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CONEROICHNUS MARINUS ICHNOGENUS ET ICHNOSPECIES NOV., A FOSSIL TRACKWAY OF MARINE REPTILE IN THE MAIOLICA FORMATION (UPPER JURASSIC-LOWER CRETACEOUS) FROM MOUNT CONERO, MARCHE, ITALY

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ABSTRACT – An uncommon ichnofossil, constituted of a sequence of eleven imprints, named as *Coneroichnus marinus* ichnog. et ichnosp. nov., is described from Mount Conero, Province of Ancona, Italy. The trackway is impressed in whitish micritic limestone of the Maiolica Formation (Upper Jurassic–Lower Cretaceous), herein interpreted as the passage on the sea bottom of a marine reptile, softly interfering in the sediment-water interface. Its gait can be defined as half-swimming, that is the swimming in exploratory and punting propulsive contact with the mud at the bottom. We discuss the probable trackmaker and we suggest it was probably a pliosaurid Plesiosauria. The extreme rarity of ichnofossils of tetrapods on the deep-sea bottom in the whole world is herein confirmed.

Keywords: Early Cretaceous, *Coneroichnus marinus* ichnog. et ichnosp. nov., pelagic reptile trackway.

RESUMO – Um raro icnofóssil, ou seja, uma sequência de onze impressões em micrite calcária da Formação Maiolica (Jurássico Superior–Cretáceo Inferior), é aqui nomeado como *Coneroichnus marinus* ichnog. et ichnosp. nov. sendo detalhadamente descrito. A pista se encontra no Monte Conero, na Província de Ancona, Itália. Ela é atribuída à passagem sobre o fundo do mar de um réptil marinho, o qual deformou a superfície na interface sedimento-água. Seu deslocamento pode ser definido como semi-natação, que corresponde a uma natação de caráter exploratório e propulsivo em contato com a lama do fundo. Discute-se o produtor desta pista, possivelmente um pliosaurídeo Plesiosauria. A extrema raridade de icnofósseis de tetrápodes no substrato marinho profundo em todo o mundo é confirmada.

Palavras-chave: Cretáceo Inferior, *Coneroichnus marinus* ichnog. et ichnosp. nov., pista de um réptil pelágico.

INTRODUCTION

There is quite a lot of literature on swim-tracks or bottom-walking tracks in shallow waters by aquatic tetrapods such as fresh- and salt-water sea turtles and crocodiles, and even by dinosaurs (Gaillard *et al*., 2003; Avanzini *et al*., 2005; Lockley & Foster, 2006; Vila *et al*., 2014; Lichtig *et al*., 2018; Reolid *et al*., 2018; Leonardi & Carvalho, 2021). Half-swimming gait or punting gait is the progression of animals that swim in shallow waters and make progress by setting their feet against the bottom. The corresponding trackways are frequently incomplete. Footprints or trackways of this kind could also be made by trackmakers completely submerged, that is "above their head", as hippos strike the bottom of rivers in this way. These classes of footprints consist principally of scratches or indentations left by the claws or hooves. Fossil tracks with this kind of gait are found in layers of formations from the Permian to the present. On the contrary, the literature on tracks on deep sea sediments is extremely scarce (Manni *et al*., 1999; Zhang *et al*., 2014; Natali *et al*., 2019). On the trail described by Manni *et al*. (1999) we will write below. The trackways produced by the nothosaurs with their punting progression, such as those described by Zhang *et al*. (2014), although belonging to a completely different period, are however useful for comparison with the trackway in question. These marine reptilians, in fact, swam close to the marine bottom, probably for the purpose of looking for and catching prey on the seabed for nourishing. So, they left on the marine ooze the imprints of their fore paddles, in a way quite similar to the tracks we are talking about. Unlike this, however, the nothosaurs tracks show that they "rowed" with both forelimbs in unison rather than with an alternate bike.

This article is focused on the paleoichnological allocation of one trackway from deep sea sediments (Natali *et al*., 2019). We formally erect herein for it a new ichnotaxon (an ichnogenus and ichnospecies), related to the study of the tracks in question. We also suggest an attribution to its trackmaker.

GEOLOGICAL SETTING AND STRATIGRAPHY

The area, known as "Placche dei Gabbiani", consists of large, fractured, structural surfaces that plunge uniformly towards the sea and are formed by the layers of the Maiolica Formation (upper Tithonian–lower Aptian) (Micarelli *et al.*, 1977; Centamore & Deiana, 1986; Centamore & Micarelli, 1991; Deiana *et al.*, 2002). This formation consists basically of compact micritic limestones of pelagic environment, except for the terminal upper portion. On the basis of ongoing and not yet published studies, the layer containing the imprints under study should belong to the Berriasian–Hauterivian series, with a backdating of a few million years compared to the previous studies (Natali *et al.*, 2019). The outcrop belongs to the Umbrian-Marchean succession and is the oldest on Mount Conero (Figure 1). The Figure 2 shows the simplified scheme of the Umbrian-Marchean region succession.

The layer containing the trackway represents the lowermost portion of the Maiolica Formation and consists of micrite, which is attributed to a deep pelagic environment,

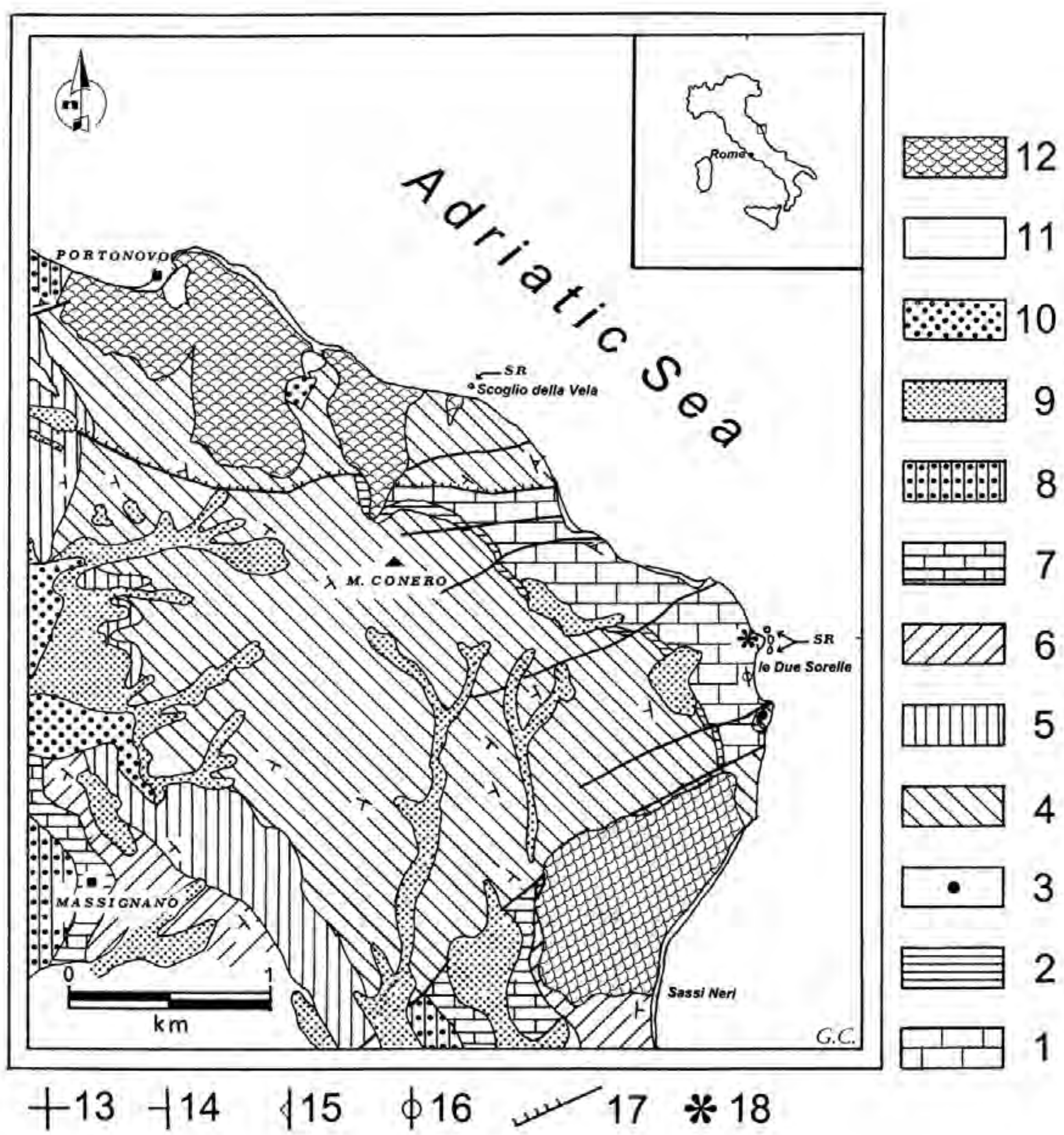

Figure 1. Simplified geological scheme relating to the paleontological area of discovery at Mount Conero, modified from Coccioni *et al.* (1997) (see Natali *et al.*, 2019). **Captions: 1**, Maiolica (Upper Tithonian–Lower Aptian *p.p.*); **2**, Marne a Fucoidi (Lower Aptian *p.p.* –upper Albian *p.p.*); **3**, Scaglia Bianca (Upper Albian *p.p.* –lower Turonian *p.p.*); **4**, Scaglia Rossa (Lower Turonian *p.p.* –Lutetian *p.p.*); **5**, Scaglia Variegata (Lutetian *p.p.* –Bartonian *p.p.*); **6**, Scaglia Cinerea (Bartonian *p.p.* –Aquitanian *p.p.*); **7**, Bisciaro (Aquitanian *p.p.* –Burdigalian *p.p.*); **8**, Schlier (Burdigalian *p.p.* –Tortonian *p.p.*); **9**, Slope deposits; **10**, Fluid turbidity conoid deposits; **11**, Current coastal deposits; **12**, Active landslides. **Strike, dip, and inclination of the layers: 13**, horizontal; **14**, 10–45°; 15, 46–85°; **16**, vertical; **17**, faults (the teeth indicate the lowered part); **18**, location of the ichnological site; **SR**, Scaglia Rossa.

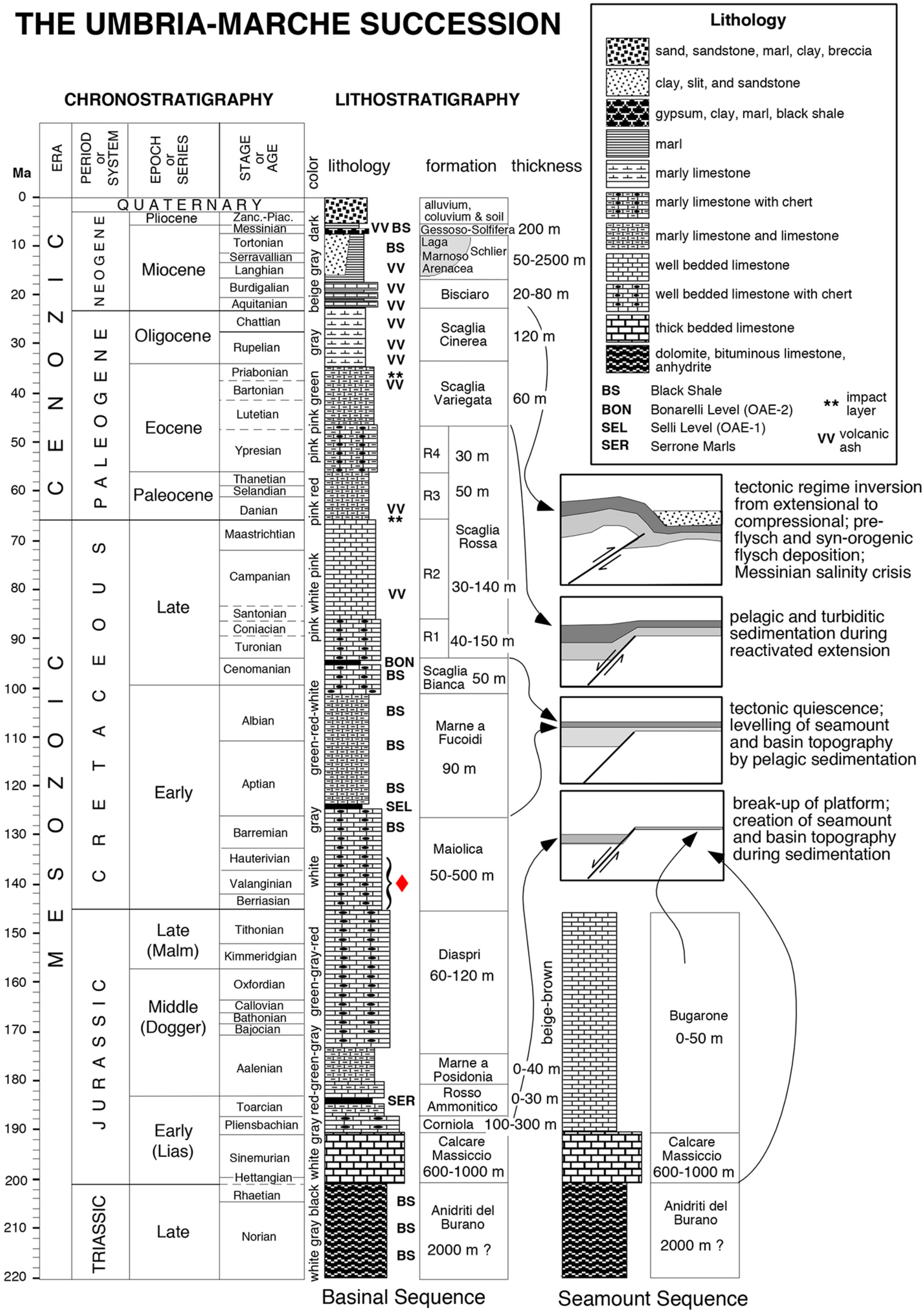

Figure 2. Chronostratigraphy and lithostratigraphy of the Umbrian–Marchean succession, indicating the area containing the imprints (♦). Taken and modified from Montanari & Koeberl (2000).

to a marine setting below 200 m depth, without the effects of storm waves (Centamore & Deiana, 1986; Centamore & Micarelli, 1991; Deiana *et al*., 2002). Furthermore, there is no ripple marks or evidence of synsedimentary subaerial exposures (Natali *et al*., 2019).

MATERIAL AND METHODS

The fieldwork was possible thanks to the help of rock-climbing equipment in an area off limits to the public for safety reasons (Figure 3). A cast of some imprints (prints or tracks 1, 3 and 6) was made with silicone rubber. Vertebrate paleoichnological terminology used here mainly follows Leonardi (1987).

The eleven imprints discovered have a depth of 3–5.5 cm and variable length and width, respectively, between 8 and 16 cm and 15–26 cm. The whole trackway configuration, with a total length of about 5.20 m, is a nearly straight line (Figures 4–8). The imprints are interpreted to be true fossil footprints, and certainly are not man-made. One might perhaps suppose that these concavities are undertracks; however, it is considered that these limestone beds are locally thick to very thick; with a thickness from decametric to metric. This excludes that the concavities described may be undertracks.

The traces have an irregularly elliptical shape: in many cases (prints 1–8) there is a detectable hem along the outer perimeter, that is the displacement rim (Figure 9; see also Figures 5–7).

Print 3 also shows, on the back side, an evident "coating" of the ancient plastic sediment, that is, the original, not eroded, surface of the limestone bed (Figure 9). The imprints are generally characterized by a smooth and slightly concave surface at the deepest point of the track, for a good part of their width and for about 2–3 cm in the longitudinal direction (Figure 9; see also Figures 5–7).

Almost all of the longitudinal sections of the imprints have roughly a "V" shape with respect to the layer surface, which originally represented the seabed surface (Figure 10).

It was observed: a very high step angle close to 180°; an alternation of paces (or oblique paces) approx. 50 cm on average (min. 30 cm, max. 70 cm), with a stride approx. 100 cm on average (min. 74 cm, max. 123 cm); a reduced trackway external width (mean ~ 26 cm, range 17–37 cm) (see Figure 8 and Table 1).

Figure 3. The steep rocky slope of Maiolica Formation containing the ichnofossils. The arrows show the first and the last imprints.

Figure 4. *Coneroichnus marinus* ichnog. et ichnosp. nov. Detail of the 11 imprints (top) and close-up view of the first nine imprints (bottom).

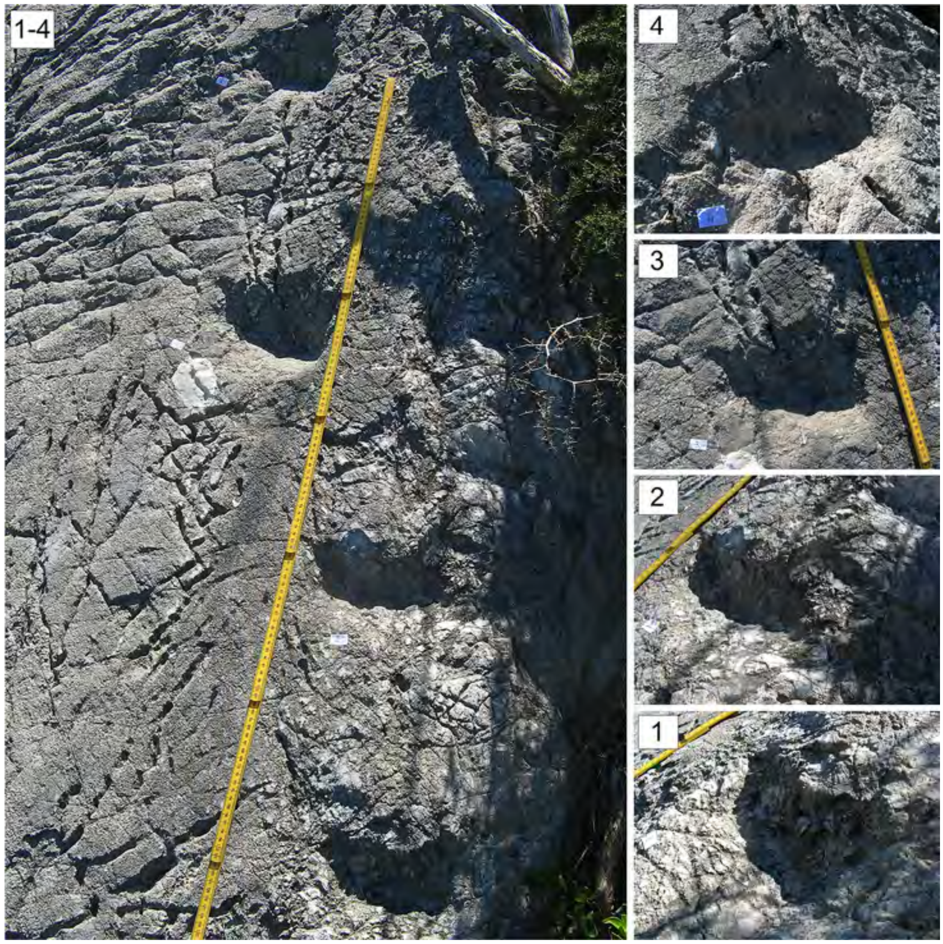

Figure 5. *Coneroichnus marinus* ichnog. et ichnosp. nov. Detail of the first four imprints. Graphic scale in cm.

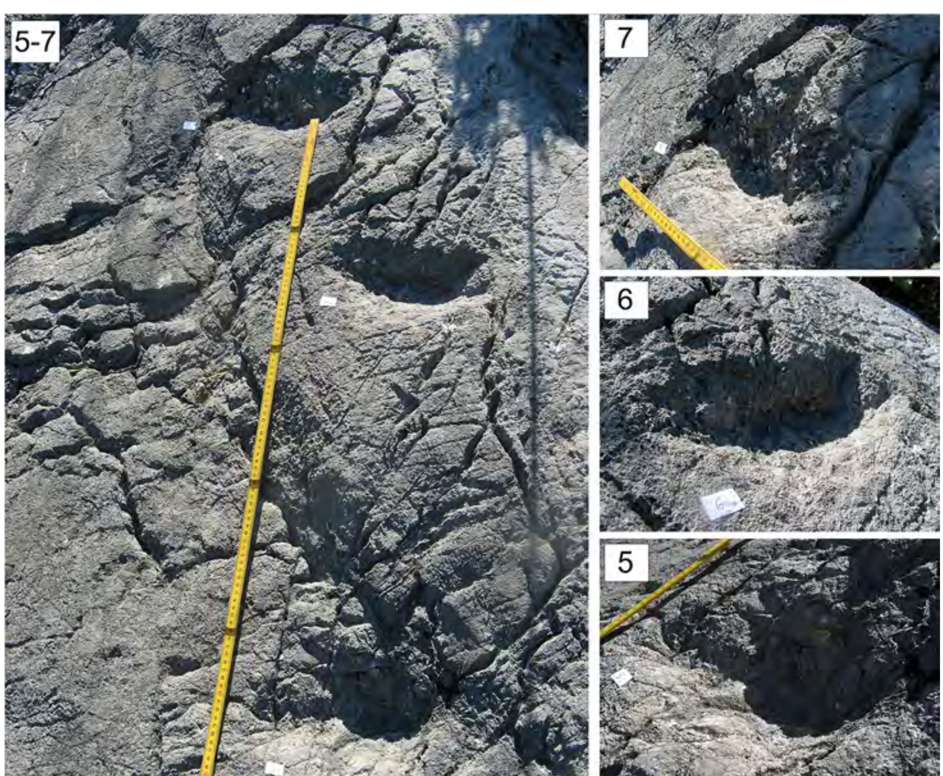

Figure 6. *Coneroichnus marinus* ichnog. et ichnosp. nov. Detail of the imprints 5, 6 and 7. Graphic scale in cm.

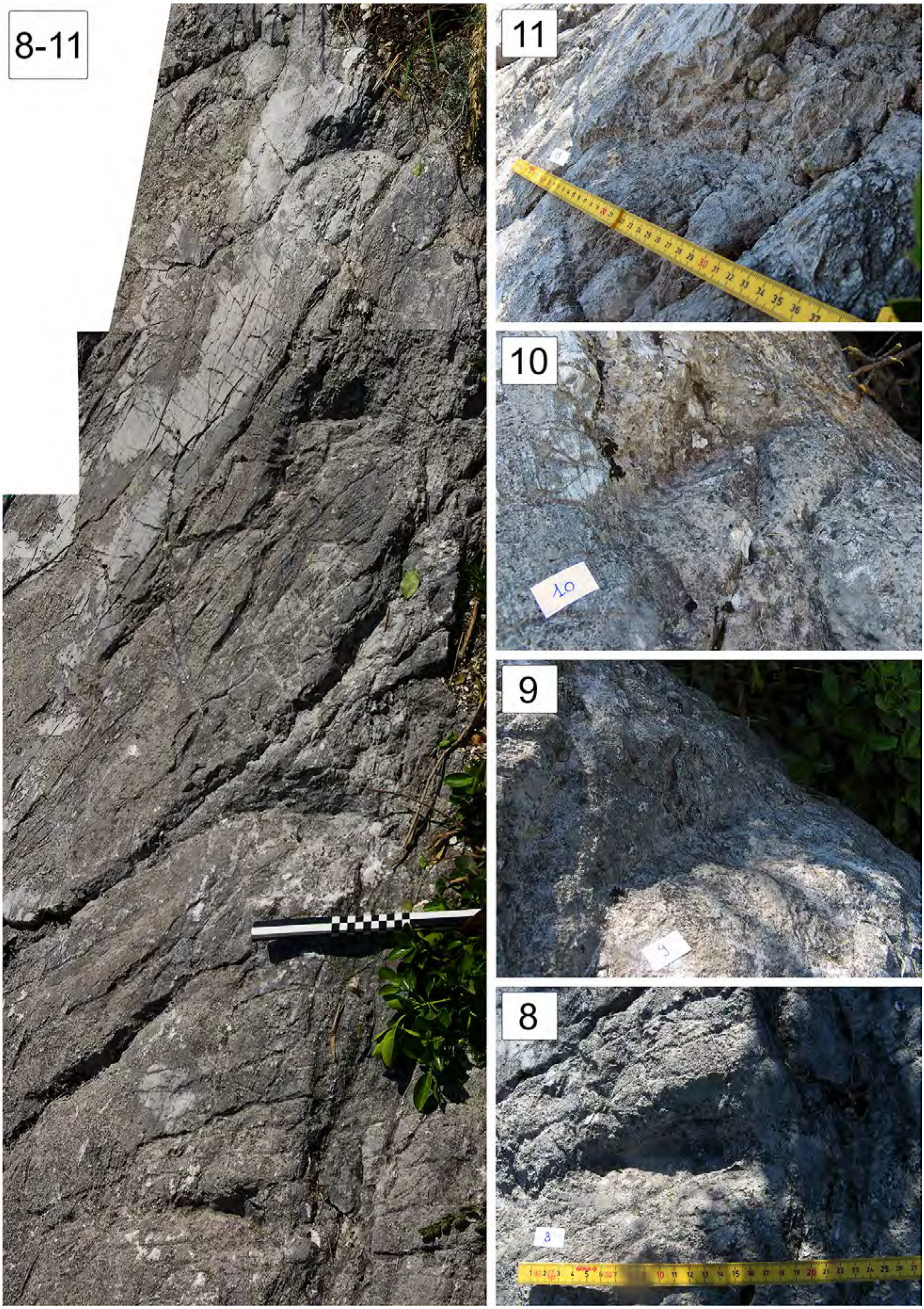

Figure 7. *Coneroichnus marinus* ichnog. et ichnosp. nov. Detail of the imprints 8, 9, 10 and 11. Graphic scale in cm.

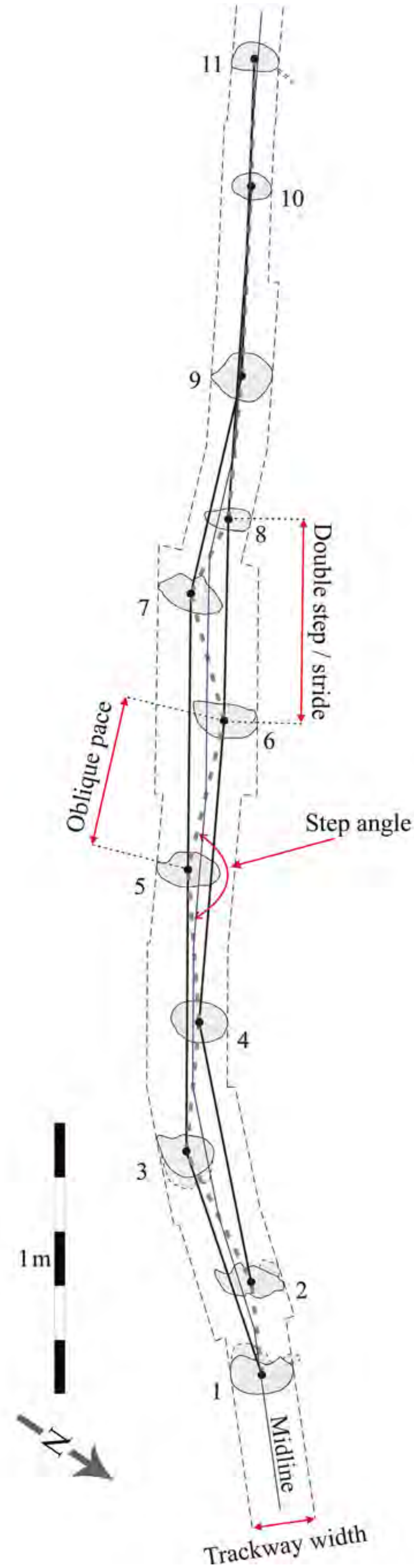

Figure 8. *Coneroichnus marinus* ichnog. et ichnosp. nov. The drawing shows the trend of the eleven imprints and some trackway parameters: the oblique pace (dotted line), the stride (bold continuous line), the step angle and the width of the trackway in relation to the midline (continuous line). The direction of animal movement is from print 1 to print 11.

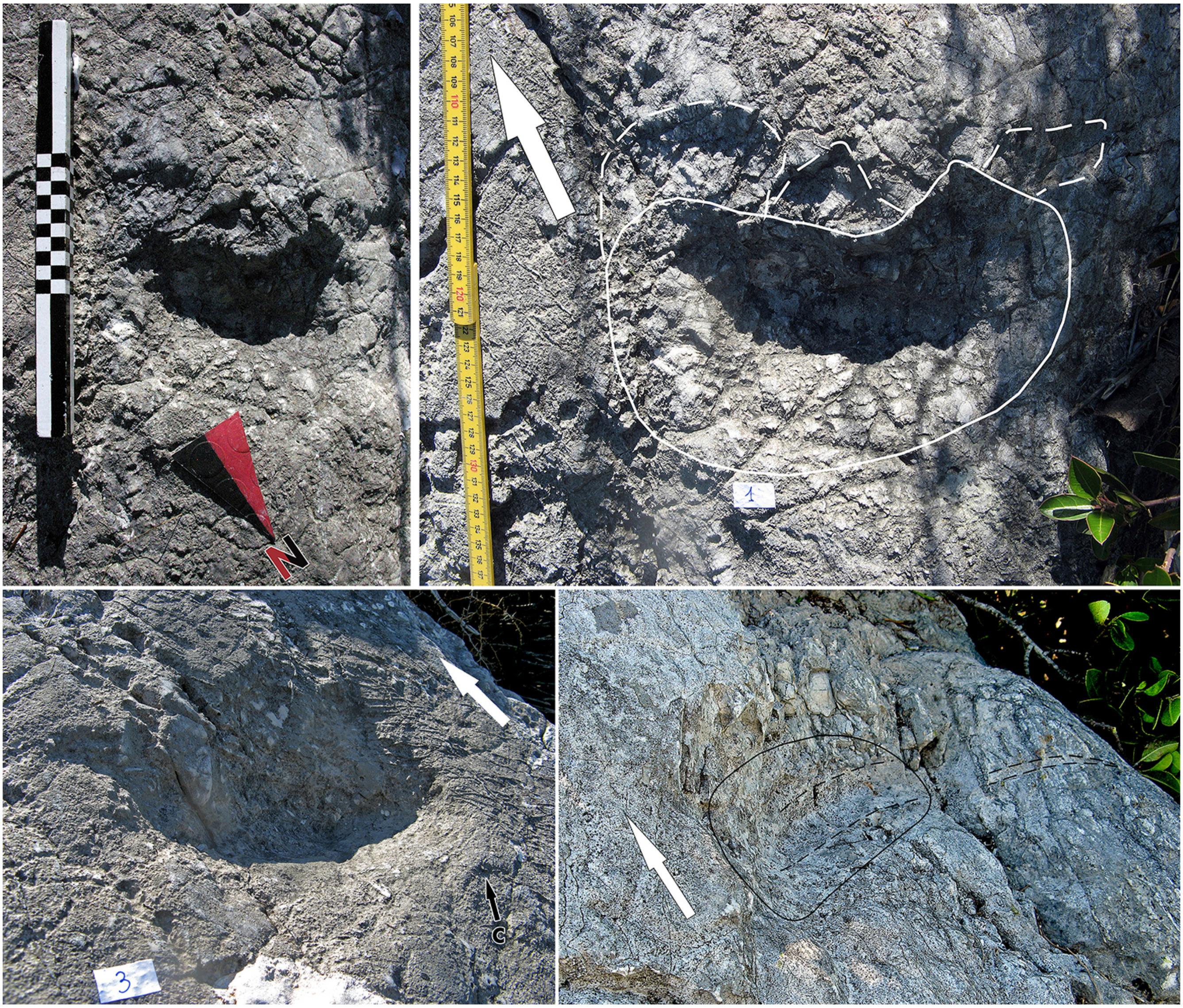

Figure 9. *Coneroichnus marinus* ichnog. et ichnosp. nov. Top (print 1): the continuous line delimits the impression; the dotted lines indicate the impressions that are interpreted as the action of the limb pressing off the soft sediment and the consequent move forward (see also Figures 8 and 11); there is, along the outer perimeter, the displacement rim; direction of movement is shown by the white arrow; graphic scale in cm. Down to the left (print 3): note the piriform aspect of the print, with the tip to the left; the letter C indicates the "coating" of the ancient plastic sediment; direction of movement is shown by the white arrow. Down to the right (print 11): the continuous line marks the outline of the imprint; the dotted lines indicate the smoothest and deepest surfaces; the thin groove on the right side of the photo, delimited by dotted lines, is interpreted as a trace left by the animal at the moment of extraction of the paddle from the sediment; direction of movement is shown by arrow.

ICHNOSYSTEMATICS

The fossil trackway described is unique in morphology, so we formally erect a new ichnotaxon (an ichnogenus and ichnospecies).

Coneroichnus ichnogenus nov.

Type ichnospecies. *Coneroichnus marinus* ichnospecies nov.
Type stratigraphic unit. As for the ichnospecies.
Type locality. As for the ichnospecies.
Derivatio nominis. From the place of discovery, the Mount Conero, in the Marche, Central Italy, on the Adriatic coast. The traditional termination "*íchnus*" comes, latinized, from the Greek *ἴχνος*, which means track, imprint, trackway.
Diagnosis. The whole general structure of the trackway is almost straight; it has a very high step angle and a very narrow internal and external trackway width. The breadth between tracks has negative values; as long as the trackway is to be considered complete, as it was found, and as it currently appears; see also the discussion, later, on this point. In the first part of the trackway, the tracks are arranged somewhat zigzag, then towards the end they are arranged in a straighter way. This implies a somewhat variable swimming and punting progression. The imprints are rarely roundish, and almost always ellipsoid, with the longest axis transverse to the midline. We do not see indications of digits, but the

Table 1. Main dimensional parameters of the 11 imprints (measured in cm and degrees). The degree of inclination (**dip**) refers to the dip of the rock slope at the print. **Abbreviations: R** and **L** indicate right and left prints. Step angles (**angle**) of the trackway.

n.	length	width	depth	dip	print	expulsion rim	angle	
1	13	21	4	45°	L	x		
2	13	25	4.2	42°	R		160°	
3	16	21	5.5	50°	L	x	148°	
4	16	21	5.5	56°	R	x	170°	
5	14	24	5	50°	L		162°	
6	13	26	4.5	50°	R		152°	
7	12	25	5	55°	L		139°	
8	8	18	3	50°	R		160°	
9	16	21	4	50°	L		183°	
10	11	15	3	60°	R		180°	
11	8	18	3.5	60°	L			
							183°	max
							139°	min
M	12.73	21.36	4.3				161°	

imprints are generally characterized by a smooth and slightly concave surface at the deepest point of the tracks (See above and ahead). So, the animal could not possibly perform a quadrupedal gait. That is, it did not realize a "punting gait" or "punting swim", that is a contact propulsion with all four (cf. Zhang *et al*., 2014).

Paleoecology. Given the paleoenvironmental characteristics of the stratigraphic unit, the trackmaker probably swam in deep water, and had to be very adapted to the pelagic life. Sedimentological data suggest in fact that this calcareous mud has been deposited in very deep waters. In this area where the visibility is minimal, called dystopic or mesopelagic band, organisms can show adaptations to this condition. If the organism was a predator, these adaptations, which served mainly in the detection of the prey, could be of different types (Natali, 2022, p. 43). In the twilight of the seabed consisting of calcareous smudge, lived worms, brachiopods, bivalves and other mollusks, such as ammonites or belemnites which could be prey to marine predators, along with fish adapted to live at those depths.

Coneroichnus marinus ichnospecies nov.
(Figures 3–12)

Holotype. A trackway about 5.20 meters long, with 11 imprints.

Depository. *In situ*, in an area difficult to reach and off limits to the public for safety reasons, protected by the Conero Natural Park.

Plastotype. Casts of the prints 1, 3 and 6, in silicone, are housed in the Museum System - Museum of Sciences of the University of Camerino (UNICAM), Camerino, Macerata, Marche.

Type locality. On a rock cliff known as the "Placche dei Gabbiani", near the beach "Due Sorelle", at the altitude of about 124 m a. s. l., inside the Conero Natural Park, in the Municipality of Sirolo, in the Province of Ancona, region of Marche, in Central Italy (Foglio I.G.M. 118 – Quadrante IV SE – Sirolo, 43°32'50,7" N – 13°37'29,7"E).

Type stratigraphic range. Lower beds of the Maiolica Formation belonging to the Umbrian–Marchean succession.

Age. Age of the Maiolica Formation: Latest Jurassic (late Tithonian) to Early Cretaceous (Berriasian–early Aptian). The level with the tracks can be considered between Berriasian and Hauterivian.

Meaning of name. The Latin adjective *marinus* refers to the impression of the trackway in a marine aquatic environment of the deep sea, and to the pelagic life conducted by the author of the tracks.

Description of the ichnospecies. The whole trackway configuration (Figure 8; Table 1) is a nearly straight line, with a very high step angle close to 180°, or at an angle of 180° or more (in one case equal to 180°. And, in another, more than 180°; min. 139°, max. 183°), and a very low external trackway width (mean ~ 26 cm, range 17–37 cm). The breadth between tracks (or inner width of the trackway) always has negative values. One observes an alternation of paces (or oblique paces) of approx. 50 cm on average (min. 30 cm, max. 70 cm), with a stride of approximately 100 cm on average (min. 74 cm, max. 123 cm). The trackway shows a slight convexity towards the current southeast direction in its proximal portion, then it becomes straighter. It seems to be the trackway of a marine tetrapod consisting of eleven imprints, with an irregularly sub-circular or elliptical shape. The imprints are generally characterized by a smooth and slightly concave surface at the deepest point of the track, for a good part of their width and for about 2–3 cm along the longitudinal direction (see above and Figure 9). The erosion and fracturing of the mycritic limestone and in particular some effects of karst make it difficult to draw in detail safely the outline of the prints, but there are some aspects that can be described and that are repeated in subsequent prints or at least in some of them.

Almost all of the anterior-posterior sections of the imprints have a "V" shape with respect to the layer surface, which originally represented the seabed surface (Figure 10). The anterior side (and in the direction of the animal's progression) of the prints is steeper than the posterior side (and in the opposite direction to that of the progression). On the opposite side, backwards, there are in some cases slight rims of pressure and displacement (prints 1–8).

Some prints (prints 2, 3, 5, 6, 8, 9), usually at their left margin (towards SE), have a tip, and a general appearance slightly pyriform. One other has this pointed aspect at the right margin (towards NW) (print 6). In this specimen the imprints are rather small (mean length and width 12.73 cm and 21.36 cm respectively; min. length 8 cm; max. length 16 cm; min. width 15 cm.; max. width 26 cm).

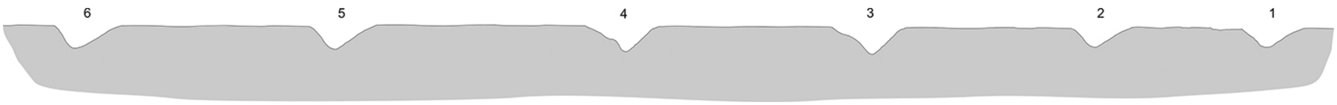

Figure 10. *Coneroichnus marinus* ichnog. et ichnosp. nov. Cross-section of the prints 1–6.

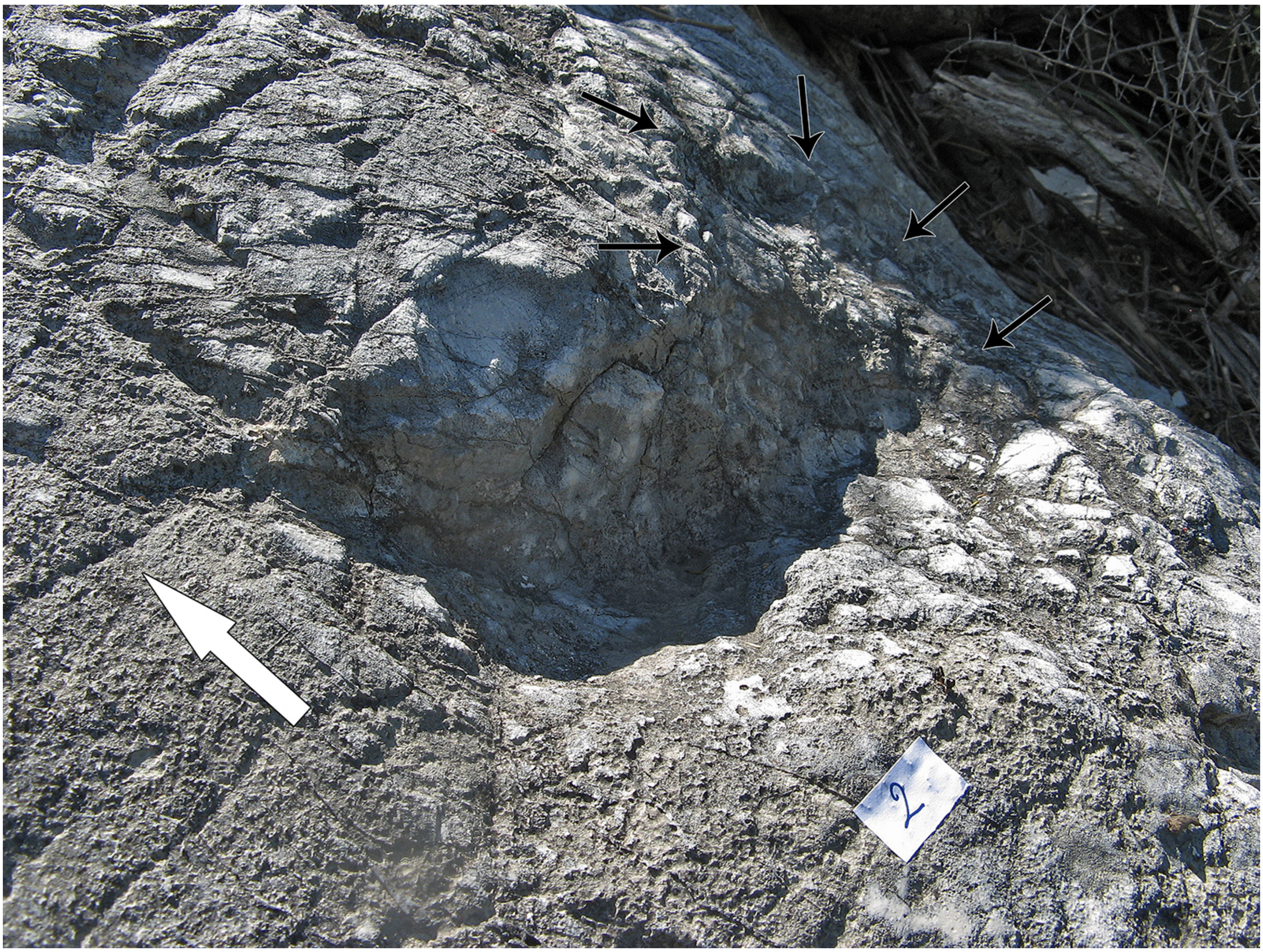

Figure 11. *Coneroichnus marinus* ichnog. et ichnosp. nov. Print 2. Note the piriform aspect of the print, with the tip to the left. The black arrows indicate the impression depending by the action of the limb pressing off the soft sediment and the consequent move forward (see also Figures 9 and 10). Direction of movement is shown by the white arrow.

In almost all prints, the longer axes are roughly parallel to each other, and they are inclined with an acute angle forward facing, compared to the midline of the trackway. This can be observed in Figures 4–7, while taking into account the perspective; and also, in Figure 8. The prints that present this phenomenon are those of number 1, 2, 3, 4, 5, 6, 7, 8, 10, 11 (10 cases out of 11); while the above-mentioned axes seem to be orthogonal to the midline in the numbered print 9. The sequence of tracks, especially if viewed in perspective as in Figure 4 looks like a fish-bone. The average angle of inclination of the long axes of the 11 tracks on the midline is 81°.

There is no groove or impression related to the tail or other parts of the trackmaker. Similarly, no furrows have been observed on Conero rocky slopes, that can be interpreted as foraging gutters, possibly produced by plesiosaurs or ichthyosaurs, which push their rostrum through the seabed ooze, in search of food, such as those reported from the Middle Jurassic (Callovian) of Liesberg, Switzerland (Geister, 1998; Zhang *et al*., 2014).

Remarks. The direction of animal movement, taking into account the morphology of the imprints, steep and deep in the front and less steep in the back, is to be understood from print 1 to 11, with an east-north-east west-south-west trackway orientation trend (Figure 8). This hypothesis is supported by the evident “coating” of the ancient plastic sediment, as mentioned above, present in the rear part of the print 3, and is evidence produced by the limb at the moment of the forward thrust, when, by kinetic action of the limb itself, a shift of the soft sediment towards the back was determined, *i.e*., in the opposite direction to the movement of the animal (Figure 9). In the front of prints 1 and 2 there are impressions that can be

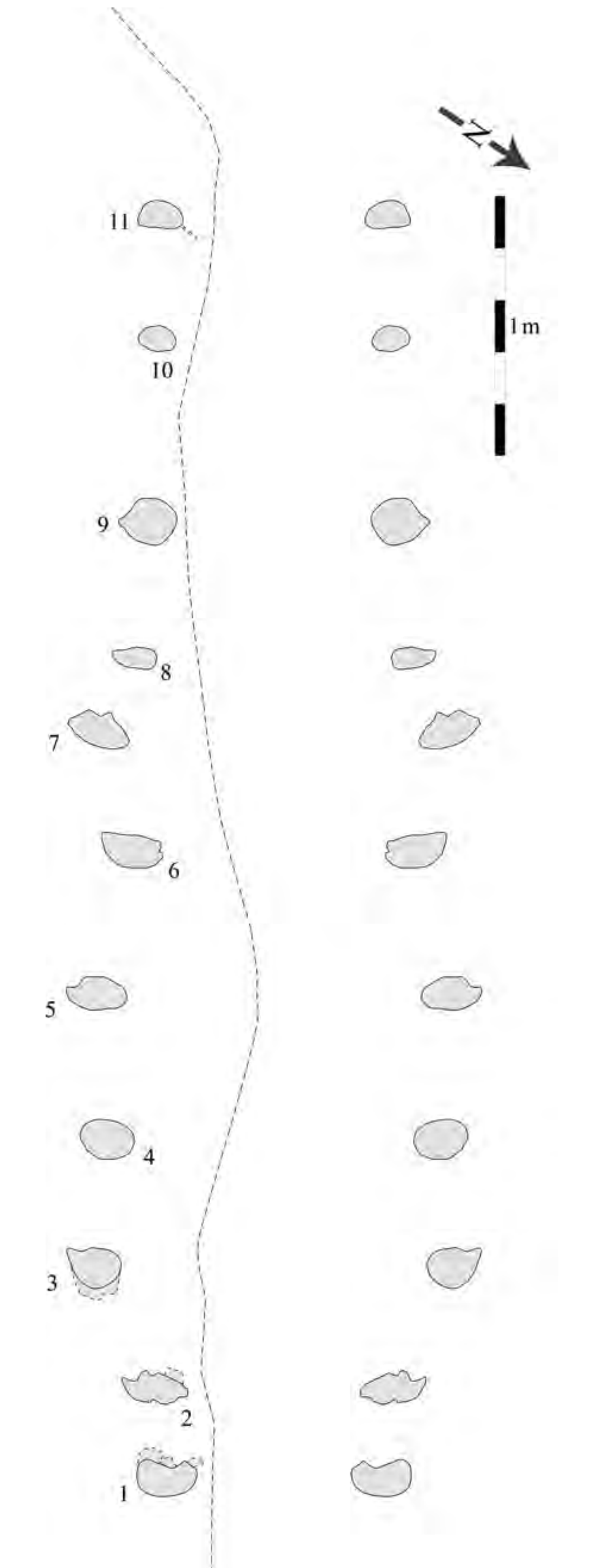

Figure 12. *Coneroichnus marinus* ichnog. et ichnosp. nov. The figure shows on the left the imprints preserved and probably impressed by the left front limb; while on the right the imprints that hypothetically could have been lost following the collapsing of the layer. The margin of the existing layer containing the imprints is shown in dashed lines.

interpreted as the action of the limb loading the soft sediment and the consequent movement forward (Figures 9 and 11). Laterally and in continuation to print 11, a smooth groove (about 8 cm long, about 1 cm wide) can be interpreted as a trace left by the animal at the moment of extraction of the paddle from the sediment (Figure 9).

However, the linearity and the very low width of the trackway, as well as the very high step angle as said before, creates some problems of interpretation. For example, the shape of the imprints of this trackway is rather similar to that of the imprints considered to pertain to the front limbs in the trackway found in Pliensbachian sediments about 5 km north of Cantiano, that is *Accordiichnus natans* Manni, Nicosia & Nobili, 1999 (Pesaro, Italy; Manni *et al*., 1999); even their dimensions are compatible with each other, even if those of Mount Conero are wider. And yet, while the step angle on the *Accordiichnus natans* track is very low (on average, for our calculation, 49°20'), the trackway step angle we are studying corresponds to almost 180°. The step angle, sometimes, in this case, has negative values (Table 1), *i.e*., it is >180°. That may seem strange, because, in a common trackway of continental tetrapods, without the logical upper limit of 180° for the step angle, as the speed increased, the animal would start to cross its legs and possibly stumble (Leonardi & Carvalho, 2021, p. 286-287). We could interpret the series of footprints that exist, such as those of the left side of the trackmaker, while those on the right side would have been destroyed by erosion, and would have fallen in the gully that is to the NW of the surface occupied by the preserved trackway. See Figure 12 how the complete trackway could have been, in this case.

DISCUSSION OF THE IDENTITY OF THE TRACKMAKER

At the passage between the Jurassic and Cretaceous, in the seas, lived several large vertebrate animals: bony fish, sharks and marine reptiles. The fish and many marine reptiles (ichthyosaurs and, at least in part, the marine crocodiles, besides some other diapsids) used the tail as their main propeller for swimming, whilst the fins were used mainly for stabilization and the changes of direction (Taylor, 1987; McGowan, 1992; Sedor *et al*., 2001; Silva *et al*., 2009; Zammit *et al*., 2013).

The only animals known to us that used fins as paddles for swimming, in the Early Cretaceous, and were able to produce prints similar to those found on the Mount Conero, were: the sea turtles (Gaillard *et al*., 2003; Avanzini *et al*., 2005; Lockley & Foster, 2006; Vila *et al*., 2014; Lichtig *et al*., 2018; Reolid *et al*., 2018), and the reptiles of the order Plesiosauria (Manni *et al*., 1999).

Sea turtles were generally relatively small in size (see *e.g*.: Avanzini *et al*., 2005; Lichtig *et al*., 2018), with some exceptions (see, *e.g*., Gaillard *et al*., 2003). All seem to have left a morphology of the trackway and each single footprint (usually with the signs of the nail scratches) such as to exclude those that may have been responsible for the traces of the study in question.

Manni *et al*. (1999) described, from the Pliensbachian layers of the Corniola Formation, a trackway about 3.20 m long, consisting of more than forty tracks, impressed by a marine reptile in a micritic sediment devoid of structures attributable to a shallow sea. This trackway was, partially and somehow, similar to that, this paper is talking about. Manni *et al*. (1999) demonstrated the possibility that tetrapod tracks were imprinted in the carbonate ooze of the seabed, and that these could be preserved over time. The microbial mats could, also in this case, have facilitated the impression and the conservation of tracks (Carvalho *et al*., 2013).

As for the marine crocodiles of the Late Jurassic or Early Cretaceous, the clade that in some way could be considered one of the candidates as makers of the trackway in question, is that of the Metriorhynchoidea (Middle Jurassic to Early Cretaceous; Toarcian, possibly up to early Aptian).

Specimens of this clade have been discovered in Italy such as *Neptunidraco ammoniticus* Cau & Fanti, 2011, a Bajocian–Bathonian pelagic metriorhynchid geosaurine (the so-called "Portomaggiore crocodile"; Leonardi, 1956; Cau & Fanti, 2011). It possibly includes also Lombard specimens (Delfino & Dal Sasso, 2006). However, the limbs of these pelagic metriorhynchid crocodiles, turned into paddles, all seem too short for the need.

After this examination, ichthyosaurs and plesiosaurs remain to be considered. The choice of the trackmaker, in this case, depends on the interpretation on the completeness, or not, of the tracks in question. In fact, if the trackway is to be considered completely preserved, then it is difficult to attribute it to a plesiosaur. These marine reptilians, in fact, seem to us too wide to be able to produce such a narrow track with such a high step angle; that, also if, less likely, they proceeded with the paddles under the body, in a vertical position or even facing inwards.

The track in question could then be produced by an ichthyosaur, an animal with a rather narrow and deep body, provided with rather long fins. As for the ichthyosaurs, it should be remembered here that these, although rare, are not unknown in Italy. Some few, often fragmentary or disarticulated, bones of Jurassic ichthyosaurs, and some other of the Early Cretaceous were found especially in the northern Apennines, in the provinces of Modena, Bologna and Parma (Sirotti & Papazzoni, 2002); a rostrum was also found in the Lessini mountains (Verona; Fornaciari *et al*., 2014).

It is especially interesting the presence, in the Province of Ancona, where the trackway in question was discovered, and in the Upper Jurassic terrains (upper Kimmeridgian–lowest Tithonian) of the so-called "ichthyosaur of Genga" (Fastelli & Nicosia, 1980; De Marinis & Nicosia, 2000), an Ophthalmosauridae, *Gengasaurus nicosiai* Paparella, Maxwell, Cipriani, Roncacè & Caldwell, 2017 (Paparella *et al*., 2017). This almost complete specimen was found, during the excavation of a road tunnel, near Genga (Ancona, Marche, Italy), in the territory of the village of Camponocecchio.

It comes from the 'Calcari ad aptici e Saccocoma' Formation, dated to the late Kimmeridgian–earliest Tithonian. This formation corresponds to a pelagic environment, from a sea whose bed had variable depth, with ups and downs (Paparella *et al*., 2017); and is located, from the stratigraphical point of view, just below the Maiolica Formation, from whose bottom comes the trackway that is the subject of this paper.

The presence of remains of ichthyosaurs in Italy and also specifically in the Marche region put ichthyosaurs among the possible authors of the tracks in study. And yet, ichthyosaurs are believed to have used the tail as propeller, and the fins were used for balance and direction.

It may be suggested that the trackway referred to corresponds to the left side of the trackway, and that its right side would have been collapsed with a portion of the layer in the gully NW of the surface occupied by the preserved trackway. If that is the way it is, then we would have a completely different, double-sided trackway, that could be produced by an animal much more fully built, flat-bodied. In this case, the trackmaker, in Early Cretaceous pelagic rocks, could be found among the plesiosaurians, obligate aquatic sauropterygian. We therefore suggest that the most likely trackmaker of the trackway of Mount Conero, is a marine reptile of the clade of Plesiosauria de Blainville, 1835 and specially Pliosauroidea Welles, 1943.

The remains of Italian plesiosaurians are rather rare, despite the area corresponding to present Italy being occupied mainly by marine environments of the Tethys during the Mesozoic. On the other hand, the bony remains of plesiosaurians are rare not only in Italy, but in all southern Europe (Welles, 1943).

As for Italy, we can remember the discovery of an isolated right humerus of a juvenile Pliosauridae from the Santonian–Campanian of Varzi, Pavia Province (Renesto, 1993; Dalla Vecchia *et al*., 2005); one isolated tooth, was also attributed to a pliosaurid from the stratigraphic unity Argille Varicolori, Cenomanian–Campanian of Castelvecchio di Prignano, Modena (Dalla Vecchia *et al*., 2005); some vertebrae were attributed to indeterminate plesiosaurians from the Sette Comuni Plateau (Vicenza; Aptian–Turonian; Dalla Vecchia *et al*., 2005). But, above all, there is the skeleton of a pliosaurid Plesiosauria from Mount Kaberlaba (Asiago, Vicenza), Red Ammonite Formation, Middle Jurassic (Cau & Fanti, 2014). To this clade we attribute with greater confidence the author of the tracks of *Coneroichnus marinus* ichnog. et ichnosp. nov.

To realize a reasonable scenario of environmental reconstruction, we choose to represent, in an open-sea underwater environment, a pliosaurid Plesiosauria. The pliosaurid, illustrated here (Figure 13), as hypothetical author of *Coneroichnus marinus* ichnog. et ichnosp. nov., is inspired by *Leptocleidus* Andrews, 1922 (White, 1940; Ketchum & Benson, 2010, 2011; Benson & Druckenmiller, 2014; Quesada *et al*., 2019), a plesiosaur with a rather short neck, whose fossil remains have been found also in Italy (Cau & Fanti, 2014). Nothing, however, excludes that it was another plesiosaurid (such as *Brancasaurus* Wegner, 1914 which is seen in the background on the right, a typical plesiosaur with a long neck) or another pliosaurid (Wegner, 1914; Cruickshank, 1997; Ketchum & Benson, 2010, 2011).

Figure 13. The image shows marine reptiles of the order Plesiosauria, on the seabed of the Tethys Ocean. The plesiosaur shown here in the foreground, together with the one on the left, is inspired by *Leptocleidus*, a short-necked plesiosaur, as an example of the supposed author of the trackway under study. In the background on the right side, one sees another plesiosaurid: *Brancasaurus*, a typical long-necked plesiosaur, another hypothetical author of the trackway. Art by Marco Astracedi.

CONCLUSIONS

In the present paper we have allocated from an ichnotaxonomical and ichnological point of view a trackway, from deep pelagic environment, on the seabed of the Tethys Ocean, which then became a limestone bank of the Maiolica Formation, of the Berriasian–Hauterivian, Early Cretaceous of Mount Conero (Sirolo, Marche, Italy). We have updated the most likely stratigraphic position of the outcrop bearing the sequence of tracks; we have assigned to them the name of *Coneroichnus marinus* ichnog. et ichnosp. nov.

We concluded that its gait can be defined as the half-swimming manner of gait, that is the exploratory and propulsive contact swimming with the mud saturated with water on the bottom. Since this kind of underwater progression happens, in this specific case, in contact with the sea bottom, it was here also defined as a punting and foraging manner of gait.

Only two other tracksites with tracks attributed to fossil marine reptiles had been so far found in sediments from the deep seabed paleoenvironment, not only in Italy, but in the entire world. Mount Conero is the third ichnosite in the world with deep-marine fossil trackways. It will be useful to carry out more intense research along all the outcrops of Maiolica at Mount Conero and along the Adriatic Sea, but also in other areas, on tabular surfaces of layers not too eroded, looking for other specimens of marine reptile tracks like these or similar to them.

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REFERENCES

Andrews, C.W. 1922. Description of a new plesiosaur from the Weald Clay of Berwick (Sussex). *Quarterly Journal of the Geological Society*, **78**:285–298. *doi:10.1144/GSL.JGS.1922.078.01-04.11*

Avanzini, M.; García-Ramos, J.C.; Lires, J.; Menegon, M.; Piñuela, L. & Fernandez, L.A. 2005. Turtle tracks from the Late Jurassic of Asturias, Spain. *Acta Palaeontologica Polonica*, **50**:743–755.

Benson, R.B.J. & Druckenmiller, P.S. 2014. Faunal turnover of marine tetrapods during the Jurassic-Cretaceous transition. *Biological Reviews*, **89**:1–23. *doi:10.1111/brv.12038*

Carvalho, I.S.; Borghi, L. & Leonardi, G. 2013. Preservation of dinosaur tracks induced by microbial mats in the Sousa Basin (Lower Cretaceous), Brazil. *Cretaceous Research*, **44**:112–121. *doi:10.1016/j.cretres.2013.04.004*

Cau, A. & Fanti, F. 2011. The oldest known metriorhynchid crocodylian from the Middle Jurassic of North-eastern Italy: *Neptunidraco ammoniticus* gen. et sp. nov. *Gondwana Research*, **19**:550–565. *doi:10.1016/j.gr.2010.07.007*

Cau, A. & Fanti, F. 2014. A pliosaurid plesiosaurian from the Rosso Ammonitico Veronese Formation of Italy. *Acta Palaeontologica Polonica*, **59**:617–634. *doi:10.4202/app.2012.0117*

Centamore, E. & Deiana, G. 1986. *La Geologia delle Marche*. Studi Geologici Camerti, special volume, 145 p.

Centamore, E. & Micarelli, A. 1991. *Stratigrafia*. In: *L'ambiente Fisico delle Marche: geologia – geomorfologia – idrogeologia*, Giunta regionale, Assessorato urbanistico – ambiente, Firenze, S.E.L.C.A, p. 5–58.

Coccioni, R.; Moretti, E.; Nesci, O.; Savelli, D.; Tramontana, M. & Veneri, F. 1997. *Carta Geologica del Monte Conero con itinerari geologico-escursionistici*. Parco Naturale del Conero, Carta Geologica a colori, scala 1:20.000. Firenze, S.E.L.C.A.

Cruickshank, A.R.I. 1997. A Lower Cretaceous Pliosauroid from South Africa. *Annals of the South African Museum*, **105**:207–226.

Dalla Vecchia, F.M. *et al*. 2005. Il Cretaceo Marino. *In*: L. Bonfiglio (ed.) *Paleontologia dei Vertebrati in Italia. Evoluzione biologica, significato ambientale e paleogeografia*, Memorie del Museo Civico di Storia Naturale di Verona, Vo. 2, sezione Scienze della Terra, p. 101–116.

de Blainville, H.M.D. 1835. Description de quelques espèces de Reptiles de la Californie, précédée de l'analyse d'une système général d'erpétologie et d'amphibiologie. *Nouvelles Annales du Muséum d'Histoire naturelle*, **4**:233–296.

De Marinis, G. & Nicosia, U. 2000. *L'Ittiosauro di Genga*. Castelferretti, Ancona, Cassa di Risparmio di Fabriano e Cupramontana Edizioni, 220 p.

Deiana, G.; Pierantoni, P.P.; Centamore, E. & Cantalamessa, G. 2002. *Cartografia Geologica – Nota illustrativa*. Progetto n. 2 – Zona Sud (Realizzazione della Cartografia Geologica e Geotecnica e dei relativi supporti informatici alla scala 1:10000. Ancona, Regione Marche, Servizio urbanistico e cartografia.

Delfino, M. & Dal Sasso, C. 2006. Marine reptiles (Thalattosuchia) from the Early Jurassic of Lombardy (northern Italy). *Geobios*, **39**:346–354. *doi:10.1016/j.geobios.2005.01.001*

Fastelli, C. & Nicosia, U. 1980. L'Ittiosauro di Genga (Ancona). In: G. Parisi & G. Seppi (eds) *I vertebrati fossili italiani*, Catalogo della Mostra, p. 95–101.

Fornaciari, B.; Maxwell, E.E.; Zorzin, R. & Papazzoni, C.A. 2014. *A new Platypterygius rostrum from the Lower Cretaceous of Lessini Mts (N Italy)*. *In*: EUROPEAN ASSOCIATION OF VERTEBRATE PALAEONTOLOGISTS MEETING, 12, 2014. *Abstract Book*, Torino, p. 62.

Gaillard *et al*. 2003. A giant Upper Jurassic turtle revealed by its trackways. *Lethaia*, **36**:315–322. *doi:10.1080/00241160310004611*

Geister, J. 1998. Lebensspuren von Meersauriern und ihren Beutetieren im mittleren Jura (Callovien) von Liesberg, Schweiz. *Facies*, **39**:105–124. *doi:10.1007/BF02537013*

Ketchum, H.F. & Benson, R.B.J. 2010. Global interrelationships of Plesiosauria (Reptilia, Sauropterygia) and the pivotal role of taxon sampling in determining the outcome of phylogenetic analyses. *Biological Reviews*, **85**:361–392. *doi:10.1111/j.1469-185x.2009.00107.x*

Ketchum, H.F. & Benson, R.B.J. 2011. A new pliosaurid (Sauropterygia, Plesiosauria) from the Oxford Clay Formation (Middle Jurassic, Callovian) of England: Evidence for a gracile, longirostrine grade of Early-Middle Jurassic pliosaurids. *Special Papers in Palaeontology*, **86**:109–129.

Leonardi, G. (ed.). 1987. *Glossary and Manual of Tetrapod Imprint Palaeoichnology*. Brasília, Departamento Nacional de Produção Mineral, 117 p.

Leonardi, G. & Carvalho, I.S. 2021. *Dinosaur Tracks from Brazil – A Lost World of Gondwana*. Bloomington, Indiana University Press, 455 p.

Leonardi, P. 1956. Notizie preliminari sul "Coccodrillo di Portomaggiore". *Bollettino della Società Geologica Italiana,* **75**:88–90.

Lichtig, A.J.; Lucas, S.G.; Klein, H. & Lovelace, D.M. 2018. Triassic turtle tracks and the origin of turtles. *Historical Biology*, **30**:1112–1122. *doi:10.1080/08912963.2017.1339037*

Lockley, M.G. & Foster, J.R. 2006. Dinosaur and turtle tracks from the Morrison Formation (Upper Jurassic) of Colorado National Monument, with observations on the taxonomy of vertebrate swim tracks. *New Mexico Museum of Natural History and Science Bulletin*, **36**:193–198.

Manni, R.; Nicosia, U. & Nobili, G. 1999. An unusual tetrapod trackway from Lower Jurassic marine sediments of Central Italy: *Accordiichnus natans* n. ichnogen., n. ichsp. *Geologica Romana*, **35**:167–187.

McGowan, C. 1992. The ichthyosaurian tail: sharks do not provide an appropriate analogue. *Palaeontology*, **35**:555–570.

Micarelli, A.; Potetti, M. & Chiocchini, M. 1977. Ricerche microbiostratigrafiche sulla Maiolica della Regione umbro-marchigiana. *Studi geologici Camerti*, **3**:57–86.

Montanari, A. & Koeberl, C. 2000. *Impact Stratigraphy: The Italian Record*. Heidelberg, Springer Verlag, 364 p.

Natali, L. 2022. *SIRO e il mistero delle sue impronte. La scoperta sul Monte Conero delle orme di un antico rettile marino*. Macerata, Edizioni Simple, 52 p.

Natali, L.; Blasetti, A. & Crocetti, G. 2019. Detection of lower Cretaceous fossil impressions of a marine reptile on Monte Conero (Central Italy). *Cretaceous Research*, **93**:143–150. *doi:10.1016/j.cretres.2018.09.014*

Paparella, I.; Maxwell, E.E.; Cipriani, A.; Roncacè, S. & Caldwell, M.W. 2017. The first ophthalmosaurid ichthyosaur from the Upper Jurassic of the Umbrian-Marchean Apennines (Marche, Central Italy). *Geological Magazine*, **154**:837–858. *doi:10.1017/S0016756816000455*

Quesada, J.M.; Pérez-García, A.; Gasulla, J.M. & Ortega, F. 2019. Plesiosauria remains from the Barremian of Morella (Castellón, Spain) and first identification of Leptocleididae in the Iberian record. *Cretaceous Research*, **94**:8–24. *doi:10.1016/j.cretres.2018.10.010*

Renesto, S. 1993. A Cretaceous plesiosaur remain (Reptilia, Sauropterygia) from the Argille Varicolori of Varzi (Pavia, Lombardy, Northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, **99**:101–106. *doi:10.13130/2039-4942/8947*

Reolid, M.; Márquez-Aliaga, A.; Belinchón, M.; García-Forner, A.; Villena, J. & Martínez-Pérez, C. 2018. Ichnological evidence of semi-aquatic locomotion in early turtles from eastern

Iberia during the Carnian Humid Episode (Late Triassic). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **490**:450–461. *doi:10.1016/j.palaeo.2017.11.025*

Sedor, F.A.; Costa, R. & Leonardi, G. 2001. Icnofósseis de Mesosauridae (Proganosauria) na Formação Irati (Neopermiano da Bacia do Paraná), Estado do Paraná, Brasil. *In*: CONGRESSO BRASILEIRO DE PALEONTOLOGIA, 17, 2001. *Boletim de resumos*, Rio Branco, p. 22.

Silva, R.C. da; Sedor, F.A. & Fernandes, A.C.S. 2009. Ichnotaxonomy, functional morphology and paleoenvironmental context of Mesosauridae tracks from Permian of Brazil. *Revista Brasileira de Geociências*, **39**:705–716.

Sirotti, A. & Papazzoni, C. 2002. On the Cretaceous ichthyosaur remains from the Northern Apennines (Italy). *Bollettino della Società Paleontologica Italiana*, **41**:237–248.

Taylor, M.A. 1987. A reinterpretation of ichthyosaur swimming and buoyancy. *Palaeontology*, **30**:531–535.

Vila, B.; Castanera, D.; Marmi, J.; Canudo, J.I. & Galobart, À. 2014. Crocodile swim tracks from the latest Cretaceous of Europe. *Lethaia*, **48**:256–266. *doi:10.1111/let.12103*

Wegner, T. 1914. Brancasaurus brancai *n. g. n. sp., ein Elasmosauride aus dem Wealden Westfalens*. Berlin, Bornträger, p. 235–305.

Welles, S.P. 1943. Elasmosaurid plesiosaurs with a description of the new material from California and Colorado. *Memoirs of the University of California*, **13**:125–254.

White, T.E. 1940. Holotype of *Plesiosaurus longirostris* Blake and classification of the plesiosaurs. *Journal of Paleontology*, **14**:451–467.

Zhang *et al*. 2014. Nothosaur foraging tracks from the Middle Triassic of southwestern China. *Nature*, **3973**:1–12. *doi:10.1038/ncomms4973*

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