Available online at www.sciencedirect.com
SCIENCE DIRECT®

C. R. Palevol 2 (2003) 45–66

COMPTES RENDUS PALEVOL

Systematic Palaeontology / Paléontologie systématique
(Vertebrate Palaeontology / Paléontologie des Vertébrés)

Dinosaurs of Italy

Dinosaures d'Italie

Dinosauri d'Italia

Cristiano Dal Sasso

Sezione di Paleontologia dei Vertebrati, Museo Civico di Storia Naturale, Corso Venezia 55, 20121 Milano, Italy

Received 28 August 2002; accepted 21 October 2002

Written on invitation of the Editorial Board

Abstract

In recent years, the idea that Italy was lacking dinosaurs has been denied by a striking series of finds. Several Triassic and Jurassic dinosaur tracksites were discovered in the mid-eastern Alps, in particular within the Dolomia Principale Fm. (Norian) and the Calcari Grigi Fm. (Hettangian to Pliensbachian), while thousands of Cretaceous (Santonian) prints came to light in Puglia (southern Italy). Three skeletal remains are known so far; they all belong to new, possibly endemic species that evolved during Sinemurian (Saltrio theropod), Albian (*Scipionyx*) and Santionian (Trieste hadrosaurs) times. Both footprints and bony remains come from coastal deposits and indicate a peculiar palaeobiogeographic condition. The model of Bahamas-like small islands is no longer consistent with the presence of large dinosaurs, which could only survive in definitely terrestrial ecosystems. As documented by the wide temporal range of the dinosaur-bearing Italian outcrops, the Mesozoic carbonate platforms of the Middle-Eastern Tethys might have emerged several times, and quite extensively. ***To cite this article: C. Dal Sasso, C. R. Palevol 2 (2003) 46–66.***

Résumé

Ces dernières années, l'idée selon laquelle l'Italie manquait de dinosaures a été démentie par une série étonnante de découvertes. Plusieurs sites recelant des pistes ont été trouvés dans les Alpes centro-orientales, en particulier au sein de la formation Dolomia principale (Norien) et de la formation Calcari Grigi (Hettangien à Pliensbachien), cependant que des milliers d'empreintes crétacées (Santonien) étaient mises au jour dans les Pouilles (Sud de l'Italie). Trois restes de squelettes sont connus jusqu'à présent ; ils appartiennent tous à de nouvelles espèces, probablement endémiques et qui ont évolué durant le Sinémurien (théropode de Saltrio), l'Albien (*Scipionyx*) et le Santonien (hadrosaures de Trieste). Les empreintes de pas et les restes osseux proviennent de dépôts côtiers et indiquent un environnement paléobiogéographique particulier. Le modèle de petites îles de type

E-mail address: cdalsasso@yahoo.com (C. Dal Sasso).

DOI: 10.1016/S1631-0683(03)00007-1

Bahamas n'est plus compatible avec de grands dinosaures, qui n'ont pu survivre que dans un écosystème nettement terrestre. Comme le prouve le large étalement dans le temps des affleurements italiens comportant des dinosaures, les plates-formes carbonatées de la Téthys centro-orientale devraient avoir été émergées plusieurs fois et sur de grandes étendues. ***Pour citer cet article : C. Dal Sasso, C. R. Palevol 2 (2003) 46–66.***

Riassunto

L'idea che in Italia fosse impossibile trovare dinosauri è stata smentita da una incredibile serie di scoperte recenti. Numerosi siti con impronte dinosauriane di età triassica e giurassica sono stati individuati sulle Alpi centro-orientali, specie nella Dolomia Principale (Norico) e nei Calcari Grigi (Hettangiano-Pliensbachiano), mentre migliaia di orme riferibili al Cretacico (Santoniano) sono venute alla luce in Puglia. I tre resti scheletrici finora scoperti appartengono a nuove specie, probabilmente endemiche, evolutesi durante il Sinemuriano (teropode di Saltrio), l'Albiano (*Scipionyx*) e il Santoniano (adrosauri di Trieste). Tutte le impronte e i resti ossei provengono da depositi costieri e indicano una situazione palaeobiogeografica particolare: il modello di un arcipelago di piccole isole non è più compatibile con la presenza di grandi dinosauri, che potevano vivere solo in un ecosistema francamente terrestre. Come documenta l'ampia distribuzione temporale dei giacimenti italiani a dinosauri, nel Mesozoico le piattaforme carbonatiche della Tetide centro-orientale devono quindi essere emerse più volte, e piuttosto estesamente.

Keywords: dinosaurs; Italy; tracksites; bony remains; soft-tissue preservation; palaeobiogeography

Mots clés : dinosaures ; Italie ; empreintes de pas ; restes osseux ; conservation de tissu mou ; paléobiogéographie

Parole-chiave: dinosauri; Italia; orme; resti ossei; conservazione delle parti molli; palaeobiogeografia

Version abrégée

Introduction

On a toujours considéré que l'Italie ne possédait pas de restes de dinosaures, en raison de son histoire géologique mésozoïque, gouvernée par les mers (Téthys centro-orientale et ses petits bassins [37]) et les plates-formes carbonatées (domaine péri-Adriatique). Ainsi, le fossile décrit (Fig. 1) par Huene en 1941 [47], sous le nom de *Coelurosaurichnus* (synonyme jeune de *Grallator* [52]), était-il considéré comme une réelle exception. Cette petite empreinte de pas tridactyle, trouvée au mont Pisano (Toscane) est datée du Carnien et représente, non seulement le premier, mais aussi le plus ancien dinosaure italien (probablement un théropode coelophysoïde). Au cours des 17 dernières années, de nombreuses découvertes exceptionnelles ont révélé que les « terribles lézards » se promenaient et abandonnaient leurs os, même en Italie [19,51]. La séquence rapide des ces découvertes a été aussi anormale que la longue absence de preuves.

Empreintes de dinosaures triasiques et jurassiques dans le Nord de l'Italie

Des empreintes de dinosaures de la fin du Trias et du début du Jurassique ont été découvertes dans les Alpes orientales et dans plusieurs localités des Dolomites. La première découverte a été faite en 1985 sur un gros bloc appartenant à la formation Dolomia Principale (Carnien supérieur) et tombé du mont Pelmetto (province de Belluno, Vénétie). Cinq traces de pas laissées par de petits ornithopodes bipèdes, par des théropodes et par un plus grand dinosaure semi-bipède, probablement un prosauropode [56], étaient imprimées sur le bloc (Fig. 2). Deux ans plus tard, un second affleurement triasique fut trouvé près de Lerici (province de La Spezia, Ligurie), dans les Alpes maritimes : une centaine d'empreintes de pas de dinosaures et d'autres archosaures [76] furent identifiées au sein de dépôts deltaïques du Carnien-Norien (formation Montemarcello). Entre 1992 et 2000, des sites noriens ont été localisés dans la Dolomia Principale de Tre Cime di

Lavaredo, mont Averau (dans les Dolomites bellunaises, Vénétie) et à Cima Puez (province de Bolzano, Haut-Adige [51]). Le « Parco Naturale delle Dolomiti Friulane » (province de Pordenone, Frioul) est également digne d'être mentionné, car des empreintes de cératosaures (Fig. 3), de prosauropodes et d'archosaures variés y sont présentes [32].

Le site jurassique le plus riche, trouvé en 1988, est d'âge Hettangien et Sinémurien et est représenté par un vaste lot d'empreintes (plusieurs centaines), qui affleurent à Lavini di Marco, non loin de Rovereto (Trentin). On rencontre divers niveaux fossilifères au sein de la formation Calcari Grigi ; c'est pourquoi il est probable que les dinosaures aient fréquenté ces marécages tidaux pendant quelques millions d'années. Selon les plus récentes études [5,51], de grands ornithopodes graviporteurs et/ou des tyréophores de base, des théropodes (avec prédominance de cératosauriens de taille petite à moyenne), des sauropodes primitifs et de petits ornithopodes bipèdes se promenaient à Lavini de Marco (Figs. 4–7). D'autres pistes jurassiques, appartenant à différents horizons de la formation Calcari Grigi (Hettangien à Pliensbachien) ont été trouvées en Vénétie occidentale et dans le Trentin méridional depuis 1990 [19,51] : dans les monts Lessini (province de Vérone), le mont Pasubio, Becco di Filadonna, Chizzola et Marocche di Dro (Province de Trente). La prospection continue et fournit de nouvelles découvertes.

Les sites d'empreintes crétacées du Sud de l'Italie

Si l'on exclut les sites riches en fossiles localisés au-delà de la frontière orientale de l'Italie, dans la proche péninsule d'Istrie (Slovénie, Croatie) [23–25,27,28,30,33–36], les traces de dinosaures crétacés sont restées inconnues en Italie, jusqu'en 1994, quand fut découvert, sur la jetée de Ravenne, un bloc du calcaire hauterivien-barrémien (de la formation Calcare del Cellina), avec une empreinte de théropode et de sauropode [26,31] ; ce bloc provient d'une carrière des montagnes de Cansiglie (province de Pordenone, Frioul). Néanmoins, les découvertes les plus excitantes ont été faites ces dernières années dans les Pouilles, dans le Sud de l'Italie. Au printemps 1999, dans une carrière privée près d'Altamura (province de Bari), des géologues ont trouvé des milliers d'empreintes fossilisées sur des calcaires fins santoniens (Figs. 8–10). Il semble que seuls des dinosaures herbivores aient fréquenté ces marécages tidaux [60], à savoir des hadrosaures et, peut-être, des ankylosaures nodosauridés. Au contraire, des empreintes de théropodes ont été détectées dans un second site [42], daté du Crétacé inférieur (Hauterivien-Barrémien) dans le promontoire de Gargano (province de Foggia). En 2000, une douzaine d'empreintes de pas tridactyles a été trouvée sur la jetée de Mattimata (côte de Gargano). Selon des études préliminaires [14], les blocs proviennent d'affleurements proches de la fin du Jurassique (formation de Sannicado) et conservent une association dominée par les théropodes. Ce troisième niveau, riche en dinosaures, de la plate-forme d'Apulie, prouve qu'une partie du Sud de l'Italie a été habitée, pendant une longue période, par de grands dinosaures.

Scipionyx samniticus

Les premiers restes d'un dinosaure italien (comportant des tissus mous, jamais observés auparavant dans quelque spécimen que ce soit [20]), ont été mis au jour en 1993 [50]. En fait, la découverte exceptionnelle a été faite en 1980 [19], dans la craie en plaquettes crétacée de Pietraroia (un dépôt d'âge Albien) des montagnes du Matese (province de Benevento, Campanie, mais *Scipionyx samniticus* n'a été reconnu réellement, avec toute sa signification scientifique, que 30 ans plus tard, lorsque celui qui l'a découvert (un collectionneur de fossiles) a été contraint de remettre le fossile à la surintendance archéologique de Salerne, où il a été préparé [22] et nommé [20]. Les proportions du corps, la dentition et l'ossification incomplète du tout petit dinosaure indiquent que *Scipionyx* était à peine plus que sorti de l'œuf (Figs. 11–14), ce qui est tout à fait rare dans les archives de fossiles [10]. Quoique semblable en taille et en forme à *Sinosauropteryx*, *Scipionyx* n'est pas compsognathe. Chez le théropode italien coexistent, en une combinaison unique, des caractères qui, d'habitude, déterminent différents clades [41,46], mais ne permettent pas l'attribution à une quelconque famille de cœlurosauriens connue. Des données paléobiogéographiques [11, 81] corroborent l'hypothèse selon laquelle *Scipionyx samnitiens* a évolué sur des terres asséchées, isolées ou limitées, au Crétacé dans la Téthys centrale (plate-forme apennine). Le caractère le plus étonnant de *Scipionyx* est la conservation des organes internes (Fig. 16) [19,21].

L'intestin complet est fossilisé dans la région abdominale, en grande partie antérieure à la ceinture pelvienne, partiellement supportée par les gastralia ; des fibres musculaires peuvent être observées sous la queue, tandis que, dans la région pectorale, des restes de trachée et des griffes cornées sont aussi conservés. Un grand halo rougeâtre peut être interprété comme des restes de foie [20,72].

Les hadrosaures de Trieste et le théropode de Saltrio

Après *Scipionyx*, des restes de squelette de deux autres types de dinosaures ont été découverts en Italie. Ceux-ci sont encore en cours d'étude et n'ont pas reçu de nom scientifique. Les hadrosaures ont été déterrés dans les calcaires de la fin du Crétacé (Santonien-Campanien), près de Trieste (Frioul), à partir de 1994 [8]. Le spécimen surnommé « Antonio » est déposé au musée d'histoire naturelle de Trieste et semble représenter le plus ancien dinosaure ornithorynque jamais trouvé en Europe (Fig. 17). En dépit de sa taille relativement petite (4,5 m), Antonio peut être considéré comme un individu adulte, en raison de son haut degré d'ossification et de la fusion des éléments de son squelette. Le fossile appartient à un nouveau taxon, présentant des plumes primitives, avec des caractères plus avancés [9,28] ; sous certains aspects, il ressemble à *Telmatosaurus*, un hadrosaurien « nain » du Maastrichtien de Roumanie [79], mais il montre aussi des caractères uniques. Ceci suggère que les hadrosaures italiens sont les ancêtres des transylvaniens et que leurs parents ont pu marcher sur des zones sèches depuis la plate-forme Adriatique-Dinarique jusqu'à la région d'Hateg, via le bloc austro-alpin [28,30]. En dernier lieu, en 1996, des restes d'un théropode de 8 m de long ont été trouvés dans les terrains du début du Jurassique (Sinémurien) des collines alpines de Saltrio (province de Varèse, Lombardie). Le fossile, en cours d'étude au musée d'histoire naturelle de Milan [18,19], est crucial dans la connaissance de l'évolution des théropodes, en ce sens qu'il pourrait représenter le plus ancien et grand tétanurien dans les archives des fossiles [44,75]. En effet, dans le spécimen de Saltrio, quoiqu'il soit très fragmentaire, il y a une évidence d'une main tridactyle, tandis qu'une vraie turcula a été retrouvée (Figs. 18–21). Les cératosauriens, qui sont en général considérés comme les dinosaures prédateurs dominants dans les périodes fin Trias-début Jurassique, ont des mains à quatre doigts et une paire de clavicules non encore fusionnées [55,81]. Prétendre à l'existence d'une furcula cœlophysoïde [78] et à des caractères de type cératosauriens dans le théropode de Saltrio requiert une analyse plus approfondie en la matière. Le contenu paléontologique et la sédimentologie de la formation de Saltrio [53,75], de même que les évidences taphonomiques, indiquent que la carcasse du dinosaure a été fossilisée non loin du rivage, dans un bassin marin peu profond. Par conséquent, des terres émergées face au Bassin liguro-piémontais ont existé en Lombardie du Nord-Ouest, au commencement du Jurassique, mais il est impossible de savoir si elles étaient reliées ou non aux habitats contemporains de Rovereto-Lavini di Marco (plate-forme de Trente).

Conclusion

Tous les restes de squelette de dinosaures italiens appartiennent à de tout nouveaux genres, probablement endémiques. Avec les empreintes de pas, ces documents fossiles proviennent de dépôts marins côtiers, représentatifs d'une situation paléogéographique particulière. Contrairement à des études géologiques antérieures, ces découvertes contraignent à l'évidence que, durant des temps mésozoïques, le territoire italien actuel n'a pas été complètement submergé par la Téthys. Le modèle d'îlots dans une plate-forme carbonatée est, en outre, insuffisant pour expliquer la présence de grands animaux terrestres, étant donné que les dinosaures occupent le sommet d'une pyramide alimentaire complexe, définitivement terrestre. Il est plus probable que les plates-formes péri-Adriatiques ont fonctionné comme des ponts continentaux temporaires, qui reliaient Laurasia et Gondwana dans la Téthys médio-centrale, permettant des migrations entre les deux hémisphères. Ensuite, l'Europe mésozoïque méridionale aurait joué un rôle majeur dans la dispersion des dinosaures, en représentant un véritable carrefour ; ces conditions, telles qu'elles sont documentées par le large intervalle de temps qu'offrent les affleurements italiens à dinosaures, se sont reproduites plusieurs fois (Figs. 22 et 23). L'histoire des dinosaures italiens n'en est qu'à son commencement ; dans un futur proche, elle devrait s'étoffer très rapidement.

1. Introduction: the land of no dinosaurs?

To vertebrate palaeontologists, Italy has represented a curious exception for almost 200 years. While all over Europe and other continents, dinosaur bones emerged everywhere, the giant reptiles of the Mesozoic seemed to have deserted the Boot Country. According to geological studies, during the 'Age of Reptiles' the Italian peninsula was completely covered by the Tethys Ocean [37]. In fact, starting in the Middle Triassic, a large gulf from the Middle East began penetrating westwards into the present southern European countries and formed wide marine, epeiric domains. These shallow marine deposits allowed the preservation of a rich fossil fauna, including a variety of fishes and aquatic reptiles on which, since the 18th century, most of the vertebrate palaeontology in Italy has based its tradition. Through Jurassic and Cretaceous times, the Tethys opened more and more, dividing the northern lands of Eurasia from the southern supercontinent of Gondwana, and finally began to close again. Between these two landmasses, above the first stretching, then colliding carbonate platforms later gave rise to the Italian peninsula, that evidently some land occasionally emerged.

As large, definitely terrestrial animals, dinosaurs bear witness to the presence of land more dramatically than sedimentology [3,19]. In fact, the first evidence that the 'terrible lizards' walked on Italian soil was found only 60 years ago, much later than the pioneer geological studies by Ulisse Aldrovandi or Giovanni Arduino.

The first and most ancient trace of an Italian dinosaur came from Monte Pisano, Tuscany (Fig. 1). Represented by a tridactyl footprint dated back to the Carnian, about 230 Myr, it was described by the German palaeontologist Friedrich von Huene in 1941 [47] and named *Coelurosaurichnus* (now a junior synonym of *Grallator* [52]). The little track, 6-7 cm long, is housed at the 'Museo di Geologia e Paleontologia dell'Università di Firenze' (specimen IGF 5200) and belongs possibly to a small, primitive theropod that, assuming its early Late Triassic age, should be referred to the Coelophysoidea rather than to the Coelurosauria.

Except for this single footprint, all the known records of dinosaurs in Italy came to light in the last 17 years (detailed account in [19]). The rapid sequence of the recent discoveries has been as anomalous as the long absence of proofs.

Fig. 1. This single footprint from the Carnian of Monte Pisano (Tuscany), now housed in Florence (Museo di Geologia e Paleontologia, specimen IGF 5200), represents the first dinosaur trace in Italy and one of the most ancient in the world. Scale bar in cm.
Fig. 1. Empreinte unique du Carnien du mont Pisano (Toscane), actuellement déposée au musée de Géologie et de Paléontologie de Florence (specimen IGF 5200), représentant la première trace de dinosaure en Italie et l'une des plus anciennes au monde. Échelle en centimètres.

2. Dinosaur tracks in northern Italy

2.1. Early dinosaurs: the Triassic footprints

Nobody, while walking up on the steep cliffs and the snowy peaks that make the Alpine Arch a classic mountain scenery, thought of a dinosaur. Nobody until 1985, when Vittorino Cazzetta, amateur of prehistoric human and animal life, noted some non-random depressions lined up along a 60-m^2 surface of a large boulder (Fig. 2) fallen from the overhanging rocky wall of Monte Pelmetto, in the heart of the Dolomites (Belluno Province, Veneto). The boulder, later shown to Paolo Mietto (University of Padua), turned out to belong to the Dolomia Principale, a typical formation of Upper Carnian age derived from tidal deposits, and to bear five trackways left by small bipedal ornithopods (fabrosaurids and/or heterodontosaurids) and theropods (ceratosaurs), as well as by a larger semibipedal dinosaur, possibly a prosauropod [56].

This first record from the Alps once again aroused the attention of geologists and mountaineers, who began to find other ichnosites. Actually, the second Triassic outcrop was discovered in the Maritime Alps, not

Fig. 2. The boulder of Monte Pelmetto (Veneto): the track diagonally climbing the top is attributed to a small primitive ornithischian, the larger one (bottom to right) to a prosauropod.
Fig. 2. Bloc du mont Pelmetto (Vénétie) : la trace montant en diagonale vers le haut est attribuée à un petit Ornitischien primitif, la plus grande (en bas à droite) à un Prosauropode.

far from the shore of the Tyrrhenian Sea. In 1987, a 12-year-old student identified about 100 footprints of dinosaurs and other archosaurs, preserved in Middle Carnian-Norian deltaic deposits (Montemarcello Formation) at Lerici (La Spezia Province, Liguria). According to Sirigu and Nicosia [76], dinosaurs are represented by small coelophysoids, prosauropods and fabrosaurids (*Grallator, Pseudotetrasauropus* and the most ancient record of *Anomoepus*).

Between 1992 and 2000, several Norian sites were discovered in the Dolomia Principale Formation, mainly in the eastern Alps [51]. At the foot of the spectacular Tre Cime di Lavaredo (Bellunese Dolomites, Veneto), a couple of 30-cm-long *Eubrontes*-like footprints were recorded in 1992 by Paolo Mietto; recently the same author found a well preserved sauropod track in the Durrenstein Formation of Monte Averau, not far from Monte Pelmetto. A tridactyl pes print was noticed in 1994 nearby Cima Puez (Bolzano Province, Alto Adige) by Giuseppe Leonardi; isolated prints were finally recovered in the detrital slope surrounding the Monte Pelmetto boulder.

Worth mention, for its variety, is a new locality in Friuli (Pordenone Province), which is still under study [32]. In the 'Parco Naturale delle Dolomiti Friulane', on the surface of a dozen blocks, footprints left by medium and large sized ceratosaurs (up to 35 cm in length), prosauropods and archosaurs such as aetosaurs and rauisuchians are present (Fig. 3).

Fig. 3. Parco Naturale delle Dolomiti Friulane (Friuli). *Eubrontes*-like footprint, possibly left by a large ceratosaur, preserved on a block of Dolomia Principale near Casera Casavento. Coin for scale.
Fig. 3. Parco Naturale delle Dolomiti Friulane (Frioul). Empreinte de type *Eubrontes*, probablement laissée par un grand Cératosaure et préservée dans un bloc de « Dolomia Principale » près de Casera Casavento. Pièce de monnaie servant d'échelle.

2.2. Climbing the Alps: the Jurassic tracksites

Only three years after the first record from the Alps (Monte Pelmetto), evidence of the most spectacular dinosaur tracksite of northern Italy was found. Luciano Chemini, an amateur naturalist, one morning at the end of 1988 was walking around the steep slopes of Monte Zugna, near Rovereto (Trento Province, Trentino), where Early Jurassic limestones of Hettangian–Sinemurian age (about 200 Myr) had come to light after a giant medieval landslide. Chemini noticed some strange, rounded depressions along a ‘colatoio’ (ribbon-like rock surface cleared away by water flow). These holes were regularly spaced and surrounded by a rim, but many of them were still filled by earth and grass, so that only after a proper cleaning did they turn out to be dinosaur footprints (Fig. 4).

Studies of the Rovereto (Lavini di Marco) ichnosite began in 1992 [49] and are still going on [51]; they are revealing the extensive presence of hundreds of well-preserved prints of many bipedal and quadrupedal dinosaurs, including what seems to be the oldest sauropod record in Europe. The ancient environment in which the tracks were made is now known in detail and indicates a semiarid coastal habitat in the tropical western margins of the Tethys [2]. Because the footprints are in different levels within the Calcari Grigi Formation, it is likely that dinosaurs frequented these tidal flats for some million of years.

At Lavini di Marco, among the most intriguing tracks is the one labelled ROLM 9, because its author is still an enigma (Fig. 4). Based on the semi-bipedal gait and to the deep, suboval footprints, the trackmaker is supposed to be a large graviportal ornithopod, possibly an ancestor of the iguanodontids [51], but according to a second hypothesis it might be a basal thyreophoran similar to *Scelidosaurus*. The latter interpretation seems to be supported by very recent findings in a near and coeval locality [5].

Besides the enigmatic large Ornithischia, about 75% of the tracks are referred to Theropoda (Fig. 5) with a prevalence of small to medium sized Ceratosauria (*Grallator*, *Eubrontes*); about 15% belong to primitive, *Vulcanodon*-like Sauropoda (*Parabrontopodus*, Fig. 6) and about 5% to small bipedal Ornithopoda (*Anomoepus*). Maybe Prosauropoda are also present, but scanty. The sitting *Anomoepus* of Lavini di Marco are worth mention, because they represent the first record in the European Early Jurassic [4]. This ichnogenus is referred to a small ornithopod, possibly a sort of fabrosaurid that, sitting on its ankles, left a pair of long grooves behind the feet. Most of the fossils are actually underprints. The prevalence of theropods is apparent and is obviously due to their higher activity levels [38].

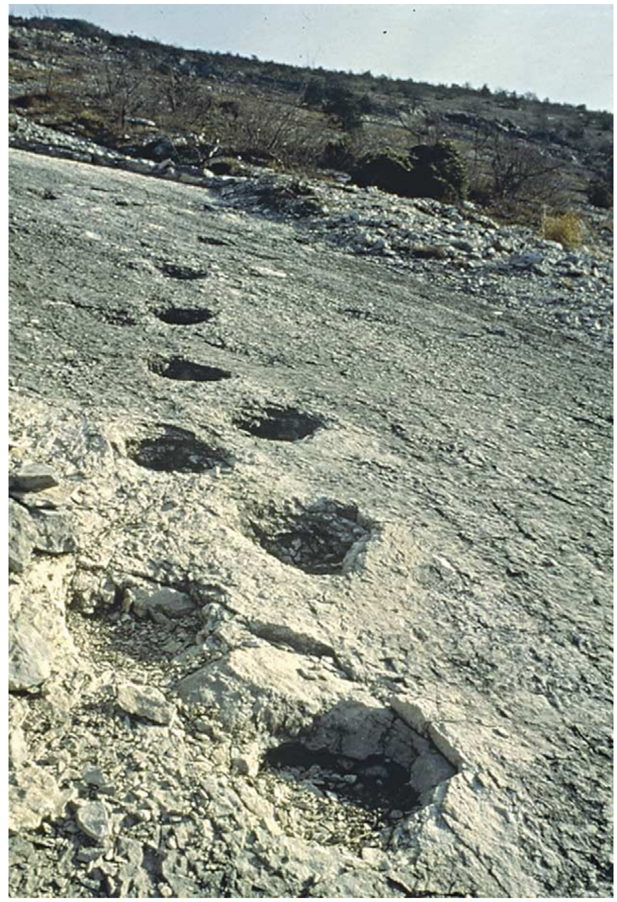

Fig. 4. The first dinosaur track discovered at Lavini di Marco (Trentino) in 1988 is now labelled ROLM 9 and is referred to a large graviportal, semibipedal ornithopod or basal thyreophoran.
Fig. 4. Première trace de dinosaure découverte à Lavini di Marco (Trentin) en 1988, actuellement labellisée ROLM 9 et se rapportant à un grand Ornithopode graviporteur, semi-bipède ou à un thyréophore de base.

According to Leonardi and Mietto [51], the dinosaur footprints of Rovereto reflect low walking speeds. The main problem concerning their biology, however, is related to the primary food sources (plants), which on such very wide tidal flats were apparently inadequate for animals as large as a 12-m-long sauropod

Fig. 5. Lavini di Marco (Trentino). A well-marked tridactyl footprint from a medium-sized theropod (?Ceratosauria).
Fig. 5. Lavini di Marco (Trentin). Empreinte tridactyle bien marquée, laissée par un théropode de taille moyenne (?Cératosaurien).

(Fig. 7). It has been suggested that the Lavini, rather than a feeding area, was a migratory corridor, but the question remains still unsolved [19,51].

Other tracksites - all dated back to the Early Jurassic but belonging to different horizons within the Calcari Grigi Formation - were discovered in western Veneto and Trentino since 1990 [19,51]. Guido Roghi [57,58] found a number of large theropod tracks (*Kayentapus*) and some possible sauropod footprints in five different Pliensbachian levels at Bella Lasta, in the Monti Lessini (Verona Province, Veneto). Marco Avanzini reported Sinemurian outcrops, again with theropod and sauropod footprints, at Monte Pasubio and Becco di Filadonna (Trento Province, Trentino) [1], and on the northern Lessini (Verona Province). Very recently

Fig. 6. Lavini di Marco (Trentino). ROLM 26, a track made by a primitive sauropod (*Parabrontopodus*), seems to climb the slope of Monte Zugna, nearby Rovereto (background).
Fig. 6. Lavini di Marco (Trentin). ROLM 6, une trace laissée par un sauropode primitif (*Parabrontopodus*) qui semble grimper la pente du mont Zugna, près de Rovereto (arrière-plan).

Matteo Campolongo found a Pliensbachian site in the massive landslide of Marocche di Dro (Sarca Valley, Trento Province), where Prosauropoda and basal Thyreophora also seem to be present [5]. Finally, Giuseppe Leonardi [51] discovered the site of Chizzola, 3 km from Lavini di Marco and of the same age, where a 33-cm-long ceratosaurian pes (*Eubrontes*) was reported in 1994, before it was destroyed by roadwork. Prospecting is still going on and providing new findings that cannot be included in this paper.

3. From Altamura to Mattinata: latest ichnosites in the Cretaceous of southern Italy

Despite the fact that in the near-Istrian Peninsula (Slovenia–Croatia) dinosaur footprints were common and well studied [23–25,27,28,30,33–36], Cretaceous tracks remained unknown from Italy until 1994, when prints of a theropod pes and a sauropod manus were discovered by chance on the pier of Ravenna [26,31]. The block of limestone is supposed to have come from a quarry located in the Cansiglio Mountains (Pordenone Province, Friuli) and dated to the Hauterivian-Barremian (Calcare del Cellina Formation). Nevertheless, the most exciting findings have been made in the last three years in Puglia, southern Italy.

In the spring of 1999, the geologists Massimo Sarti and Michele Claps (University of Ancona) were looking for oil deposits near the city of Altamura (Bari

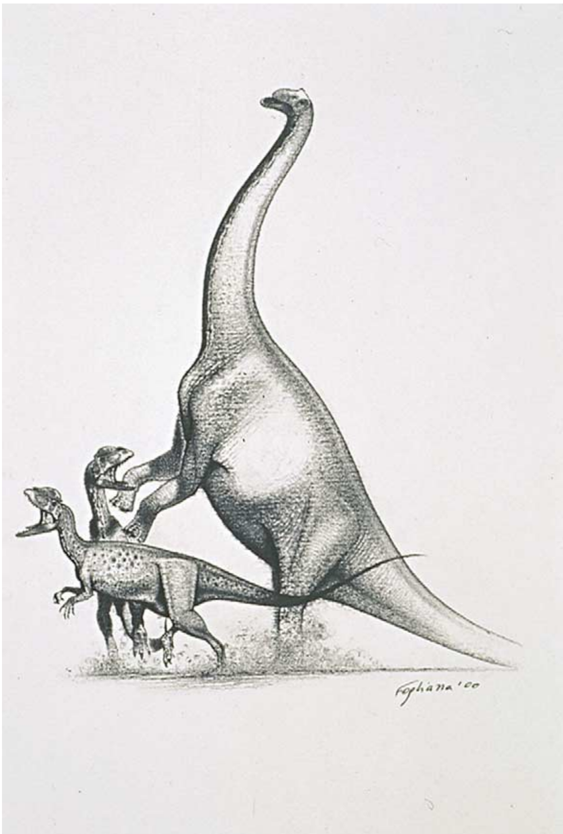

Fig. 7. Restoration of some possible trackmakers of the Early Jurassic prints at Lavini di Marco (Trentino): a couple of ceratosaurian theropods teasing a *Vulcanodon*-like sauropod (from [19]).
Fig. 7. Reconstitution de possibles auteurs des empreintes du Jurassique inférieur à Lavini di Marco (Trentin) : un couple de théropodes cératosauriens taquinant un sauropode de type *Vulcanodon* (d'après [19]).

Province), when they suddenly had a vision: in a private quarry, a layer of hard, fine-grained limestone containing thousands of rounded depressions had been unearthed. In the sunset light, each depression appeared so well marked and so precise in shape that it could not be anything else but a dinosaur footprint (Fig. 8). Surprisingly, the quarrymen had ignored the nature of those tracks for years and had left in place the fossiliferous layer by chance, probably because it was too hard to be removed and economically inconvenient [19]. The site of Altamura is now protected by Italian law as a palaeontological treasure and is under study by Umberto Nicosia (University of Rome); long considerable fieldwork must still be done because many footprints are filled-in by matrix. At present the ex-

Fig. 8. Altamura (Puglia). Partial view of the quarry 'De Lucia', where about 30 000 Cretaceous dinosaur prints were found in 1999.
Fig. 8. Altamura (Pouilles). Vue partielle de la carrière « De Lucia », dans laquelle furent trouvées, en 1999, environ 30 000 empreintes de dinosaures crétacés.

posed rock surface in the 'De Lucia' quarry covers an area of about 12 000 m^2 and the prints are estimated to be around 30 000 in number, a very high density [60]. On closer inspection, many marks apparently scattered in irregular directions and intersecting each other show their actual arrangement in trackways; the longest one is composed of 176 footprints and is referred to a small-sized hadrosaur that walked on four legs (Fig. 9). According to preliminary studies [60], only herbivorous dinosaurs frequented this place in Santonian times. Hadrosaurs (mainly in quadrupedal gait) are the most common; quite interesting are some four-fingered, blunt-toed, well-spaced footprints (Fig. 10), because they might belong to medium-sized, advanced Thyreophora, namely Ankylosauria (a taxon that is rare in the ichnological record). The fact that nodosaurid ankylosaurs lived in the Cretaceous of Europe is documented by bony remains of *Polacanthus*, unearthed in the present United Kingdom [69,71], and of *Struthiosaurus*, found in Spain, France, Austria, Romania and Hungary [69,70].

Like the Lavini di Marco, the Altamura limestones are shallow marine deposits. Sedimentological analysis, the presence of thin laminae, and the lack of expulsion borders suggest that the footprints were impressed on a soft substrate, most probably covered by microbial mats, in a supratidal environment. Nevertheless, the presence of so many large, herbivorous, definitely terrestrial animals is compelling evidence that on the Apulia Platform, in the central Tethys, wide land areas

Fig. 9. Altamura (Puglia). Close-up of the longest track, composed of 176 prints. The trackmaker is supposed to be a hadrosaur in quadrupedal gait.
Fig. 9. Altamura (Pouilles). Gros plan de la plus longue piste, composée de 176 empreintes. L'auteur des traces est supposé être un hadrosaure à démarche quadrupède.

Fig. 10. A nodosaurid ankylosaur similar to *Struthiosaurus* (above) is the possible author of this wide-fingered footprint currently under study at Altamura (Puglia). Pen for scale.
Fig. 10. Ankylosaure nodosaurien analogue à *Struthiosaurus* (au-dessus), auteur possible de l'empreinte de pas à larges doigts, en cours d'étude à Altamura (Pouilles). Stylo servant d'échelle.

and not only small islands emerged during the Late Cretaceous. Actually, it was not only at that time. In 2000, geologists from the University of Ferrara [42] reported tens of prints in the Gargano Promontory, near the village of San Giovanni Rotondo (Foggia Province). The footmarks, ranging from 15 to 40 cm each, belong to medium-sized and large theropods that lived in the Early Cretaceous, about 120 Myr (Hauterivian-Barremian). Finally, in the fall of the same year, a dozen footprints were found on three blocks of limestone in the pier of Mattinata, along the Gargano coast. According to current studies [14], the blocks might have been quarried from the Late Jurassic Sannicandro Limestone Formation, which outcrops only in the Gargano area. The ichnocoenosis includes elongate, tetradactyl footprints of an unusual theropod (Theroplantigrada sp.), medium-sized theropod footprints (?*Therangospodus* sp.), isolated footprints (*Megalosauripus* sp.) and a few marks of difficult attribution, due either to bad impression or to too generalised shape. This theropod-dominated association represents a third dinosaur-rich level in the Apulian Platform; together with the findings mentioned above, it reveals a succession of chronoichnofaunas and demonstrates that part of the southern Italy was inhabited by large dinosaurs for quite a long time.

4. *Scipionyx*: first skeleton, and not only bones

The first body remains of an Italian dinosaur abruptly came to the limelight in 1993 [50]. Actually they were something more than the usual fossil remains that palaeontologists are familiar with: *Scipionyx samniticus* is a striking specimen, preserving soft tissues never seen before in any dinosaur [20].

The exceptional find occurred at Pietraroia, a small village nestled in the Matese mountains, about 80 km northeast of Naples (Benevento Province, Campania). The story of *Scipionyx*'s discovery is original in itself

[19]; in fact the specimen, found in 1980 by the fossil collector Giovanni Todesco and then almost forgotten in the basement of his house, was recognised for its scientific importance only thirteen years later, when the finder asked palaeontologists from the 'Museo di Storia Naturale di Milano' to examine the unknown fossil. According to Italian law, Todesco was forced to give the specimen to the 'Soprintendenza Archeologica di Salerno', where it was subsequently prepared [19,22] and better examined [20,21]. It is still housed there and awaiting detailed study.

The Pietraroia Plattenkalk, known since the 18th century for its beautiful fossil fishes, is a Lower-Cretaceous formation of Albian age, dated to about 110 Myr. Fine marly limestones were deposited in a shallow lagoon environment during cyclic anoxic periods; those very peculiar environmental conditions allowed fossilisation of soft tissues in association with animal bony remains, making the Pietraroia outcrop a Konservat-Lagerstätte [7]. It is likely that the terrestrial fauna associated with fishes and marine invertebrates was carried into the sea by rivers or during violent storms, but it is difficult to know whether the dinosaur was drowned or died because of other reasons.

The skeleton of *Scipionyx*, preserved in almost perfect anatomical articulation except for its hindlimbs and tail (both distally missing), is 237 mm long (Fig. 11). The incomplete ossification of the vertebral column (neural arches unfused to their centra [17]), the body proportions (skull/presacral ratio higher than in any adult theropod [13,59,64]), the short and deep antorbital region, the rounded and oversized orbital foramina, the symmetrical development of tooth series in both maxillary rami (consistent with first tooth replacement being not yet occurred), and the low denticle count [62] indicate that *Scipionyx* is little more than a hatchling (a rarity in the fossil record [10]) (Fig.12).

Although similar in shape and size to *Sinosauropteryx* [48], *Scipionyx* is more puzzling than a compsognathid (Fig. 13). The Italian baby theropod shows a true mosaic of characters that does not allow attribution to any known coelurosaurian family [19,21]. Most elements of the skull recall the Dromaeosauridae [16,64,77]: the maxilla is excluded from the posterior margin of the external naris by thin premaxillary-nasal contact, the splenial emerges externally on the lateral surface of the mandible, and the tooth count and shape

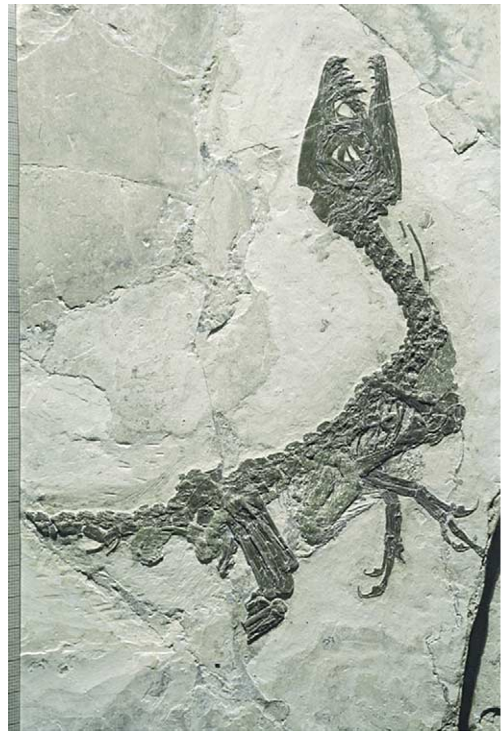

Fig. 11. *Scipionyx samniticus,* found in the Albian Lagerstätte of Pietraroia (Campania), is now at the Soprintendenza Archeologica, Salerno. The preservation of internal organs associated to its perfectly articulated skeleton (only 23 cm long) cannot be seen in any other dinosaur.

Fig. 11. *Scipionyx samniticus*, trouvé dans le gisement albien de Pietraroia (Campanie), actuellement à la superintendance archéologique de Salerme. La conservation des organes internes associés au squelette, parfaitement articulé (seulement 23 cm de long), n'a pas été observée chez un autre dinosaure.

are typically dromaeosaurid. Other characters (e.g., L-shaped quadratojugal with equal rami) are synapomorphic with the Troodontidae [15,73,74]. Plesiomorphic characters include the stout, L-shaped lachrymal and the large prefrontal, whereas the elongate dentary, which does not end posteriorly at the maxillary level but continues under the orbital midline, represents a unique feature (Fig. 14). The powerful forelimbs are elongate and raptorial, and have dromaeosaurian ratios and shapes [61,64–66] except for a slighter curvature in the manual claws and a shorter first digit. On the other hand, the girdles retain many primitive traits, recalling in particular the Ornithomimidae [6], the Compsognathidae [46,67] and in general primitive Coelurosauria [41,45,46,63]: pronounced scapular acromion, fan-like coracoid with rounded caudal end, pos-

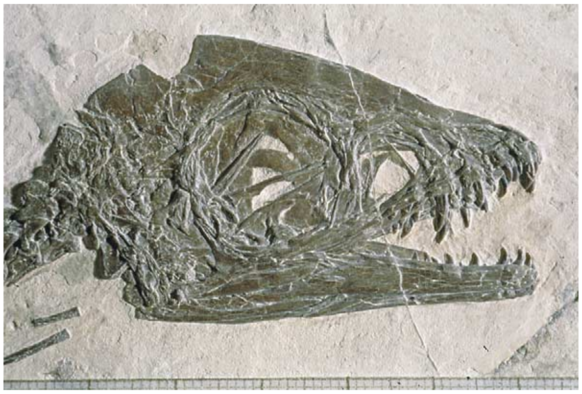

Fig. 12. Close-up of the skull of *Scipionyx*. The short antorbital region, the large and rounded orbital foramen and the symmetrical tooth development on both maxillae are juvenile features. Scale bar = 1 cm.

Fig. 12. Gros plan du crâne de *Scipionyx*. La région ante-orbitale étroite, le foramen orbital grand et arrondi et le développement symétrique des dents sur les deux maxillaires sont des traits juvéniles. Barre d'échelle = 1cm.

teriorly facing glenoid, orthopubic pelvis, ilium anteriorly hooked and posteriorly truncated, and an ischium three-quarters of pubic length, with a forward-pointing foot (Fig. 11).

Therefore, in the Pietraroia dinosaur, there co-exists a unique combination of primitive and derived characters that usually mark different clades [41,46]. Because the fossil comes from an outcrop of Albian age, a time when the known families of Maniraptoriformes were already differentiated, this mixture suggests that *Scipionyx samniticus* could represent a relict clade of basal maniraptoriform coelurosaurs that perhaps has retained many primitive features as a consequence of taking an independent evolutionary path [19].

Fig. 13. Hypothetical restoration of *Scipionyx samniticus* (lifesize model by F. Fogliazza).

Fig. 13. Hypothétique reconstitution de *Scipionyx samniticus* (modèle grandeur nature par F. Fogliazza).

Paleobiogeographical data [11,81] support the hypothesis that the southern Italian theropod evolved on isolated, emergent lands in the Cretaceous Central Tethys Sea (the Apennine Carbonate Platform, roughly corresponding to the present Campania and Basilicata regions, during Early-Cretaceous times was separated from the larger, eastward Apulia Platform by a deep and narrow basin). Isolation within the peri-Adriatic Domain, in the form of a small island no larger than the present Corsica, could have led to biological consequences such as the evolution of endemic species [19] (Fig. 15).

The most striking feature of *Scipionyx* is the preservation of soft tissues [19,21] (Fig. 16), above all, the intestine. Its surface bears transverse, anastomized folds that reveal a surprising fossilization of the mucosa as an endocast. Most of the gut (tenuis [43]) is positioned more forward than generally thought [68]; the posterior colon [43] passes through the pelvic canal close and parallel to the vertebral column and ends, with the cloacal tract, just above the ischiadic foot. Interestingly, the gastralia show that they constituted effective support for the intestine, while the pubic bones had no role in this function [68]. The digestive tube is surprisingly short and deep in section, suggesting a high absorption rate.

At the base of the tail, in the form of some fibres that converge forward in a striped bundle, part of the *M. caudifemoralis longus* [40] is preserved; large isolated tendons are present more posteriorly (Fig. 11). Muscle fibres are fossilised in the pectoral region as well, with scattered acicular cells clearly visible under 50 × magnification. In the centre of the same area, right above the furcula, some cartilaginous, hyaline tracheal rings are clearly preserved. The incomplete fossilization of the rings might indicate that, as in many amniotes, the rings were open dorsally, and were completed by elastic connective tissue.

A large, reddish halo was tentatively interpreted as liver remnants because of its post-sternal position

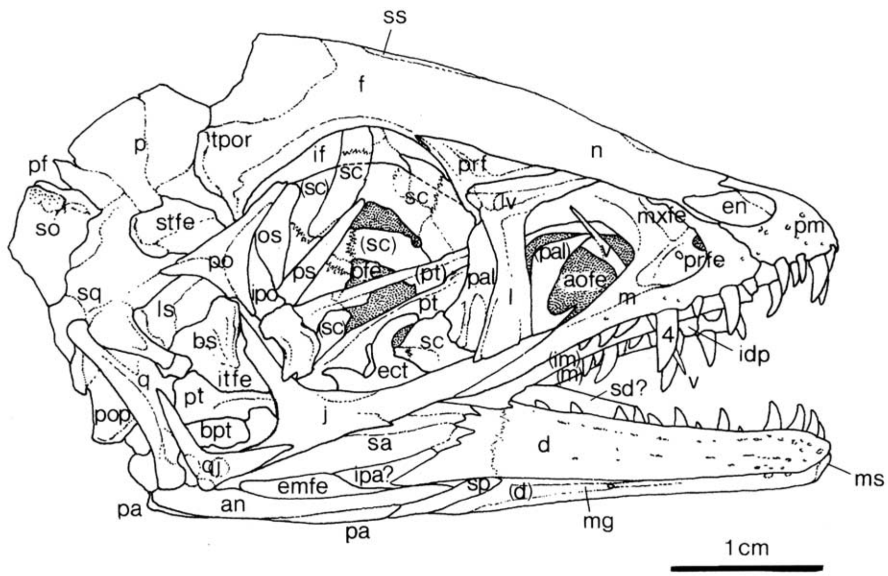

Fig. 14. Sketch of the skull of *Scipionyx*. Abbreviations: an, angular; aofe, antorbital fenestra; bpt, basipterygoid; bs, basisphenoid; ect, ectopterygoid; emfe, external mandibular fenestra; en, external naris; f, frontal; idp, interdental plates; if, inner (orbital) wall of frontal; im, inner (lingual) wall of maxillary; ipa, inner prearticular; ipo, inner (orbital) wall of postorbital; itfe, infratemporal fenestra; j, jugal; l, lachrymal; ls, laterosphenoid; lv, lachrymal vacuity; m, maxillary; mg, meckelian groove; ms, mandibular symphysis; mxf, maxillary foramen; n, nasal; ofe, orbital fenestra; os, orbitosphenoid; p, parietal; pa, prearticular; pal, palatine; pf, parietal flange; pm, premaxillary; pno, pneumatic opening; po, postorbital; pop, paroccipital process; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sc, sclerotic plates; sd, supradentary; so, supraoccipital; sp, splenial; sq, squamosal; ss, sagittal suture; stfe, supratemporal fenestra; tpor, transverse postorbital ridge; v, vomer; 4, fourth maxillary tooth. Left side elements are among brackets. Scale bar = 1 cm. (From [21]).

Fig. 14. Schéma du crâne de Scipionyx. Abréviations : an, angulaire ; aofe, fenêtre ante- orbitale ; bpt, basiptérygoïde ; bs, basisphénoïde ; ect, ectoptérygoïde ; emfe, fenêtre mandibulaire externe ; en, naris externe ; f, frontal ; idp, plaques interdentaires ; if, paroi (orbitale) interne du frontal ; im, paroi interne (linguale) du maxillaire ; ipa, préarticulaire interne ; ipo, paroi interne (orbitale) du post-orbital ; itfe, fenêtre infratemporale ; j, jugal ; l, lacrymal ; ls, latérosphénoïde ; lv, vide lacrymal ; m, maxillaire, mg, bouquet meckélien ; ms, symphise mandibulaire ; mxf, foramen maxillaire ; n, nasal ; ofe, fenêtre orbitale ; os, orbitosphénoïde ; p, pariétal ; pa, préarticulaire ; pal, palatin, pf, bourrelet pariétal ; pm, prémaxillaire ; pno, ouverture pneumatique ; po, postorbital ; pop, processus paroccipital ; prf, préfontal ; ps, parasphénoïde ; pt, ptérygoïde ; q, carré ; qj, quadratojugal ; sa, surangulaire ; sc, plaques sclérotiques ; sd, supra-dentaire ; so, supra-occipital ; sp, splénial ; sq, squamosal ; ss, suture sagittale ; stfe, fenêtre supra-temporale ; tpor, crête post- orbitale transverse ; v, vomer ; 4, quatrième dent du maxillaire ; les éléments du côté gauche sont entre parenthèses. Barre d'échelle = 1cm (d'après [21]).

(Fig. 16) and its haematitic composition [20]. Observations under ultraviolet illumination not only confirmed the former hypothesis, but also revealed an even deeper organ [72]. Finally, of note is the preservation of the horny claws that still cover the manual ungual phalanges of *Scipionyx*: they are composed of gray-blackish keratin on the dorsal horny talons, toward the tips, and yellowish keratin on the palmar talons [19].

Once allowed, samples of those tissues analysed by electron microscopy and biochemical techniques should provide data otherwise never obtainable. On the other hand, the chance to find a second specimen is remote but not impossible and this is one of the purposes of the new systematic excavations that began in 2001 in the Pietraroia Lagerstätte, under the aegis of the local Superintendency, through the 'Museo di Storia Naturale di Milano' [18].

5. Still unnamed: hadrosaurs from Friuli and a second large theropod from Lombardy

5.1. The hadrosaurs of Villaggio del Pescatore

Scipionyx was not alone. Some 20 Myr later, in the present Friuli Region (northeastern Italy), herds of herbivorous dinosaurs were grazing along the Tethys coasts. Near Trieste, laminated carbonates of Santonian-Campanian age revealed well-preserved remains of Hadrosauridae starting in 1994 [8]. After the

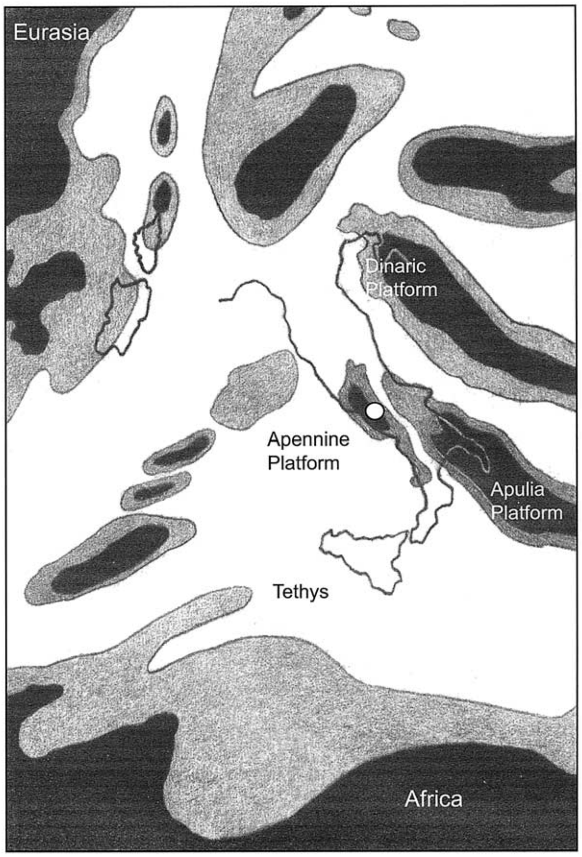

Fig. 15. 110 Ma, most of the present Italian peninsula was submerged by the Tethys (white) and was fragmented in various carbonate platforms (grey), which were partially emersed (black). *Scipionyx* lived on a portion of the Apennine Platform (circle). (From [19], modified).
Fig. 15. Il y a 110 Ma, la plus grande partie de l'actuelle péninsule italienne était submergée par la Téthys (en blanc) et était fragmentée en plates-formes carbonatées (en gris), partiellement émergées (en noir). *Scipionyx* vivait sur une portion de la plate-forme Apennine (cercle). (D'après [19], modifié).

unexpected discovery of some bones emerging on the surface of vertically positioned strata, the abandoned quarry of Villaggio del Pescatore was reopened by the Italian Ministry of Culture and a long and hard excavation was done by Stoneage (a private corporation officially allowed to dig). In 1999, a complete, 4.5-m-long specimen was finally recovered within some large blocks, together with at least three partial individuals and with crocodilian and pterosaur remains as well.

Reassembled and acid-prepared, the hadrosaur specimen (nicknamed 'Antonio', State Collection

Fig. 16. Close-up of the abdomen of *Scipionyx*, showing the striking fossilisation of the intestine (centre) and a reddish macula that might represent the remains of the liver (right). Graph paper for scale.
Fig. 16. Gros plan sur l'abdomen de *Scipionyx*, montrant la remarquable fossilisation de l'intestin (au centre) et une tâche rougeâtre qui pourrait représenter les restes du foie (à droite). Papier quadrillé comme échelle.

Number 57021) is housed at the 'Museo Civico di Storia Naturale di Trieste' and is still under study [9]. It seems to represent the most complete and most ancient hadrosaur ever found in Europe, and is at least 10 Myr older than the North American forms. Despite its relatively small size, the specimen can be considered an adult individual by its high degree of ossification and fusion of skeletal elements (Fig. 17). This animal lacks any narial or fronto-parietal crest, so there are no doubts about its relationships with the subfamily Hadrosaurinae.

According to Dalla Vecchia [28], who made some preliminary observations at the time of his scientific direction of the quarry, the fossil belongs to a new taxon, presenting primitive features together with more advanced characters. Among plesiomorphic traits, later confirmed by Buffetaut, Delfino and Pinna [9], are the relatively narrow premaxilla, the presence of strong denticles on the premaxilla and predentary, the low number of maxillary tooth emplacements, and the very broad condyle of the quadrate. Specialised and possibly autapomorphic characters are the very long jugal bone and the very large infratemporal fenestra, the complete loss of digit 5 in the manus, the very long ischium, the femur shorter than the tibia, the unusual phalangeal shape and formula in the pes, the backwardly positioned first chevron, the distally booted

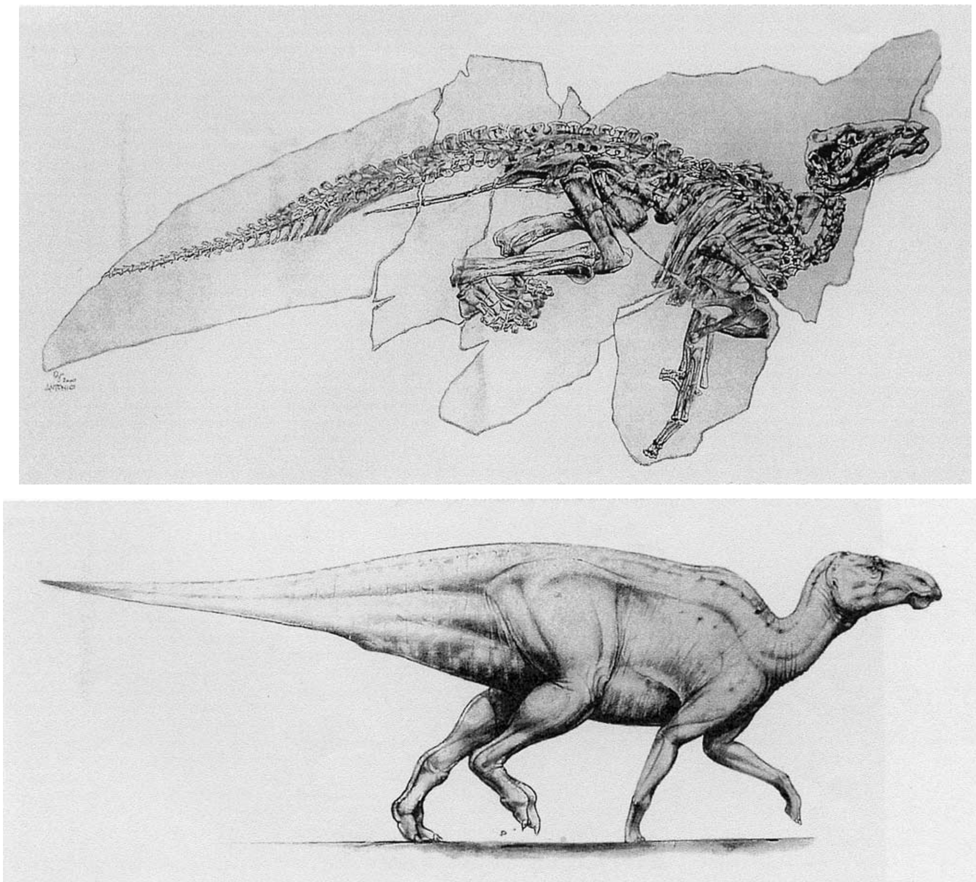

Fig. 17. The hadrosaur 'Antonio' (specimen 57021, Museo di Storia Naturale di Trieste), from Villaggio del Pescatore (Friuli): sketch of the skeleton after chemical preparation (above) and a restoration of its possible life appearance (below).
Fig. 17. L'hadrosaure « Antonio » (spécimen 57021, Musée d'histoire naturelle de Trieste), provenant de Villaggio del Pescatore (Frioul) : schéma du squelette, après préparation chimique (en haut), et reconstitution de son apparence possible de son vivant (en bas).

chevrons and the distal caudal vertebrae that are strongly flattened dorsoventrally.

In some respects, the Italian hadrosaur resembles *Telmatosaurus*, a primitive 'dwarf' hadrosaurine from the Maastrichtian of Romania [79]. But it bears peculiar characters, such as dentary teeth not sensibly larger than the maxillary teeth, a scapula dorsally very broad, and a strong angular deltopectoral crest in the humerus. Clearer affinities with the Romanian hadrosaurs might eventually emerge when more complete material will come to light in Transylvania, as the structure of the pelvis, limbs and chevrons of *Telmatosaurus* are still poorly known.

The palaeogeographical implications of the hadrosaurs from Villaggio del Pescatore, taken together with recent crocodile and dinosaur findings in Slovenia, are of primary importance. It has been demonstrated that duck-billed dinosaurs were gregarious animals that needed to feed and migrate through wide territories; therefore their occurrence in the Adriatic-Dinaric Carbonate Platform is a dramatic evidence that even part of the northern Italy was not under the sea level in the Late Cretaceous. Moreover, their affinities with the Transylvanian hadrosaurs suggest that from Santonian to Maastrichtian times the possible ancestors of *Telmatosaurus* could have walked on dry land to the Hateg region via the Austroalpine block [28,30].

5.2. The Saltrio theropod

Beyond the tiny *Scipionyx* from Pietraroia and the hadrosaurs from Villaggio del Pescatore, a third kind of

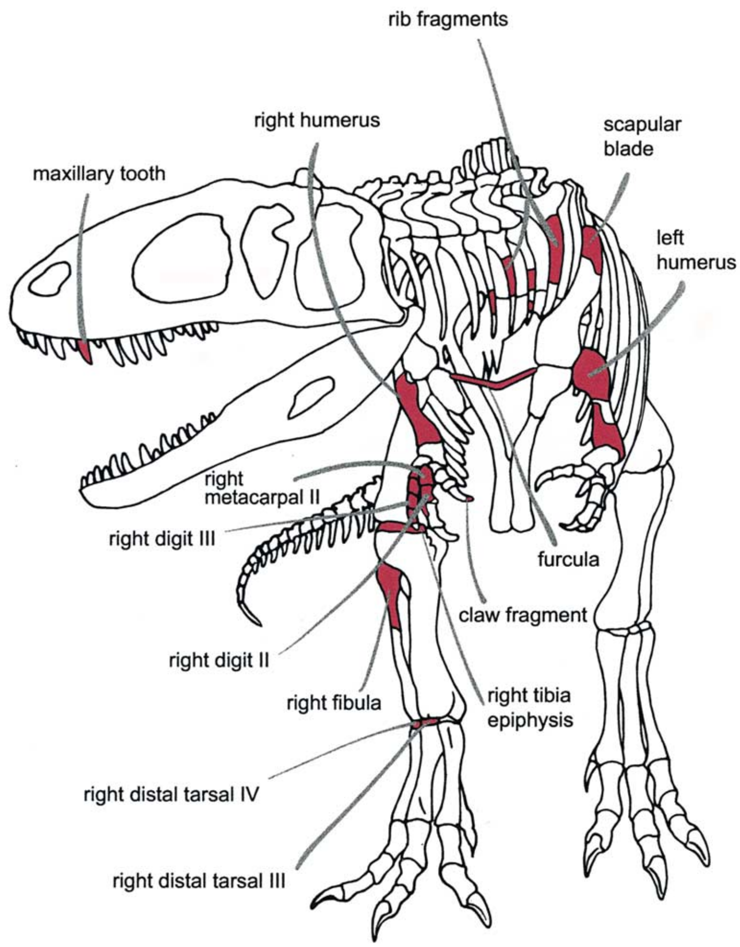

Fig. 18. The theropod from Saltrio (Lombardy): less than 10% of the skeleton was recovered (red). Nevertheless, 21 limb bones are allowing a reliable diagnosis. (From [19], modified).

Fig. 18. Le théropode de Saltrio (Lombardie) : moins de 10 % du squelette a été récupéré (en rouge). Néanmoins, 21 os du flanc permettent une diagnose fiable (selon [19], modifié).

dinosaur is known from skeletal remains from Italy. As in the above-mentioned localities, the discovery of this last and more recent specimen was accidental [19].

In the summer of 1996, a huge quarry located in the Alpine foothills, at the Swiss-Italian border near Saltrio, less than 80 km north of Milan (Varese Province, Lombardy), gave up some bones of a large reptile. The Saltrio quarry is well known since the 15th century as one of the finest sites of marble production (the 'Saltrio Stone' provided high-quality matter during building of famous Italian monuments, such as the Scala Theatre). But in these massive, whitish Early Jurassic marine limestones, Angelo Zanella (a fossil amateur and collaborator of the 'Museo di Storia Naturale di Milano') was used to look for ammonites and other small fossil invertebrates. One day Zanella collected some blocks that included large bones; he reported them to the Museum, which arranged a rapid expedition and recovered more remains. The research was difficult because the dynamite used for industrial quarrying had blown up the fossil-bearing layer and had broken it into hundreds of pieces.

In 1999, after 1800 hours of chemical preparation in the laboratory of the Museum of Milan, 119 remains were recovered. Although fragmentary, rib remains and 21 limb bones were revealed to be part of a large theropod dinosaur (Fig. 18). The Saltrio specimen (MSNM V3664) became popular by the name 'Saltriosaur' but it is still under study [18]. Actually, even though it may be sometimes latinized [29], any pseudo-scientific name given to a specimen cannot be valid, because it lacks a proper diagnosis (which is also beyond the aim of the present contribution).

According to preliminary morphometric comparisons with an *Allosaurus* skeleton mounted in the Museum of Natural Sciences of Bergamo, the Saltrio theropod would have reached 8 m in length and 1.5 t in weight. Considering the age of the Saltrio Formation, which is dated to the Sinemurian (about 200 Myr [75]), this specimen represents the most ancient large predatory dinosaur known from skeletal remains.

It is generally thought that in the Sinemurian the ruling theropod dinosaurs were the primitive Ceratosauria. The bones from Saltrio show anatomical features typical of more evolved theropods (Tetanurae) because there is evidence of a three-fingered manus and an exquisite furcula has been luckily recovered.

Although the best-preserved elements belong to the right forelimb, the specimen is really fragmentary and the manus is far from complete (Fig. 19). Nevertheless, one can deduce the phalangeal formula by observing, in the third digit, the proximal articular facet of the first phalanx. That articulation consists of a single fossa, rather than two fossae separated by a median ridge. In the four-fingered ceratosaurs [55,80] the same bone seems to bear two fossae, in order to articulate with a pair of condyles of the third metacarpal, which is very similar to the second one; in the Tetanurae [54], due to loss of the fourth digit and to reduction of the third digit, the third metacarpal has only one condyle.

Another character that recalls the Tetanurae is the low degree of supination of the manual phalanges, which is comparable to that of *Allosaurus*. In the Ceratosauria and in more primitive forms, the supination capabilities are much higher and clearly plesiomorphic, possibly reminiscent of the quadrupedal gait of the theropod ancestors [39].

A third tetanurine character [46] of the Saltrio theropod is the presence of a true furcula (Fig. 20). This rarely preserved bone of the pectoral girdle seems to be absent in the Ceratosauria, where the two rami are separate and constitute the clavicles, whereas in the Tetanurae they become fused into a typical, boomerang-shaped element. The bone from Saltrio is without doubt a furcula and cannot be misinterpreted as gastral basket element because the two rami are stout, lack any longitudinal groove and terminate with flattened scars for the coracoid articulations; furthermore, they are medioventrally united in a clearly defined hypocleidium [12]. Claims of the existence of a ceratosaurian (coelophysoid) furcula [78] suggest a deeper analysis of the matter. Moreover, in the Italian specimen there are some features reminiscent of Ceratosauria, such as the quite short first phalanx in the central digit, and 'megalosaurian' characters such as

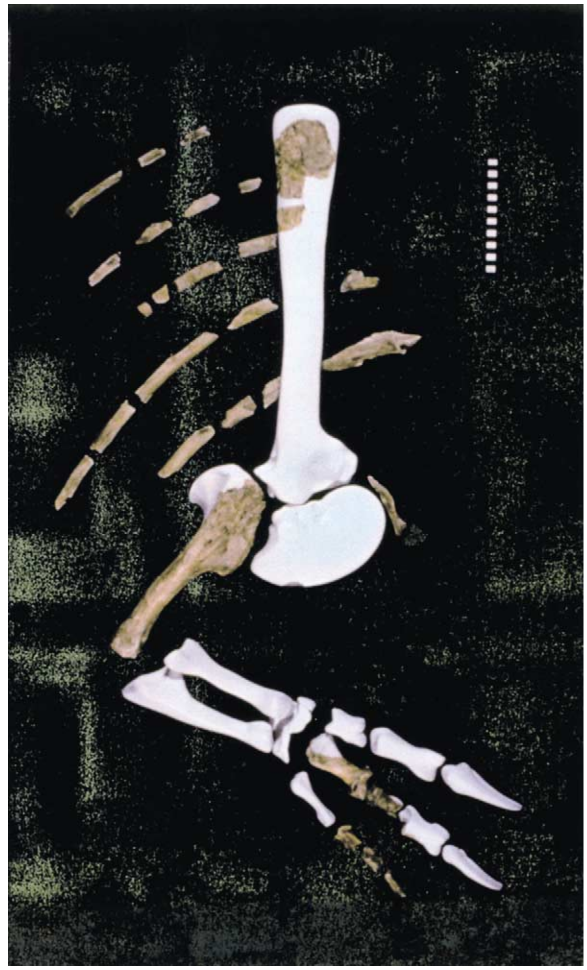

Fig. 19. Specimen MSNM V3664 (Saltrio theropod, Lombardy). Part of the preserved bones (right forelimb and ribs) restored in anatomical connection. Missing elements are white-coloured. Scale bar = 20 cm.

Fig. 19. Spécimen MSNM V3664 (théropode de Saltrio, Lombardie). Une partie des os conservés (membre inférieur droit et côtes) ont été reconstitués en connexion anatomique. Les éléments manquants apparaissent en blanc. Barre d'échelle = 20 cm.

Fig. 20. Specimen MSNM V3664 (Saltrio theropod, Lombardy). Close-up of the furcula in posterior view. Chicken wishbone for comparison, scale bar = 20 cm.
Fig. 20. Spécimen MSNM 3664 (théropode de Saltrio, Lombardie). Gros plan de la furcula en vue postérieure. Os de poulet pour comparaison. Barre d'échelle = 20 cm.

the moderately stout, non-sigmoidal humerus (Fig. 19).

The Saltrio theropod is certainly the largest predatory dinosaur that we know from fossil remains in Italy. From a frankly scientific point of view, this specimen is crucial in any case for the knowledge of theropod evolution: it might represent a transitional form between Ceratosauria and Tetanurae, a basal tetanuran or even the most ancient carnosaur in the fossil record; it shows that large, meat-eating dinosaurs with three-fingered hands (possibly the forerunners of the allosauroid kin) already existed 200 Myr ago (Fig. 21). So far, the oldest tetanuran theropod may be *Cryolophosaurus*, a bizarre crested dinosaur whose remains were discovered by a USA expedition to Antarctica [44]: the frozen rocks bearing that fossil were dated to the Pliensbachian, which is slightly younger than the Sinemurian.

The Simenurian age of the Saltrio Formation is well supported by a hundred species of marine invertebrates, among which 19 ammonites are index fossils of that time [75]. The palaeontological content and the sedimentology of the Saltrio limestone suggest that the dinosaur carcass drifted into the water after the animal died and was fossilised not far from the shore, in a shallow marine basin. This hypothesis is supported by taphonomic evidence, such as the fact that some bones of the Saltrio theropod bear feeding marks made by marine invertebrates. At the same time, fossil remains of terrestrial plants (*Ptilophyllum*, *Pagiophyllum* and

Fig. 21. Artistic restoration of the Saltrio theropod. Estimated in-life size and weight are 8 meters per 1.5 t. (Drawing by F. Fogliazza.)
Fig. 21. Reconstitution artistique du théropode de Saltrio. La taille et le poids estimé pour l'animal vivant sont de 8 m pour 1,5 t. (Dessin de F. Fogliazza.)

Brachyphyllum) confirm that emerged lands facing the Ligurian-Piemontese Basin existed in northwestern Lombardy at the beginning of the Jurassic [53]. The extent of those lands is still unknown, so it is impossible to know whether or not they might be linked to the contemporary terrestrial habitats of Rovereto-Lavini di Marco (Trento Platform).

6. Conclusion

The skeletal remains of Italian dinosaurs belong to brand new, possibly endemic species. Together with the footprints, all these records come from shallow marine coastal deposits, indicating a peculiar palaeobiogeographical situation. The model of Bahamas-like small islands within a carbonate platform is thus insufficient to explain the presence of large land animals such as the huge sauropods of Rovereto and surrounding areas, the gregarious hadrosaurs of Trieste, and the ornithopod herds of Altamura. It is more difficult to support an island-limited ecospace for the large ceratosaurs of the Dolomites, for the diverse Apulian theropods, and for the 8-m-long specimen from Saltrio, because predatory dinosaurs occupied the apex of a complex, definitely terrestrial alimentary pyramid.

It is more likely that the peri-Adriatic Platforms acted as temporary continental bridges that connected Laurasia and Gondwana in the central Tethys, allowing migrations between the two hemispheres and colonisation of the local coastal habitats. Thus Mesozoic southern Europe would have played a major role in dinosaur dispersal, acting as a true crossroad. During marine transgressions some transit land became isolated and led its terrestrial fauna to genetic drift, with typical biological consequences such as endemism and possibly dwarfism. And those conditions, as documented by the wide temporal range of the dinosaur-bearing Italian outcrops, occurred several times during the Mesozoic (Fig. 22).

Given the continuous, high frequency of recent findings, especially for the ichnosites (Fig. 23), the dinosaur record in Italy is expected to improve rapidly in the near future. The eyes of both researchers and amateurs are now familiar with dinosaurs even where, no longer than two decades ago, nobody could dream of them on his doorstep. Clearly the history of Italian dinosaurs is just at its beginning.

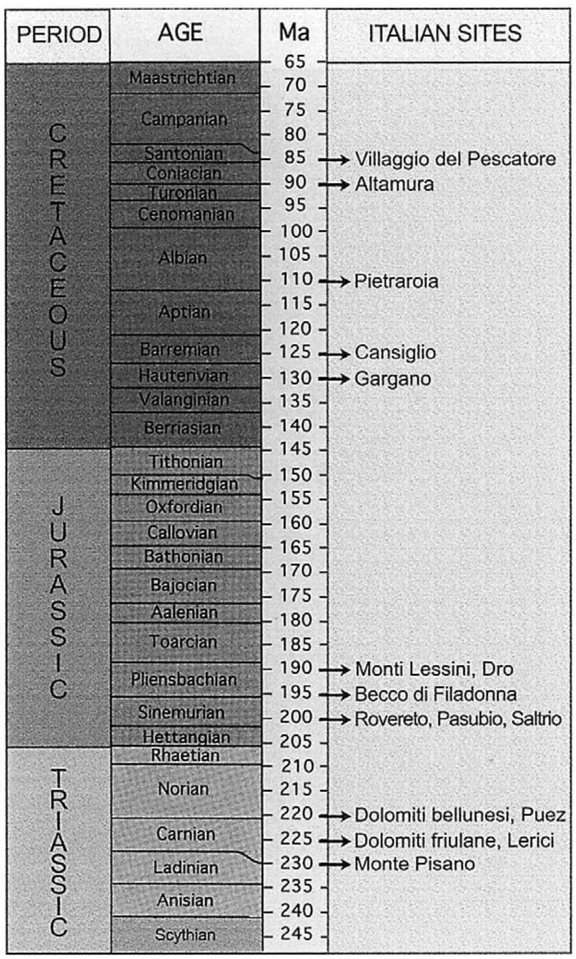

Fig. 22. Geochronological distribution of the Italian dinosaur-bearing outcrops (from [19], modified).

Fig. 22. Répartition géochronologique des affleurements comportant des restes de dinosaures (selon [19], modifié).

Fig. 23. Location of the main sites with dinosaur fossil remains in Italy (from [19], modified).

Fig. 23. Situation des principaux sites à dinosaures fossiles en Italie (selon [19], modifié).

Acknowledgements

Many thanks to R. Allain, M. Avanzini, E. Buffetaut, D. Chure, E. Cioppi, F. Dalla Vecchia, G. Leonardi, O. Matéus and U. Nicosia for informations and to the Italian Ministry of Cultural Goods & Activities for picture courtesy. Thanks also to K. Padian and to a second anonymous referee for reviewing this paper. Photos are by M. Avanzini, F. Cozzini, C. Dal Sasso, G. Palmieri (Centro Studi Ricerche Ligabue), L. Spezia, L. Vitola; drawings by F. Fogliazza, T. Perentin-Stoneage; graphics by F. Nodo, C. Pagliarin.

References

[1] M. Avanzini, Impronte di sauropodi nel Giurassico inferiore del Becco di Filadonna (Piattaforma di Trento-Italia settentrionale), Studi Trentini di Scienze Naturali, Acta Geologica 72 (1998) 193–198.

[2] M. Avanzini, S. Frisia, K. Van den Driessche, E. Keppens, A dinosaur tracksite in an Early Liassic tidal flat in northern Italy: paleoenvironmental reconstruction from sedimentology and geochemistry, Palaios 12 (6) (1997) 538–551.

[3] M. Avanzini, F.M. Dalla Vecchia, V. De Zanche, P. Giannolla, P. Mietto, N. Preto, G. Roghi, Aspetti stratigrafici relativi alla presenza di tetrapodi nelle piattaforme carbonatiche mesozoiche del Sudalpino, in: A. Cherchi, C. Corradini (Eds.), Crisi biologiche, radiazioni adattative e dinamica delle piattaforme carbonatiche, Convegno di fine progetto nazionale di ricerca COFIN97, Modena, 13-14 giugno 2000, Acc. Naz. Sci. Lett. Arti di Modena, Published abstract 21, 2000, pp. 11–14.

[4] M. Avanzini, G. Gierlinski, G. Leonardi, First report of sitting *Anomoepus* tracks in European Lower Jurassic (Lavini di Marco site - Northern Italy), Riv. Ital. Paleont. Strat. 107 (1) (2001) 131–136.

[5] M. Avanzini, G. Leonardi, R. Tomasoni, M. Campolongo, Enigmatic dinosaur trackways from the Lower Jurassic (Pliensbachian) of the Sarca Valley, Northeast Italy, Ichnos 8 (2001) 235–242.

[6] R. Barsbold, H. Osmólska, Ornithomimosauria, in: D.B. Weishampel, P. Dodson, H. Osmólska (Eds.), The Dinosauria, University of California, Berkeley, 1990, pp. 225–244.

[7] S. Bravi, A. Garassino, New biostratigraphic and paleoecological observations on the Plattenkalk of the Lower Cretaceous (Albian) of Pietraroia (Benevento, S. Italy), and its decapod crustacean assemblage, Atti Soc. Ital. Sci. Nat. 138 (1998) 119–171.

[8] T. Brazzatti, R. Calligaris, Studio preliminare di reperti ossei di dinosauri del Carso Triestino, Atti Mus. Civ. Stor. Nat. Trieste 45 (1995) 221–226.

[9] E. Buffetaut, M. Delfino, G. Pinna, The crocodilians, pterosaurs and dinosaurs from the Campanian-Santonian of Villaggio del Pescatore (northeastern Italy): a preliminary report, 6th European Workshop on Vertebrate Paleontology, Florence, 19-22 September 2001, Università degli Studi di Firenze, Abstract volume, 2001, pp. 22.

[10] K. Carpenter, Eggs, Nests and baby dinosaurs, Indiana University Press, Blooming and Indianapolis, 1999, 336 p.

[11] A. Cati, D. Sartorio, S. Venturini, Carbonate platforms in the subsurface of the northern Adriatic Area, Mem. Soc. Geol. Ital. 40 (1987) 295–308.

[12] D.J. Chure, J.H. Madsen, On the presence of furculae in some non-maniraptoran theropods, J. Vertebr. Paleontol. 16 (1996) 573–577.

[13] E.H. Colbert, Variation in *Coelophysis bauri*, in: K. Carpenter, P.J. Currie (Eds.), Dinosaur Systematics, Cambridge University Press, Cambridge, UK, 1990, pp. 81–90.

[14] M. Conti, M. Morsilli, U. Nicosia, E. Sacchi, V. Savino, A. Wagensommer, L. Di Maggio, P. Gianolla, Apulian dinosaurs, Boll. Soc. Paleontol. Ital. (in press).

[15] P.J. Currie, Cranial anatomy of *Stenonychosaurus inequalis* (Saurischia, Theropoda) and its bearing on the origin of birds, Can. J. Earth Sci. 22 (1985) 1643–1658.

[16] P.J. Currie, New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda), J. Vertebr. Paleontol. 15 (3) (1995) 576–591.

[17] P.J. Currie, X.J. Zhao, A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, Poeple's Republic of China, Can. J. Earth Sci. 30 (1993) 2037–2081.

[18] C. Dal Sasso, Update on Italian dinosaurs, 6th European Workshop on Vertebrate Paleontology, Florence, 19–22 September 2001, Università degli Studi di Firenze, Abstract volume, 2001, pp. 27.

[19] C. Dal Sasso, Dinosauri italiani, Marsilio Editori, Venezia, 2001 260 p.

[20] C. Dal Sasso, M. Signore, Exceptional soft-tissue preservation in a theropod dinosaur from Italy, Nature 392 (1998) 383–387.

[21] C. Dal Sasso, M. Signore, *Scipionyx samniticus* (Theropoda, Coelurosauria) and its exceptionally preserved internal organs, J. Vertebr. Paleontol. 18 (3 Suppl.) (1998) 37A.

[22] C. Dal Sasso, L. Magnoni, F. Fogliazza, Elementi di tecniche paleontologiche, Natura, Soc. Ital. Sci. Nat. Mus. Civ. St. Nat. Milano 91 (1) (2001) 37 p.

[23] F.M. Dalla Vecchia, Jurassic and Cretaceous Sauropod evidence in the Mesozoic carbonate platforms of Southern Alps and Dinarids, in: M.G. Lockley, V. Faria dos Santos, C.A. Meyer, A. Hunt (Eds.), Aspects of Sauropod Paleobiology, Gaia 10, Lisboa, 1994, pp. 65–73.

[24] F.M. Dalla Vecchia, Terrestrial tetrapod evidence on the Norian (Late Triassic) and Cretaceous carbonate platforms of Northern Adriatic region (Italy, Slovenia and Croatia), Proc. Int. Symp. "Mesozoic Vertebrate Faunas of Central Europe", Sargetia, ser. Sci. Nat. XVII, Deva, 1997, pp. 177–201.

[25] F.M. Dalla Vecchia, Remains of Sauropoda (Reptilia, Saurischia) in the Lower Cretaceous (Upper Hauterivian/Lower Barremian) limestones of SW Istria (Croatia), Geol. Croatica 51 (2) (1998) 105–134.

[26] F.M. Dalla Vecchia, A sauropod footprint in a limestone block from the Lower Cretaceous of northeastern Italy, Ichnos 6 (4) (1999) 269–275.

[27] F.M. Dalla Vecchia, Theropod footprints in the Cretaceous Adriatic-Dinaric carbonate platform (Italy and Croatia), in: B. Perez-Moreno, T. Holtz, J.L. Sanz, J.J. Moratalla (Eds.), Aspects of Theropod Paleobiology, Gaia 15, Lisboa, 2000, pp. 355–367.

[28] F.M. Dalla Vecchia, The Mesozoic Periadriatic Carbonate Platforms as terrestrial ecosystems: the vertebrate evidence, VII International Symposium on Mesozoic Terrestrial Ecosystems, Buenos Aires, 26 September–1 October 1999, Abstracts, 2001, pp. 20–21.

[29] F.M. Dalla Vecchia, A new theropod dinosaur from the Lower Jurassic of Italy, Saltriosaurus, Dino Press 3 (2001) 81–87.

[30] F.M. Dalla Vecchia, Cretaceous dinosaurs in the Adriatic-Dinaric carbonate platform (Italy and Croatia): paleoenvironmental implications and paleogeographical hypotheses, Mem. Soc. Geol. Ital. 57 (in press).

[31] F.M. Dalla Vecchia, S. Venturini, A theropod (Reptilia, Dinosauria) footprint on a block of Cretaceous limestone at the pier of Porto Corsini (Ravenna, Italy), Riv. Ital. Paleontol. Stratigr. 101 (1) (1995) 93–98.

[32] F.M. Dalla Vecchia, P. Mietto, Impronte di rettili terrestri nella Dolomia Principale (Triassico superiore) delle Prealpi Carniche (Pordenone, Friuli), Atti Ticinensi Sci. Terra Pavia (Serie Speciale) 7 (1998) 87–107.

[33] F.M. Dalla Vecchia, A. Tarlao, G. Tunis, Theropod (Reptilia, Dinosauria) footprints in the Albian (Lower Cretaceous) of the Quieto/Mirna river mouth (NW Istria, Croatia) and dinosaur population of the Istrian region during the Cretaceous, Mem. Sci. Geol. Padova 45 (1993) 139–148.

[34] F.M. Dalla Vecchia, A. Tarlao, G. Tunis, M. Tentor, S. Venturini, First record of Hauterivian dinosaur footprints in southern Istria (Croatia), in: I. Vlahovic, R. Biondic (Eds.), Proc. Second Croatian Geological Congress, Cavtat-Dubrovnik, 17–20 May 2000, pp. 143–149.

[35] F.M. Dalla Vecchia, A. Tarlao, G. Tunis, S. Venturini, New dinosaur track sites in the Albian (Early Cretaceous) of the Istrian peninsula (Croatia), Mem. Sci. Geol. Padova 52 (1) (2000) 227–293 52 (2) (2000) 193–292.

[36] F.M. Dalla Vecchia, G. Tunis, S. Venturini, A. Tarlao, Dinosaur track sites in the Upper Cenomanian (Late Cretaceous) of Istria Peninsula (Croatia), Boll. Soc. Paleontol. Ital. 40 (1) (2001) 25–53.

[37] J. Dercourt, L.E. Ricou, B. Vrielynck, Atlas Tethys Palaeoenvironmental Maps, Gauthier-Villars, Paris, 1993 307 p.

[38] J.O. Farlow, Predatory/Prey Biomass Ratios Community Food Webs and Dinosaur Physiology, in: R.D.K. Thomas, E. Olson (Eds.), A cold look at the warm-blooded dinosaurs, Westview Press, Boulder, 1980, pp. 55–83.

[39] P.M. Galton, Manus movements of the coelurosaurian dinosaur *Syntarsus* and opposability of the theropod hallux, Arnoldia 5 (15) (1971) 1–8.

[40] S.M. Gatesy, Caudofemoral musculature and the evolution of theropod locomotion, Paleobiology 16 (1990) 170–186.

[41] J. Gauthier, Saurischian monophyly and the origin of birds, Mem. Calif. Acad. Sci. 8 (1986) 1–55.

[42] P. Gianolla, M.D. Morsilli, F.M. Dalla Vecchia, A. Bosellini, A. Russo, Impronte di dinosauri in facies di piattaforma interna nel Cretaceo inferiore del Gargano (Puglia, Italia meridionale), Riassunti delle comunicazioni orali e dei posters, 80° Riunione Estiva S.G.I., Trieste September 6–8 2000, Published abstract, 2000, pp. 265–266.

[43] J. Guibé, L'appareil digestif, in: P.P. Grassé (Ed.), Traité de Zoologie, Tome XIV: Reptiles. Caractères géneraux et anatomie, Masson, Paris, 1970, pp. 521–548.

[44] W.R. Hammer, W.J. Hickerson, A Crested Theropod Dinosaur from Antarctica, Science 264 (1994) 828–830.

[45] T.R. Holtz, Phylogenetic taxonomy of the Coelurosauria (Dinosauria: Theropoda), J. Paleontol. 70 (3) (1996) 536–538.

[46] T.R. Holtz Jr, A new phyologeny of the carnivorous dinosaurs, in: B. Perez-Moreno, T. Holtz, J.L. Sanz, J.J. Moratalla (Eds.), Aspects of Theropod Paleobiology, Gaia 15, Lisboa, 2000, pp. 5–61.

[47] F. von Huene, Die Tetrapoden-Fährten in toskanischen Verrucano und ihre Bedeutung, Neues Jahrb. Geol. Palaeontol. Abt. B (1941) 1–34.

[48] Q. Ji, S. Ji, On discovery of the earliest bird fossil in China and the origin of birds, Chin. Geol. 233 (1996) 30–33.

[49] G. Leonardi, M. Lanzinger, Dinosauri nel Trentino: venticinque piste fossili nel Liassico di Rovereto (Trento, Italia), Paleocronache 1992-I (1992) 13–24.

[50] G. Leonardi, G. Teruzzi, Prima segnalazione di uno scheletro fossile di dinosauro (Theropoda, Coelurosauria) in Italia (Cretacico di Pietraroia, Benevento), Paleocronache 1993-I (1993) 7–14.

[51] G. Leonardi, P. Mietto (Eds.), Dinosauri in Italia, Accademia Editorale, Pisa, 2001.

[52] M. Lockley, C. Meyer, Dinosaur tracks and other fossil footprints of Europe, Columbia University Press, New York, 2000.

[53] A. Lualdi, New data on the Western part of the M. Nudo Basin (Lower Jurassic, West Lombardy), Tübingen Geowiss. Arbeiten, Ser. A 52 (1999) 173–176.

[54] J.H. Madsen Jr, *Allosaurus fragilis*: a revised osteology, Utah Geol. Miner. Surv. Bull. 109, Salt Lake City, USA, 1976 164 p.

[55] J.H. Madsen Jr, *Ceratosaurus* (Dinosauria, Theropoda): a revised osteology, Utah Geol. Survey, Misc. Publ. 00-2, Salt Lake City, USA, 2000 80 p.

[56] P. Mietto, Piste di dinosauri nella Dolomia Principale (Triassico superiore) del Monte Pelmetto (Cadore), Mem. Soc. Geol. Ital. 30 (1988) 307–310.

[57] P. Mietto, G. Roghi, Nuova segnalazione di impronte di dinosauri nel Giurassico inferiore del Subalpino: le piste della Valle di Revolto (Alti Lessini Veronesi), Paleocronache 1993-II (1993) 39–43.

[58] P. Mietto, G. Roghi, R. Zorzin, Le impronte di dinosauri liassici dei Monti Lessini Veronesi, Boll. Mus. Civ. St. Nat. Verona 24 (2000) 55–72.

[59] R.E. Molnar, Variation in theory and in theropods, in: K. Carpenter, P.J. Currie (Eds.), Dinosaur Systematics, Cambridge University Press, Cambridge, 1990, pp. 71–79.

[60] U. Nicosia, M. Marino, N. Mariotti, C. Muraro, S. Panigutti, F.M. Petti, E. Sacchi, The Late Cretaceous dinosaur tracksite near Altamura (Bari, southern Italy), Geologica Romana 35 (1999) 237–247.

[61] M.A. Norell, P. Makovicky, Important features of the dromaeosaur skeleton: information from a new specimen, Am. Mus. Novitates 3215 (1997) 1–28.

[62] M.A. Norell, J.A. Clark, D. Dashzeveg, R. Barsbold, L.M. Chiappe, A.R. Davidson, M. McKenna, A. Perle, M. Novacek, A Theropod Dinosaur Embryo and the Affinities of the Flaming Cliffs Dinosaur Eggs, Science 266 (1994) 779–782.

[63] D.B. Norman, Problematic theropoda: Coelurosaurs, in: D.B. Weishampel, P. Dodson, H. Osmólska (Eds.), The Dinosauria, University of California, Berkeley, CA, 1990, pp. 280–305.

[64] J.H. Ostrom, Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana, Bull. Peabody Mus. Nat. Hist. Yale 30 (1969) 1–165.

[65] J.H. Ostrom, The pectoral girdle and forelimb function of *Deinonychus* (Reptilia: Saurischia): a correction, Postilla 165 (1974) 1–11.

[66] J.H. Ostrom, On a new specimen of the Lower Cretaceous theropod dinosaur *Deinonychus antirrhopus*, Breviora 438 (1976) 1–21.

[67] J.H. Ostrom, The Osteology of *Compsognathus longipes* Wagner, Zitteliana 4 (1978) 73–118.

[68] G.S. Paul, Predatory Dinosaurs of the World, Simon & Schuster, New York, 1988 464 p.

[69] X. Pereda-Superbiola, A revised census of European Late Cretaceous nodosaurids (Ornithischia: Ankylosauria): last occurrence and possible extinction scenarios, Terra Nova 4 (1992) 641–648.

[70] X. Pereda-Superbiola, P.M. Galton, A revision of the cranial features of the dinosaur *Struthiosaurus austriacus* Bunzel (Ornithischia: Ankylosauria) from the Late Cretaceous of Europe, N. Jahrb. Geol. Paläont. Abh. 191 (2) (1994) 173–200.

[71] X. Pereda-Superbiola, P.M. Barrett, A systematic review of ankylosaurian remains from the Albian-Cenomanian of England, 1999, pp. 177–208.

[72] J.A. Ruben, C. Dal Sasso, N.R. Geist, W.J. Hillenius, T.D. Jones, M. Signore, Pulmonary function and metabolic physiology of theropod dinosaurs, Science 283 (1999) 514–516.

[73] D.A. Russell, A new specimen of *Stenonychosaurus* from the Oldman Formation (Cretaceous) of Alberta, Can. J. Earth Sci. 6 (1969) 595–612.

[74] D.A. Russell, Z. Dong, A nearly complete skeleton of a new troodontid dinosaur from the Early Cretaceous of the Ordos Basin, Inner Mongolia, People's Republic of China, Can. J. Earth Sci. 30 (1993) 2163–2173.

[75] G. Sacchi Vialli, Revisione della fauna di Saltrio, Atti Ist. Geol. Univ. Pavia 15 (1964) 146–161.

[76] I. Sirigu, U. Nicosia, Piste di rettili triassici nel territorio della Spezia, Atti Accad. Lunig. Sci. LXIV-LXV (1995) 251–256.

[77] H.D. Sues, The skull of *Velociraptor mongoliensis*, a small Cretaceous theropod dinosaur from Mongolia, Palaeont. Z. 51 (3/4) (1977) 173–184.

[78] R.S. Tykoski, The osteology of *Syntarsus kayentakatae* and its implications for ceratosaurid phylogeny, Unpublished Masters Thesis, University of Texas at Austin, 1998 217 p.

[79] D.B. Weishampel, D.B. Norman, D. Grigorescu, *Telmatosaurus transylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur, Palaeontology 36 (2) (1993) 361–385.

[80] S.P. Welles, *Dilophosaurus wetherilli* (Dinosauria Theropoda), osteology and comparisons, Palaeontographica Abt. A 185 (1984) 85–180.

[81] E. Zappaterra, Carbonate paleogeographic sequences of the periadriatic region, Boll. Soc. Geol. Ital. 109 (1990) 5–20.