well as the Aptian and Cenomanian tracksites of the APCP, confirms this hypothesis. The change coincides with the Early Aptian opening of an oceanic basin between the Afro Arabian continent and the Periadriatic Platforms reported in the palaeoenvironmental-palaeogeographic maps of Masse et al. (1993;

2000). The basin would have separated the platforms from the continent, rendering the dinosaur faunas on them insular. The smaller body size of the dinosaurs would be a consequence of insularity (the “island rule”; Van Valen, 1973).

However, the opening of an oceanic basin between the Afro Arabian continent and the Periadriatic Platforms is not necessary to explain the small size of the post-Barremian Periadriatic dinosaurs. A trend toward the reduction in dinosaur body size is observed also in the western Europe lands between the Late Jurassic-Neocomian and the Campanian-Maastrichtian faunas. Compare the relative frequency of large sauropod and ornithopod fossils: large sauropods (>15 m long) are only sporadically found in the Campanian-Maastrichtian faunas and ornithopods the size of an adult *Iguanodon bernissartensis* are even rarer. A large theropod like the Barremian *Baryonyx* is not recorded in the Campanian-Maastrichtian of western Europe. Probably this is not a mere matter of sampling. The size trend could be related to the formation of an European Archipelago by the sensible increase of the global sea level after Early Albian times (Haq et al., 1987) and consequent reduction of the life space, that is one of the factors affecting the body size of some vertebrates (see Burness et al., 2001).

## THE “ISLAND RULE”, DWARFISM AND CONTINENTAL CONNECTIONS

According to the “island rule”, small animals reach larger size on islands while large animals dwarf. It is worth highlighting that it is the general trend toward a small body size with respect to the body size of systematically related individuals in continental settings that is significant. Furthermore, it is often a graded trend (McClain et al., 2006).

Insular dwarfism, as well as gigantism, is observed in Pleistocene (e.g., Sondaar, 1977; Azzaroli, 1982; Lomolino, 1985; 2005; Malatesta, 1986; Roth, 1992; Burness et al., 2001; Raia et al., 2003; Millien, 2006) and living insular faunas (e.g., Lomolino, 1985; 2005; Millien, 2006; Meiri et al., 2007), and does not affect only mammals, but also chelonians, squamates and birds (e.g., Case, 1978; Case & Schwaner, 1993; Clegg & Owens, 2002; Boback, 2003; Keogh et al., 2005; Wikelski, 2005; Lomolino, 2005). Even the evolution of body size in the deep sea gastropods is consistent with the “insular rule” (McClain et al., 2006). The “insular rule” has exceptions (Meiri et al., 2005; 2007) and the phenomenon of insular dwarfism is not linear and simple at all, and is strongly dependent on autoecological and sinecological (e.g., Boback, 2003; Raia et al., 2003; Wikelski, 2005; McClain et al., 2006) and phylogenetic (Meiri et al., 2005; 2007) constraints.

Dinosaur dwarfism has previously been reported from elsewhere in the Cretaceous European Archipelago, namely the Transylvanian Island (Weishampel et al. 1991, 1993; Jianu & Weishampel, 1999). However, the insular status of the region where dinosaur lived was later argued (Jianu & Boekschoten, 1999). Le Loeuff (2005) argued

that the small Transylvanian sauropods are not dwarfs because some bones indicate the presence of large individuals (10-15 m long) and suggest “taphonomical biases, possibly linked to the existence of age-classed communities among sauropod populations” (p. 15). However, this interpretation of localized evidence of small-sized individuals of a single dinosaur clade as juveniles instead of dwarfs does not mean that dinosaur dwarfism does not exist. In fact, Sander et al. (2006) have demonstrated on osteological and growth criteria the existence of sauropod dwarfism in an European Late Jurassic island. The hypothetical presence of age-classed communities might explain one or few cases related to single taxa, but its use to account for a general trend regarding different dinosaur clades, observed at several different stratigraphic levels in many localities that were on separate islands at the time, it is not parsimonious when we know a much more common and well-known phenomenon such as insular dwarfism. The presence of a few large individuals associated with several much smaller individuals of the same taxon might be evidence of age-classed communities only if it can be demonstrated that small and large individuals belong to a same species and the same population.

It must be considered that continental taxa reaching an island have the “original” size at the beginning, and only successively they can be selected for a smaller individual size. Fluctuating and short-lasting connections with the continent due to eustatic or tectonic reasons could allow repeated arrival on the island of normally-sized individuals of the locally dwarfed species, or of a large-sized, closely related species.

Theoretically, also a sufficiently long-lasting increase in productivity of the island (linked to a climate change or to the island area increase) or, in general, a change in ecological conditions, could produce an increase in individual size (e.g., Wikelski, 2005).

The dinosaur growth strategy could also account for the presence of larger individuals in an otherwise small-sized population. If non avian dinosaurs had indeterminate growth like living non-avian diapsids, unusually old individuals had unusually large body size, a well-known phenomenon in living crocodiles and snakes.

Finally, an unusually large final body size could be an individual trait due to genetic factors (Andrews, 1982: pp. 301-302, 304).

Thus, the occurrence of larger individuals in otherwise dwarf faunas is not definitely a solid proof against the existence of dwarfism. The trend is important, not the single episode that could have several different explanations that are difficult, if not impossible, to test.

Limiting the discussion to the emergent parts of the Periadriatic carbonate platforms, nobody argues that they were islands in the Tethys during Albian-Maastrichtian times (not even Bosellini, 2002: see p. 230). As for the isolation of the platforms it is unimportant whether the basin separating the two regions was on oceanic crust or stretched continental crust, as debated by geologists (Bosellini, 2002). It can be

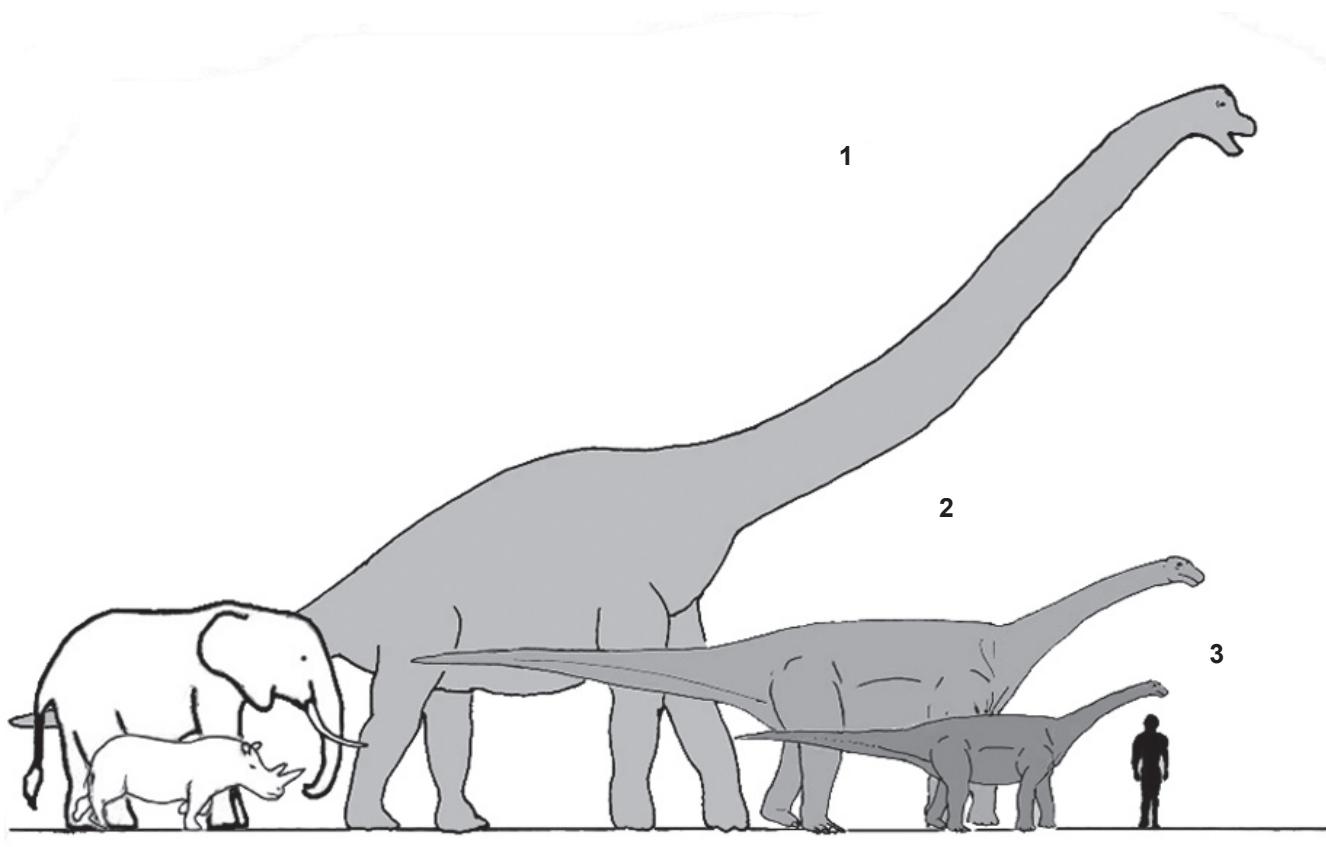
objected that the sample is not huge, but it cannot be denied that the size of dinosaurs present in the fossil record of that interval in those platforms is sensibly smaller than the size of those living at the same times in continental areas, in terms of maximum body size and frequency of large-sized individuals. The presence of a single, relatively larger sauropod in the Turonian-Lower Coniacian of Dalmatia does not change the trend; it is just an episode, not an evidence of a stable connection of ADCP with a continent during the whole Cretaceous as reported by Mezga, Meyer et al. (2006). The possibility of Late Cretaceous ephemeral and occasional connections of the ADCP with northern and eastern lands is supported by palaeontological, as well as geological, evidence (e.g., Dalla Vecchia, 2002a). Surely the uplifts related to the Eoalpine phase of the Alpine orogeny contributed to this, as well as the eustatic oscillations of the sea level.

Of course, the history of the dinosaur colonization of the carbonate platforms was much more complex than that preliminarily depicted by Dalla Vecchia (2002a; 2005).

Possibly, the change in the body size of dinosaur taxa populating the platforms was sensibly biased by the short-term eustatic oscillation of the sea level and the consequent change in the extent of the emergent part of those flat areas. The eustatic phenomenon interplayed also with tectonic phases that uplifted in different times the different platforms, as well as single parts of the platforms. This explains why evidence of emergence like bauxites, sedimentation hiatuses and the dinosaur remains themselves sometimes occur at different levels in the three Periadriatic carbonate platforms.

## DINOSAUR ICHNOLOGY AND PALEOBIOGEOGRAPHY

A palaeobiogeographic use of footprints is limited by the fact that the footprint morphology is highly influenced by the properties of the substrate, mainly in carbonate sedimentary settings (see Dalla Vecchia & Tarlao, 2000). Furthermore, the apomorphic features of the different dinosaur clades rarely occur in the feet and consequently foot morphology does not have a high systematic value (see Weishampel et al., 2004a). Late Triassic theropods, basal saurischians, some non-dinosaurian advanced archosaurs (e.g., *Silesaurus*), and possibly also bipedal basal ornithischians (e.g., *Pisanosaurus* and *Eocursor*) had, as far as it is known, feet that could produce similar footprints (e.g., Dalla Vecchia, 1998c; Dzik, 2003; Langer, 2004). Earliest sauropods, prosauropods and basal saurischians (e.g., *Herrerasaurus*, *Guaibasaurus*) have similar pedal morphologies (Langer, 2004; Galton & Upchurch, 2004). Oftentimes the systematics used by palaeoichnologists in their comparison between ichnotaxa and taxa is not updated based on current morphological phylogenetic analyses and is oversimplified. For example, the trackmaker of *Evazoum* is a prosauropod according Nicosia & Loi (2003) because the foot skeleton of *Sellosaurus* matches with the pedal print morphology (Nico-



**Figure 7** – Size of sauropods and large living mammals (elephant and rhino). 1) Large “continental” sauropod (the size is that of the African *Paralititan*, but the model is a brachiosaurid), 2) Campanian-Maastrichtian sauropod (*Ampelosaurus*) from the large Ibero-Armorican Island of the European Archipelago, 3) Cenomanian sauropod from Istria.

sia & Loi, 2003: p. 137 and fig. 10), but actually it matches also with the foot skeleton of basal saurischians such as *Herrerasaurus* and *Guaibasaurus* (see Langer, 2004: fig. 2.10), that are not considered for comparison.

The case of the Santonian *Apulosauripus* is an example of the problems that could arise with the palaeobiogeographic use of the ichnotaxa. *Apulosauripus* was referred to a hadrosaurid trackmaker (Nicosia et al., 2000b). Santonian hadrosaurids are found in Asia and North America, although they are represented only by rare, incomplete remains (Horner et al., 2004; Weishampel et al., 2004b); they later reached South America, Antarctica, and the European Archipelago and have never been found in Afro Arabia, India and Australia. The presence of a hadrosaurid trackmaker could be taken as evidence of a connection of the Apulian Platform with Asia or North America via the North European landmass as early as the beginning of the Santonian. As an alternative, those hadrosaurids could be taken as basal forms remained isolated on the APUCP during the “middle” Cretaceous.

Nicosia et al. (2000b) attributed *Apulosauripus* to hadrosaurids also because supposed skeletons of those dinosaurs were reported in the Upper Santonian of the ADCP

site of the Villaggio del Pescatore. However, those skeletal remains have actually a younger age, and their hadrosaurid status (sensu Prieto-Marquez et al., 2006 as well as sensu Horner et al., 2004) is not demonstrated yet. No hadrosaurid apomorphy occurs in the pes (Horner et al., 2004; Prieto-Marquez et al., 2006) thus preventing the distinction of a hadrosaurid from a more basal iguanodontian on the base of a footprint alone. Basal iguanodontians were present in the European Archipelago during the Santonian (*contra* Nicosia et al., 2000b). Although much more common in the European Archipelago during Campanian-Maastrichtian times (Weishampel et al., 2004b), Rhabdodontids where already present in Hungary during the Santonian (Ósi, 2005), associated with small ankylosaurians. Furthermore, hadrosaurid pedal unguals are heart or spade-shaped, whereas those of more basal iguanodontians usually are not, although “spade-shaped pedal unguals” is not considered an apomorphy of Hadrosauridae (Horner et al., 2004). The pedal unguals of the hadrosaurids should produce a characteristic arrow-point morphology in the digital print that is not observed in *Apulosauripus*. Thus, if not an ankylosaurian trackway as suggested by Gierlinski et al. (2005), *Apulosauripus* could just be that of a basal iguanodontian, without the palaeobiogeog-

graphic meaning of a hadrosaurid one.

Another example is that of Bosellini (2002: p. 217), who confused the footprints that he attributed to "Iguanodontian ornithopods" as indicative of the presence in the APUCP of the iguanodontoid *Iguanodon*, making erroneous palaeogeographic conclusions based on the palaeobiogeographic distribution of such genus. Also in this case, the attribution of the footprints can be argued as they could plausibly be theropodan because of relatively slender, long and pointed digital prints, absence of a wide "heel" print (metatarsal pad), and asymmetrical posterior development of prints of digits II and IV (pers. obs.).

Usually footprints can give only more general palaeobiogeographic information.

An exception are deinonychosaurians, which have an apomorphic hind foot that allows more clearcut identification of their footprints. To date this derived theropod clade is not represented in the footprint sample from the Periadriatic Carbonate Platforms. Only the fully tridactyl mesaxonic footprints of plesiomorphic theropod feet occur, with the exception of the much rarer and yet undescribed tetradactyl footprints in the Upper Jurassic (Nicosia et al., 2005).

The well-preserved, saurodalan manual prints in the Upper Albian of Istria (*Titanosaurimanus*) show that the track makers lacked the claw as well as the manual phalanges and were Titanosauriformes more derived than *Brachiosaurus*, possibly titanosaurs (Dalla Vecchia, 2005). Therefore, advanced titanosauriforms extended their geographic distribution to the ADCP during Albian times.

## PALAEOBIOLOGICAL IMPLICATIONS OF THE PERIADRIATIC DINOSAURS: A SUGGESTION FOR FUTURE RESEARCH

During Albian-Cenomanian times the ADCP was not comparable as surface to a continental land like Afro-Arabia or the Western North America, even if it were completely emergent and united to the APUCP. Albian-Cenomanian sauropods living in Istria were much smaller than coeval "continental sauropods". However, they were relatively large animals compared to top-herbivores of the Late Pleistocene-Holocene islands (Burness et al., 2001), in between the size of living African elephants and rhinos (fig. 7). Normally-sized elephants and rhinos never populated islands stably: they extinguished or dwarfed, probably because islands offer limited food resources and because of other ecological factors. This suggests that the Periadriatic sauropods did not have the same food requirements and, in general, the ecological needs of large, living herbivorous mammals (Dalla Vecchia, 2003b). The small Albian-Cenomanian theropods of Istria were as well larger than mammalian top-predators living on Late Pleistocene-Holocene islands (Burness et al., 2001). Furthermore, could the Periadriatic dinosaurs be inertial homeotherms, being smaller than their giant relatives living on continents? This is a stimulus for future research.

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