# Turtle tracks from the Late Jurassic of Asturias, Spain

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Although tracks of dinosaurs are well known from Upper Jurassic sediments, tracks of non-dinosaurian vertebrates are fairly rare. The Upper Jurassic Lastres Formations of Asturias in northern Spain contain many vertebrate tracksites that include footprints and trackways of non-dinosaurian tetrapods. Several of these tracks are natural casts of pentadactyl to tridactyl footprints with digits connected by arched structures. The digits are short with deep scratch marks oriented anteriorly. The Asturian tracks show a high degree of morphological similarity to other specimens previously described as possible turtle tracks. Observations from extant turtle trackways show some surprising similarities with the fossil material. The tracks are here interpreted as having been made by turtles partially buoyed by water or by turtles walking in a slightly wet subaerial environment.

Key words: Testudines, turtle tracks, gait pattern, experimental ichnology, Jurassic, Asturias.

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## Introduction

The Upper Jurassic Vega, Tereñes, and Lastres Formations of Asturias in the northern Spain contain many vertebrate tracksites. These sites preserve tracks of a wide variety of vertebrate taxa. Most are of dinosaurs, but several sites include tracks of pterosaurs, crocodilians, and probable lizards (García-Ramos et al. 2002). Although tracks of dinosaurs are well known from Upper Jurassic sediments, tracks of non-dinosaurian vertebrates are fairly rare. To date, only a few possible turtle tracks have been reported from Germany, France, and the USA (Nopcsa 1923; Bernier et al. 1982; Bernier et al. 1984; Lockley 1991; Thulborn 1989, 1990; Foster et al. 1999; Wright and Lockley 2001).

The specimens described herein were quarried from several ichnosites located along the Asturian coast near the towns of Quintueles, Oles, Tazones (Villaviciosa), and Luces (Colunga) (Fig. 1).

The tracks are preserved in the Upper Jurassic Lastres Formation. This unit, more than 300 m thick is represented by multiple intercalations of light grey to light orange-brown sandstones and siltstone, marls, and black shales related to a freshwater deltaic system at the margin of a shallow sea. Remarkable examples of depositional sequences are shown in the deltaic model including prodelta, distal bar, distributary mouth-bars, channel, and levee, interdistributary bay, swamp, as well as the typical delta abandonment facies. Sedimentation was repeatedly interrupted by local or more widespread but small trangsressive events recorded by laterally extensive shell beds. The more representative faunal assemblage is dominated by some gastropods and abundant bivalves. Rare ammonoids allow dating this formation as lower and upper Kimmeridgian (Aramburu and Bastida 1995).

*Institutional abbreviations*.—Some fossil specimens have been deposited in the Museo del Jurásico de Asturias (MUJA) near Colunga, Oviedo, Asturias, Spain, while the main slab has not been removed from the field.

*Terminology*.—The terms concerning vertebrate palaeoichnology mainly follow Leonardi (1987). To avoid repetition in the systematics, the authors and years of publication of the ichnotaxa will only be listed at the first mention. L, footprint length; W, footprint width.

## Track descriptions

The tracks are preserved as natural casts on a large sandstone slab (100 × 70 cm) that was left *in situ* (Figs. 2, 3C–H), on smaller siltstone slabs (Fig. 3A, B) and on some wide sandstone or siltstone blocks that were also left *in situ* (Figs. 3I, J, 4, 5B, D, E).

The tracks are tridactyl to pentadactyl footprints consisting of distinct digit traces connected by arched structures.

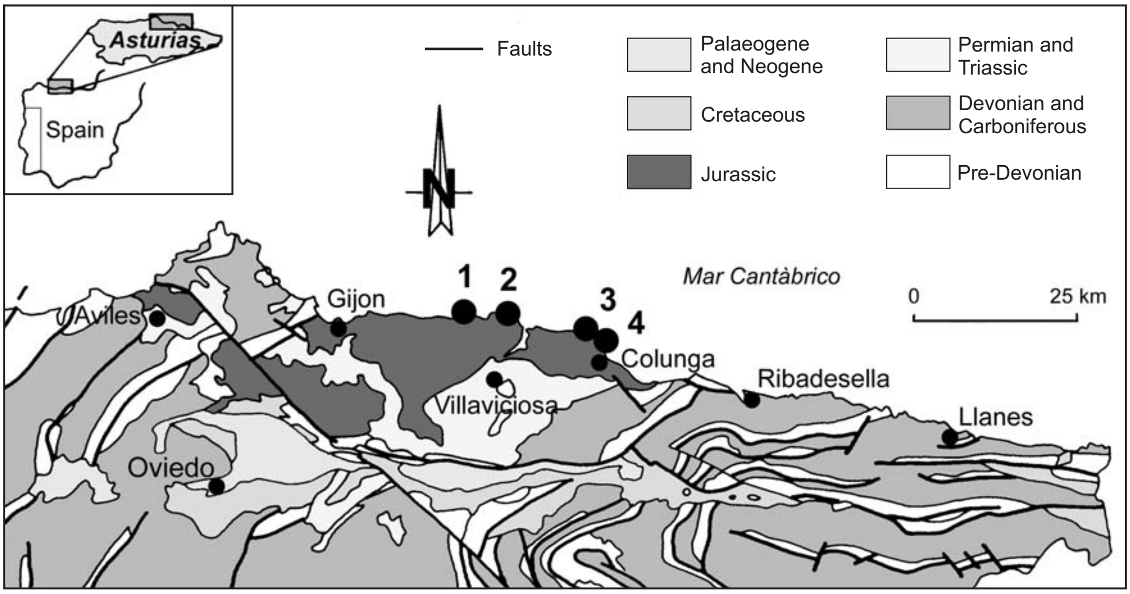


Fig.1. Schematic map showing the location of the Oles (1), Quintueles (2), Tazones (3), and Luces (4) ichnosites where the tracks were discovered.

The digit (or claw) impressions are oriented more or less anteriorly with little divarication. In some specimens, the digit impressions end with deep scratch marks.

Individual footprints range from 1.5 to 7 cm in width and from 1 to 4.5 cm in length. The depth of the tracks is generally 0.5–1 cm.

The sandstone slab of Quintueles (*in situ*) (Fig. 2) contains at least eight consecutive manus-pes sets (Fig. 3C–E). Other, randomly distributed tracks on the same surface are also recognisable (Fig. 3F–H). The consecutive manus-pes sets constitute a trackway of a single individual, while the isolated tracks probably represent a second individual (or more) moving in the same direction. In the trackway, the claws form the deepest part of the imprints. The imprint's posterior portion is transverse and perpendicular to the claw axes. The manus is digitigrade and exhibits 3 or 4 claw marks connected by a shallow and arched depression (L = 1–3 cm, W = 3–4 cm) (Figs. 3C, E, 5C). The claw marks of some prints were only slightly impressed into the substrate, resulting in a manual print consisting of an arched impression with four or five rounded anterior depressions (Figs. 3D, G, 5D). Digits II–IV are well defined in several prints. Digit III is the longest; digits II and IV are more or less equal in length, whereas digits I or V are the shortest in the manus. The pedal prints are characterised by 3 or sometimes 4 wide claw marks (Fig. 3C–E, H). The prints are generally digitigrade and the claw marks are nearly parallel and of the same length (L = 1.5–2.5 cm, W = 2.5–4 cm). The trackway is 27 cm wide, with an alternate pace angle that varies between 55 to 60° a pace length of 24 cm, and a stride of 20 cm. The manual prints are medial to the pedal prints. Manus and pes are oriented forward. The pedal digits are parallel to the midline while the ungual marks of the manus are rotated inwards or outwards. Other tracks consist of elongate scratch marks occurring in groups of 3 or 4.

Small isolated prints from the Luces outcrops (MUJA 654) show differing dimensions and morphology (Figs. 3A, B, 5E). The tracks are smaller than those described above. In these specimens, only the ungual scratch marks are well recognisable. The best-preserved manual print is 1.4 cm long and 1.8 cm wide (MUJA 654) (Fig. 3A). The four manual digits are slightly curved and deeply impressed into the substrate, while the pedal print (L = 1.5 cm, W = 1.5 cm) show only three deep and parallel ungual marks (Fig. 3B).

Three larger specimens are preserved on a wide sandstone block (*in situ*) in the Oles bay outcrops (Figs. 3I, J, 5A, B). The first one (Figs. 3I, 5A) consists of a semiplantigrade manual print with four well-developed ungual tracks (L = 5 cm, W = 7 cm). The second one consists of a manus-pes set (Fig. 3J). The manual print is semiplantigrade with four ungual impressions (L = 2.5 cm, W = 5.5 cm) and similar to the above mentioned manual print from the same locality. The pedal print is plantigrade and wider than long (L = 4.5 cm, W = 5.5 cm). The three digits (II–IV) are anteriorly oriented, little divaricated (II–IV = 60°), and connected by a rounded pad. The digit III shows a triangular robust claw. The third footprint is a plantigrade pedal print (Fig. 5B) with four ungual marks (II and III of similar length and I and IV shorter and divergent). Two other slabs with evident scratch marks come from Oles (Fig. 4) and Tazones (Villaviciosa) (Fig. 5F) bay outcrops. On the Oles sandstone slab (Fig. 4), among several scratch marks randomly oriented, a manus-pes set is well preserved. The manual print (W = 4 cm) shows four parallel ungual marks 9 cm long, the pedal print (L = 2 cm, W = 3.5 cm) shows instead three stouter and shorter ungual marks connected by a fleshy pad. The tracks from Tazones are constituted by several parallel furrows in which there is no difference between manual and pedal prints (Fig. 5F).

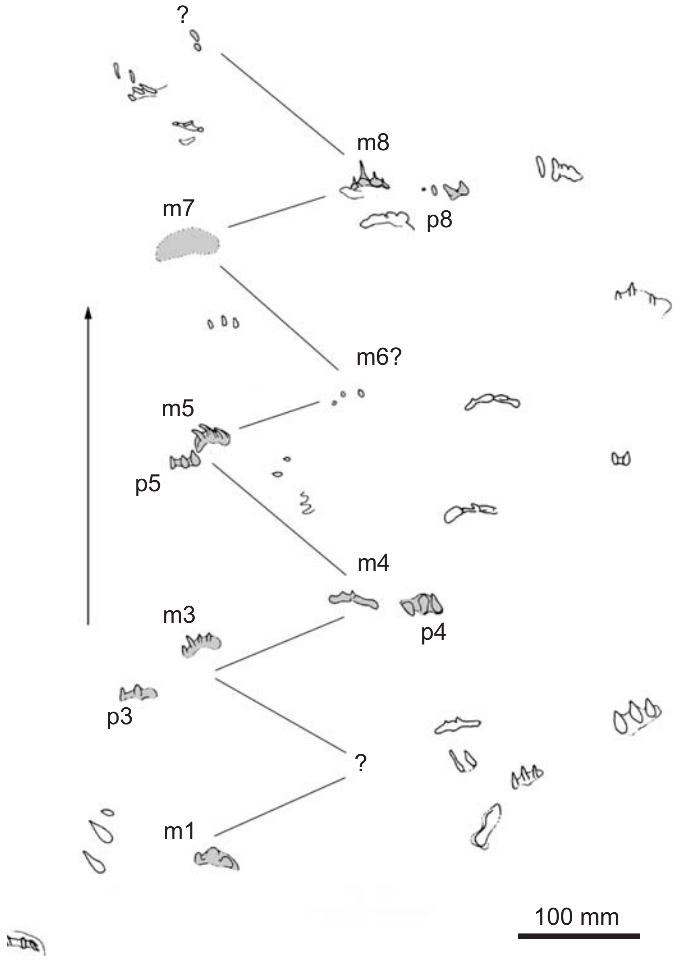


Fig. 2. Schematic drawing of the tracks from the Quintueles cliffs (Villaviciosa) site (m, manual print; p, pedal print). Specimen left in the outcrop.

# Ichnotaxonomy

The tracks were left by a quadrupedal animal with sharp claws, wide gait, and five-toed hind limbs. No dinosaur could have left these tracks and they are very different from lizard-like tracks, such as *Rhynchosauroides*, or from tracks of amphibians and crocodilians (Haubold 1984). Several purported half-swimming dinosaurs tracks show tridactyl scratch marks similar to some of the Asturian tracks (Leonardi, 1987; Romano and Whyte 2003), however, tetradactyl or pendadactyl short and symmetric traces have never been attributed to dinosaurs. *Rhynchosauroides* manus and pes are pentadactyl and asymmetric. The length of the digits increases from I to IV and the digit V is rotated outwards; very different to those of the specimens here described. Amphibians have tetra- or pentadactyl manus and pentadactyl pes with rounded tips of digits, generally without claw marks (Haubold 1984). Crocodilians could have left tracks with pronounced scratch marks. The main characteristic of the crocodilians footprints, however, is in having digit III as the longest and a pronounced heteropody. The manus is much smaller than the pes, has five toes and is usually rotated so that digit II points forward, digit IV laterally and digit V posteriorly. The pes is functionally tetradactyl and digitigrade, outwardly rotated; so very different to the short and symmetric footprints here described (Avanzini et al. in press).

The only animals that could have made the tracks described herein are turtles.

Ichnotaxonomy and interpretation of purported turtle tracks is confused (Moratalla et al. 1995). Schimper (1850) described as *Chelonichnium vogesiacum* a single tridactyl footprint from the Lower Triassic of Germany (Mittlere Buntsandstein) later declared a *nomen dubium* by many authors (Abel 1935; Haubold 1971a). Walther (1904) reported a trackway, which he named *Ichnium megapodium*, from

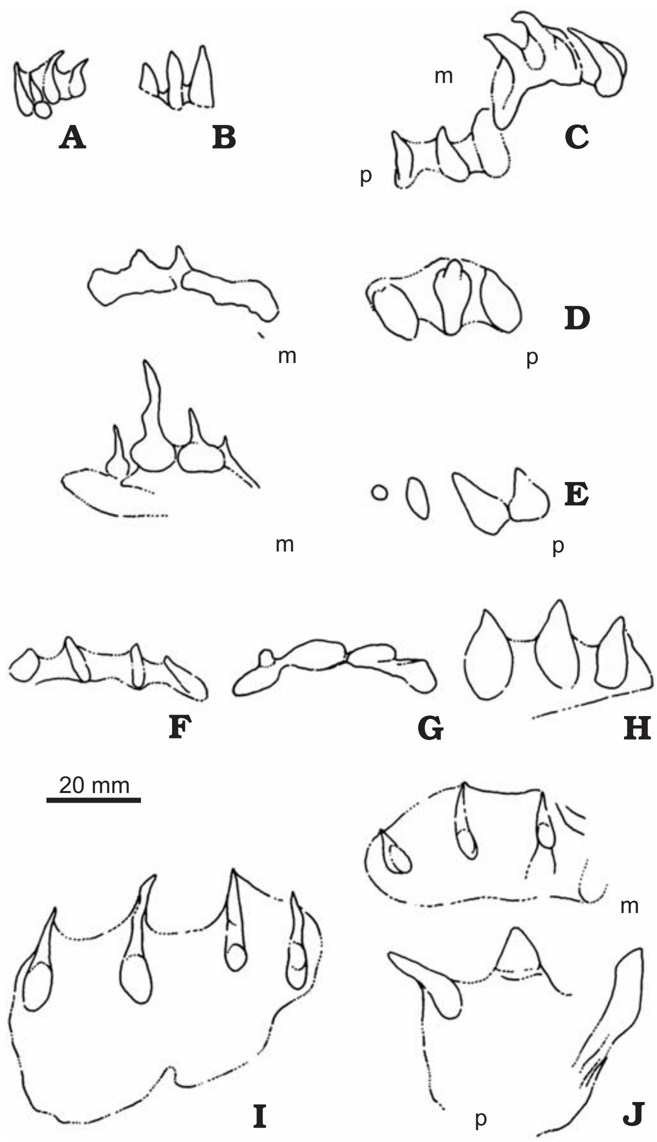


Fig. 3. Turtle tracks from the Late Jurassic of Asturias. **A**. Manual print from Luces cliffs (Colunga) (MUJA 654). **B**. Pedal print from from Luces cliffs (Colunga) (MUJA 654). **C**–**H**. Prints from the main ichnoassemblage at Quintueles cliffs (Villaviciosa), manus-pes sets (**C**–**E**), manual prints (**F**, **G**), pedal print (**H**). **I**. Manual print from Oles ichnosite. **J**. Manus-pes set from Oles ichnosite (m, manual print; p, pedal print). C–J, left in the outcrop.

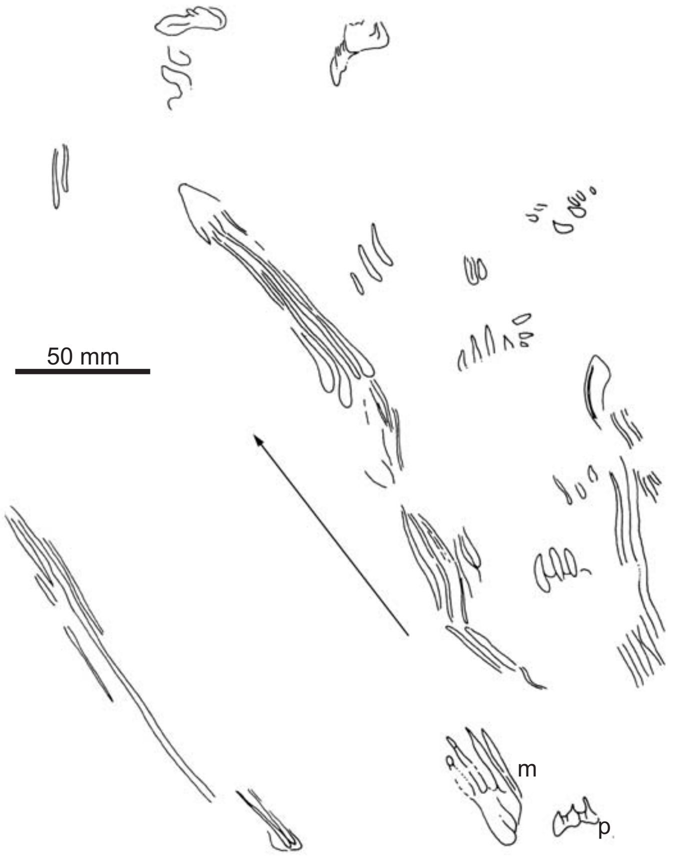


Fig. 4. Schematic drawing of a surface with evident scratch marks from Oles. A manus-pes set is recognisable (m, manual print; p, pedal print). Specimen left in the outcrop.

lithographic limestone of Solnhofen. These were later renamed *Emydichnium* by Nopcsa (1923) and attributed to swimming turtles. The validity of the *Emydichnium* ichnogenus was discussed by Seilacher (1963), who interpreted these as roll marks produced by ammonites. Although there are doubts about the origin of many purported verebrate traces in the Solnhofen limestone, the possibility of turtle tracks presence was not ruled out by Moratalla et al. (1995).

In 1939 Rühle von Liliestern named three different trackways from the Lower Triassic "Thüringischer Chirotheriumsandstein" of Europe *Chelonipus torquatus*, *Chelonipus cuneiformis*, and *Agostropus falcatus*. Of these, *Chelonipus torquatus* and *Chelonipus cuneiformis* are considered synonyms by Kuhn (1958) and the ichnogenus is diagnosed (Haubold 1971b) by its trackway width (up to 25 cm), a pace angle of 50–70°, digitigrade or semiplantigrade pes (L = 2 cm, W = 5.5 cm) with three or four digits with thin claws, manus (L = 2 cm, W = 4 cm) with four well recognisable digits which are shorter than those of the foot and connected by a fleshy, arched structure. The trackway shows an apparent oversteps with the pedal print of phase III that is placed away the manual print of the phase I (Figs. 6B, 7A). *Agostropus* is represented by only two pentadactyl small (L = 5 cm; W = 4.8 cm) footprints. Their interpretation as chelonians was discussed by Smith (1959) and Haubold (1971a, b) who reinterpreted them as theriomorph footprints and considered *Agostropus falcatus* as a junior synonym of *Dicynodontipus geinitzi* Hornstein, 1876. Haubold (1971a) confirmed the synonymy of *Chelonipus torquatus* and *Chelonipus cuneiformis* (Fig. 6G–I) and described as *Chelonipus plieningeri* a further trackway recognised but not named by Plieninger (1838) from the Upper Triassic (Mittlere Keuper) of Germany (Fig. 6F).

In 1982, a trackway of a large turtle was described and named *Chelonichnium cerinense* by Demathieu and Gaillard (in Bernier et al. 1982) from the Upper Jurassic lithographic limestone of Cerin (France) (Fig. 6J). *Chelonichnium* was used despite the fact that it has already been declared a *nomen*

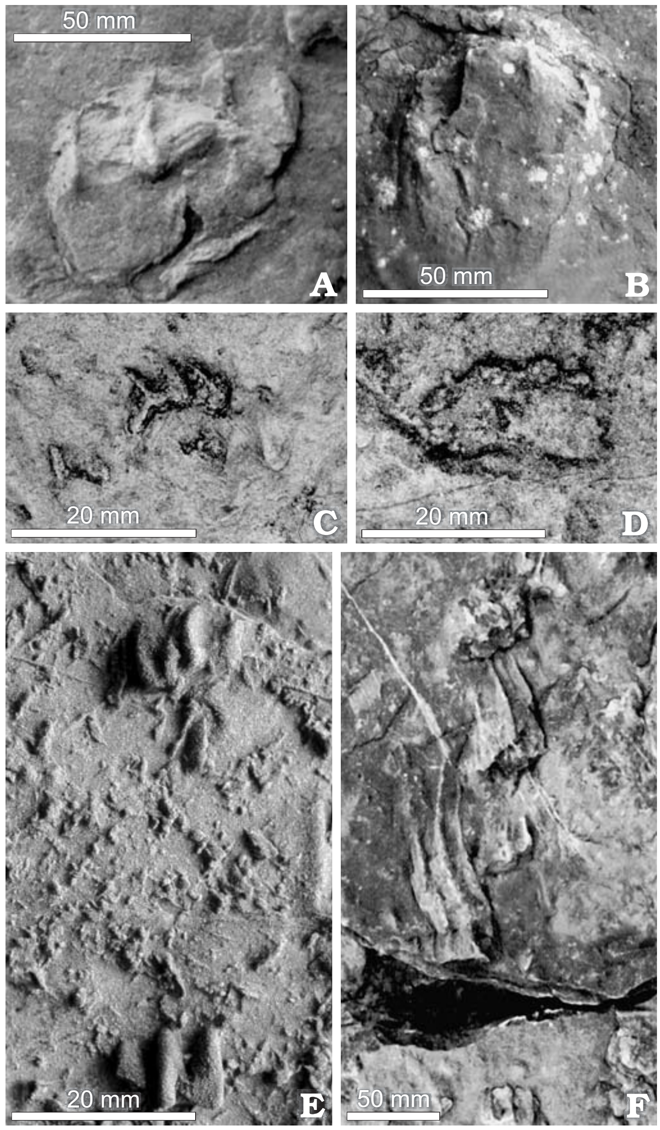


Fig. 5. Turtle tracks from the Late Jurassic of Asturias. **A**. Manual print from Oles. **B**. Pedal print from Oles. **C**. Manus-pes set from the main ichnoassociation at Quintueles cliffs (Villaviciosa). **D**. Manual print from the main ichnoassociation at Quintueles cliffs (Villaviciosa). **E**. Manus-pes set from Luces cliffs (Colunga) (MUJA 654). **F**. Scratch marks from Tazones (Villaviciosa). A–D, F, left at the outcrops.

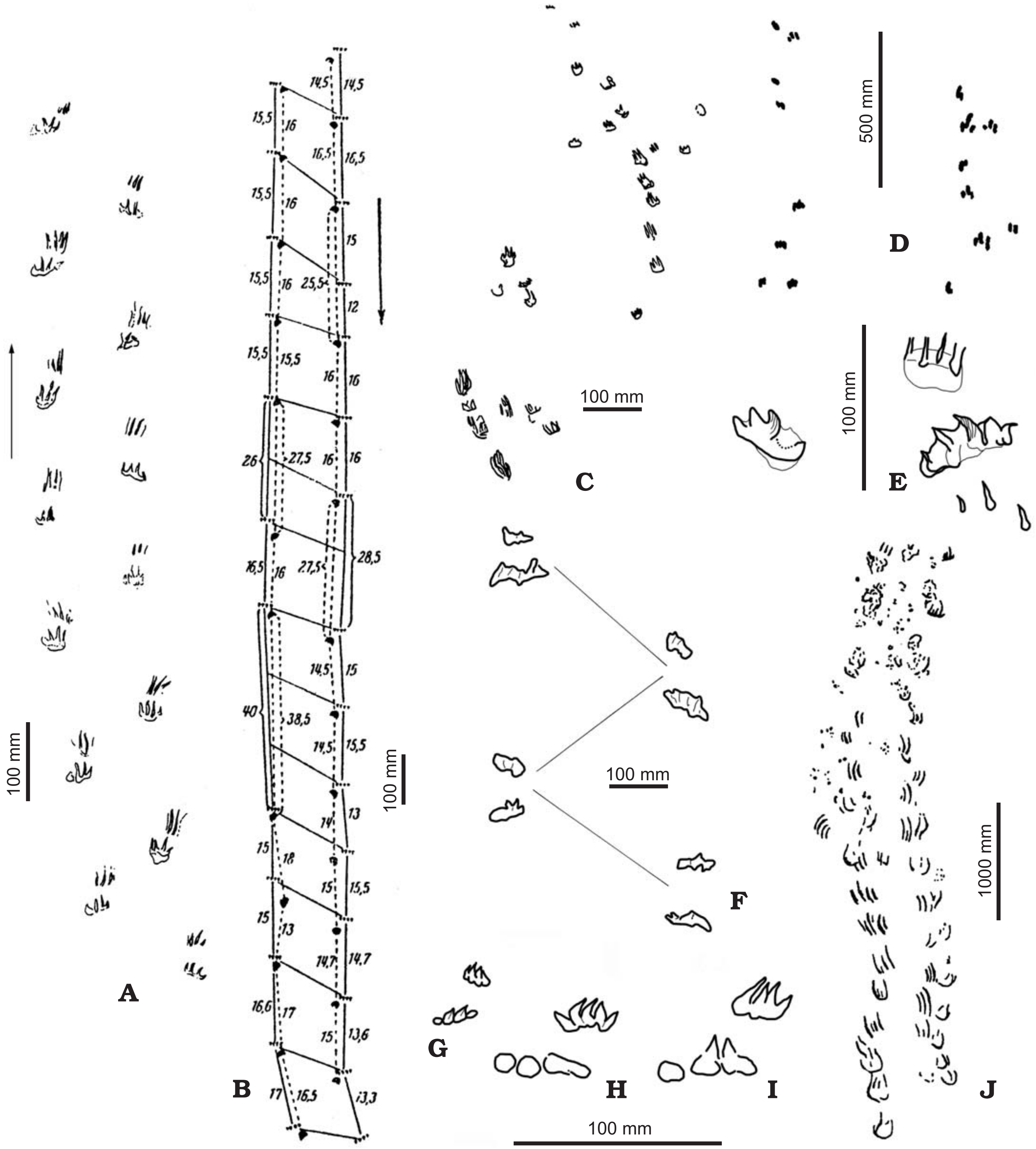


Fig. 6. **A**. *Emydhipus cameroi* Fuentes Vidarte, Meijede Calvo, F. Meijede Fuentes, and M. Meijede Fuentes, 2003, Early Cretaceous, Spain, holotype. **B**. *Chelonipus torquatus* Rühle von Liliestern, 1939, Early Triassic, Germany, holotype. **C**. Turtle tracks from the Late Jurassic Morrison Formation of Utah (after Foster et al. 1999). **D**. Turtle tracks from the Lower Cretaceous Enciso Group of the Cameros Basin, Spain (after Moratalla 1993). **E**. Turtle tracks from the Upper Cretaceous of Colorado (after Wright and Lockley 2001). **F**. *Chelonipus plieningeri* Haubold, 1971a, Late Triassic, Germany, holotype. **G**–**I**. *Chelonipus torquatus* Rühle von Liliestern, 1939 (after Haubold 1971a), Early Triassic, Germany. **J**. *Chelonichnium cerinense* Demathieu and Gaillard, 1982 (in Bernier et al. 1982), Late Jurassic, France.

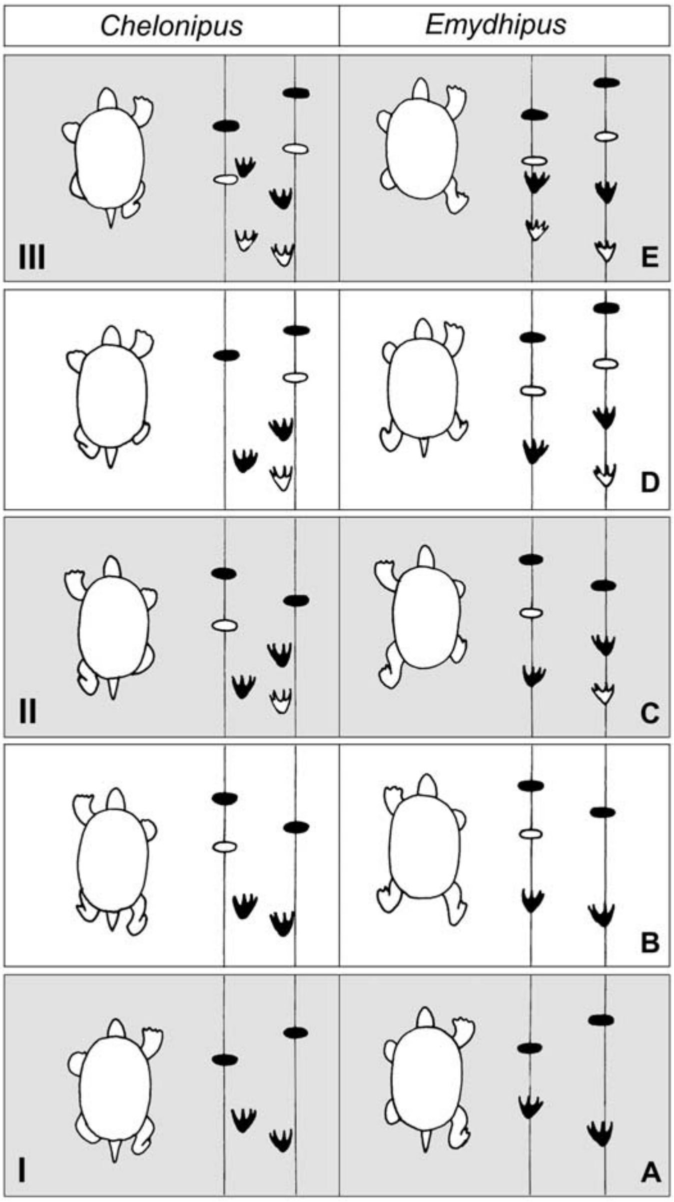


Fig. 7. Reconstructed trackways of *Chelonipus torquatus* Rühle von Liliestern, 1939 and *Emydhipus cameroi* Vidarte et al., 2003. The footprints produced as the trackmaker progresses through subsequent positions are shown. Position I and III represent the animal with all four feet on the ground in a complete step sequence.

*dubium*. Later, a large number of additional trackways were found in the same deposits (Bernier et al. 1984). These trackways were attributed to hopping dinosaurs and named *Saltosauropus latus* by Demathieu and Gaillard (in Bernier et al. 1984). Thulborn (1990) challenged the interpretation of the hopping dinosaurs and proposed that these tracks were made by a swimming turtle. New discovery of tracks similar to *Saltosauropus* in shape, but smaller in size, from the Jurassic and Cretaceous of North America and Spain (Moratalla et al. 1993, 1995; Wright et al. 1998) have been attributed to turtles that were presumably swimming. However, recently Lockley et al. (1995) and Wright et al. (1998) reinterpreted some of the *Saltosauropus* tracks as possible pterosaur tracks.

Purported but unnamed turtle tracks were reported from the Late Jurassic Morrison Formation of Utah (Foster et al. 1999) (Fig. 6C), from the Upper Cretaceous of Colorado (Wright and Lockley 2001) (Fig. 6E), and from the Middle Jurassic of the Cleveland Basin, England (morphotypes Cvi and Cvii in Romano and Whyte 2003).

A well-preserved trackway was recently reported form the Middle–Late Berriasian of the Spain by Fuentes Vidarte et al. (2003) (Fig. 6A). The track was named *Emydhipus cameroi* and diagnosed as follows (Fuentes Vidarte et al. 2003: 125): "[...] trackway by a quadrupedal animal with different hind and fore limbs. Manual print with four elongated and parallel claw marks in axis with the trackway midline (L = 1.7 cm, W = 2 cm). Pedal print plantigrade (L = 1 cm, W = 1.5 cm) with four clawed digits. Pedal digit II and III nearly equal in length and I and IV shorter and nearly divergent respect to the pes long axis. The sole is short and rounded. The trackway width is about 4.5 cm, the pace angle 63–85°. Manual and pedal prints without rotation in respect to the trackway midline".

*Emydhipus* differs from *Chelonipus* in having the manual prints with evident parallel ungual traces, slightly internal and apparently always away in respect to the pedal ones (Figs. 6A, B, 7). In our opinion such characteristics are sufficient for not considering *Emydhipus* as a junior synonym of *Chelonipus*. The different position of the manual prints in the trackway corresponds to a different trackmaker anatomy and possibly to a different vertebrate taxon (Fig. 8).

Thus, only two ichnogenera attributed to turtles seem to be currently valid (Table 1): *Chelonipus* and *Emydhipus*. However, the abandonment of *Chelonichnium* (*nomen dubium*) requests a new attribution for *Chelonichnium cerinense*; a track certainly attributable to a turtle. *Chelonich-*

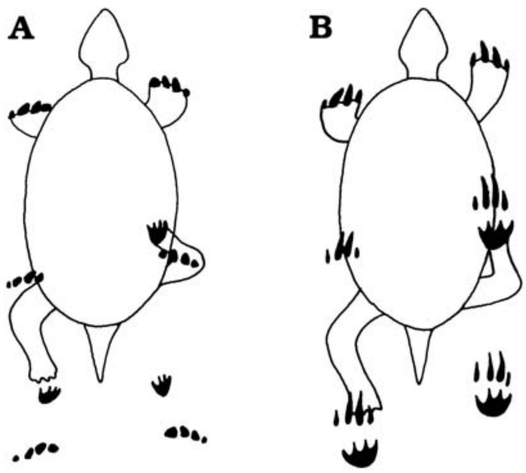


Fig. 8. **A**. *Chelonipus torquatus* Rühle von Liliestern, 1939 . **B**. *Emydhipus cameroi* Vidarte et al., 2003. *Emydhipus* differs from *Chelonipus* in having the manual prints with evident parallel ungual traces, slightly internal and apparently always away in respect to the pedal ones. The different position of the manual prints in the trackways could be related to a different trackmakers anatomy and possibly to different vertebrate taxa.

Table 1. Ichnogenera attributed to turtles.

| Ichnogenus | Age | Status | Comments |
|---|---|---|---|
| *Chelonichnium* Schimper, 1850 | Lower Triassic | *nomen dubium* | |
| *Anyropus* Hitchcock, 1858 | Lower Jurassic | | not a turtle track; possible amphibian footprint |
| *Emydichnium* Nopcsa, 1923 | Upper Jurassic | | not a turtle track; possible ammonite roll-mark |
| *Chelonipus* Rühle von Liliestern, 1939 | Lower Triassic | | walking turtle track |
| *Agostropus* Rühle von Liliestern, 1939 | Lower Triassic | synonym | not a turtle track; *Dicynodontipus* Hornstein, 1876 |
| *Saltosauropus* Demathieu and Gaillard, 1984 | Upper Jurassic | | swimming tracks attributed both to turtle and pterosaur |
| *Emydhipus* Fuentes Vidarte et al., 2003 | Lower Cretaceous | | walking turtle track |

*nium cerinensis* with the clawed manual prints slightly internal to those of the pedes, and without apparent overpass, shows a closer comparison with *Emydhipus* rather than with *Chelonipus* and so we suggest renaming *Chelonichnium cerinense* as *Emydhipus cerinensis*.

# Comparison with modern turtle tracks

Chelonians are a bizarre group of reptiles. The placement of the limb girdles inside the shell and the arrangement of the openings in the shell to allow for retraction of head, tail, and limbs has drastically limited the range of limb movements both in the horizontal and vertical planes. Chelonian limbs are greatly modified in response to the various environments in which they occur. In marine forms the manus and pes evolved into broad, flattened paddles, in the freshwater forms this has happened to a lesser extent, in terrestrial chelonians the limbs are stout, rounded structures. The terrestrial chelonians have a wider stance and tracks compared to stride length than other living tetrapods. The primitive sprawling stance has been retained as a result of the placement of the limb girdles within the shell and generates the wide trackways. During most normal locomotion three feet are on the ground at all times and equilibrium is maintained. At faster gaits (rarely used in normal situations), occasionally only two feet are on the ground (an inherently unstable stance) and loss of equilibrium results in pitch and roll of up to 10°. The demands of aquatic locomotion have resulted in significant morphological modification in aquatic forms. In freshwater turtles the hind limbs are longer, more heavily muscled and have a greater surface area in the manus than in the pes. During swimming the limb is extended lateral with the digits spread, the interdigital webbing increasing the surface area. Fore- and hind limbs contribute to propulsive locomotion. The limb is moved posteriorly in the horizontal plane with the foot at a 90° angle until it reaches the back of the stroke arc, nearly parallel to the body. The leg is flexed, the digits closed (reducing drag) and the limb moved forward next to the body with the foot at a low angle (10–20°). Normal gait is for diagonally opposed limbs to be coordinated. Forward propulsive forces are generated only during the backstroke. The forestroke results in drag (Marlow 1985).

Living turtles produce wide trackways in which the footprints commonly reveal elongate digit scrape marks (Walker 1971; Foster et al. 1999).

Rühle von Liliestern (1939) analysed the tracks of the modern turtles *Testudo graeca*, *Chrysemys ornata*, and *Testudo polyphemus* to compare their footprints to the new instituted ichnogenus *Chelonipus*. Recently, Foster et al. (1999) analysed the gait of *Chrysemys picta marginata* and *Terrapene ornata ornata* in order to reconstruct their trackways and compare them to the purported turtle tracks from Utah, Spain, and France. The conclusion was that the trackways of extant turtles were very similar in general outline to those of the fossils ones. However, the authors suggested that there are differences between trackways made by animals walking on land and those walking under water and pointed out that no studies recorded or distinguished fossil trackways of bottom walking (aquatic locomotion) from terrestrial locomotion (Foster et al. 1999).

## Material and methods

In order to compare footprints morphology and kinematics of the step cycle of extant turtle with those of the fossil ones we analysed the trackways of five living taxa of terrestrial and aquatic testudinoid turtles (*Testudo hermanni*, *Testudo marginata*, *Cuora amboinensis*, *Rhinoclemmys pulcherrima*, *Emys orbicularis*) that were produced experimentally in substrate both terrestrial and aquatic.

Species involved in the study are all cryptodirans belonging to the Testudinoidea clade. Shell shapes and limbs morphology are reflecting their mode of life, respectively terrestrial in the genus *Testudo*, terrestrial or semi-aquatic in the genera *Cuora* and *Rhinoclemmys* or fully aquatic in the genus *Emys* (Barbour and Erns 1992; Zug et al. 2001).

### Order Testudines Batsch, 1788
### Family Testudinidae Gray, 1825

*Testudo hermanni* Gmelin, 1789.—Hermann's tortoise is a small to medium sized terrestrial tortoise occurring in southern Europe. This species is a typical member of *Testudo*. Both the males and females have a large horny scale or nail on the end of their tails. Adult males tend to be smaller than females, have a slight plastral concavity, and have much larger and longer tails. Typical habitat in the wild is variable, including woods, scrub, heath, grassland, and farmland.

*Testudo marginata* Schoepf, 1792.—Marginated tortoise is a medium-sized tortoise originally native to Greece; one of the largest of the Mediterranean species. It is a terrestrial species; typical habitat is arid, scrubby, rocky hillsides, where the tortoises spend mornings and late afternoons browsing on weeds, shrubs, and flowers while resting in the shade during the hottest afternoon hours.

### Order Testudines Batsch, 1788
### Family Emydidae Lydekker, 1889
### Subfamily Batagurinae McDowell, 1964

*Cuora amboinensis* (Daudin, 1801).—Malayan box turtle. Malayan box turtle is a small to medium sized species, occurring only in lowland tropical rainforest areas of South-East Asia. It is the most aquatic of the box turtles in the world, and because they prefer still, warm water, they are found quite often in rice paddies, marshes, and shallow ponds in these tropical areas (Barbour and Erns 1992). Malayan box turtles use the typical anti-predatory behaviour characteristic of box turtles that is tucking their entire body inside their protective shell. This is possible because of their hinged plastron, which allows the bottom to close very tightly against the top.

*Rhinoclemmys pulcherrima* (Gray, 1855).—Painted wood turtle. Painted wood turtle is comprised of four subspecies, which collectively range from Sonora, Mexico to Costa Rica. It is a terrestrial lowland species, primarily an inhabitant of scrublands and moist woodlands, but also occurs in gallery forest close to streams. The species, at least in Costa Rica and Nicaragua, prefers moist habitats, and has been observed wading and swimming in streams and rain pools, especially during the dry season.

### Order Testudines Batsch, 1788
### Family Emydidae Lydekker, 1889
### Subfamily Emydinae Lydekker, 1889

*Emys orbicularis* Linnaeus, 1758.—European pond turtle. The European pond turtles, are found in southern and central Europe, northwestern Africa (roughly Morocco through to Tunisia), and in humid areas of the Middle East and Central Asia as far east as the Aral Sea. This species lives in freshwater areas, including ponds, lakes, slow-moving streams, and other lentic regions. They select terrestrial locations with open, high, and sandy soil habitats for nesting. These turtles search for habitats in shallow, fertile areas with adequate food supplies and minimal predators.

## Experimental substrate

The trackbeds were constituted of medium and very fine siliciclastic sand with different moisture content, lime mud, and of lime mud covered with 5–10 cm of freshwater.

The turtles were lured across the trackbed by the attraction of food: they walked normally.

When the turtles were recaptured, we took photographs and traced the trackbed on polystyrene film of (Figs. 9, 10). For the tracks imprinted during bottom walking, the water was drained before the drawing of the trampled surface on polystyrene film.

Terrestrial turtles, *Testudo marginata* and *T. hermanni*, were observed in their walk on firm mud or sand with low moisture content. Semi-aquatic or fully aquatic turtles as *Rhinoclemmys*, *Cuora*, and *Emys* were observed in their walk on semi-liquid mud, soft mud or very fine sand both in bottom walking (5 to 10 cm of water column), and in terrestrial walking.

### Results

*Tracks in semi-liquid mud. Terrestrial and bottom walking tracks*.—The mud was extensively disrupted during the insertion of the foot and later, especially in subaerial environment, as the result of adhesion and suction, during its withdrawal. In bottom walking, no marginal flow survived and the deformed sediments collapsed and partly flowed back into the depression partly filling it and obscuring the footprint. Nevertheless, the trackway was recognisable in our general outline with well-marked pedal traces and less marked manual ones (Fig. 9B).

*Tracks in soft mud or very fine sand. Terrestrial and bottom walking tracks*.—Soft mud has a high moisture content and low yield strength (Allen 1997). The tendency to flow and collapse, however, is less pronounced than the previous case. The footprints are poorly formed and covered sometimes with many "adhesion spikes" created as the foot was withdrawn. The footprints show a few blurred striae made by the foot during the step cycle (Fig. 9G, H). The footprints are likely to show only the grosser anatomical features.

Fine sand could preserve track of bottom walking better than semi-liquid mud. The pedal and manual ungual marks are always well recognisable, often elongated as deeply and parallel scratch marks (Fig. 9C). The manus and pes prints are slightly deformed in respect to those of the same individual imprinted in subaerial environment (stiff mud or fine sand). Pedal prints are shorter and wider (Fig. 9D) than those imprinted in terrestrial walking (Fig. 9E, F), often with the impression of the longest digits II–IV and with a displacement rim on the posterior margin. Manual prints are unguligrade without (Fig. 9C), or with only a thin arched impression of the soft tissues (Fig. 9D).

*Tracks in stiff mud or fine sand. Terrestrial walking tracks*.—Stiff mud has moderate moisture content and yield strength.

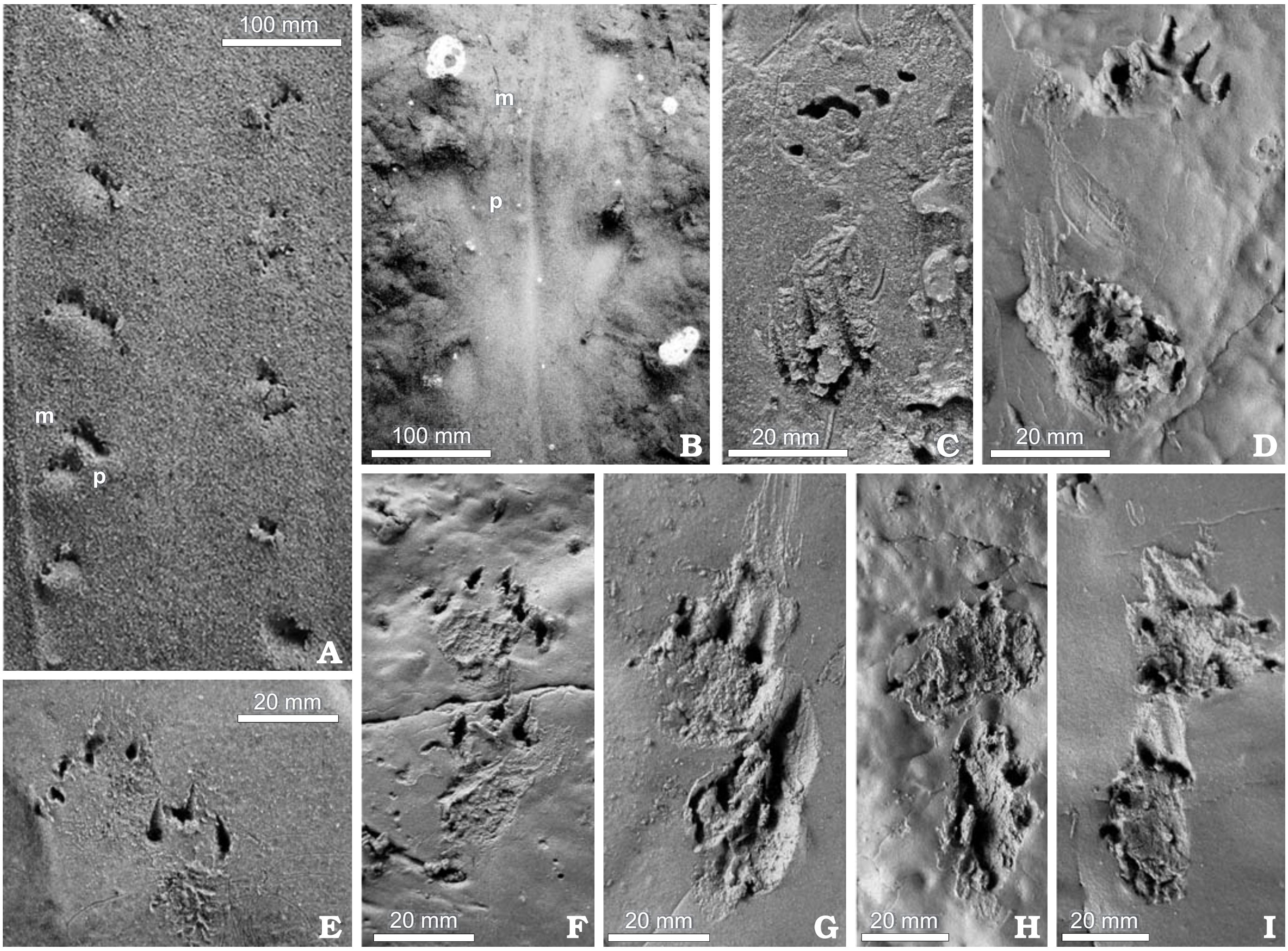


Fig. 9. Trackways and isolated footprints of living terrestrial and semiaquatic turtles. **A**. *Testudo hermanni* in terrestrial walking on firm sand. **B**. *Rhinoclemmys pulcherrima* in bottom walking on soft mud. **C**. *Emys orbicularis* in bottom walking on very fine sand. **D**. *Emys orbicularis* in bottom walking (shallow water) on very fine sand. **E**. *Emys orbicularis* in terrestrial walking on firm very fine sand. **F**. *Emys orbicularis* in terrestrial walking on firm mud. **G**. *Rhinoclemmys pulcherrima* in terrestrial walking on soft mud. **H**. *Cuora amboinensis* in terrestrial walking on hard mud. **I**. *Cuora amboinensis* in terrestrial walking on very fine sand. (m, manual print; p, pedal print).

The footprints were well defined. Marginal rims were weakly developed and in some cases limited to only side of the print. Finely grooved drag marks are sometime recognisable (Fig. 9I).

*Tracks in firm mud or sand. Terrestrial walking tracks*.—These materials are characterised by their high yield strength and their low moisture contents. Tracks left in these materials consist of shallow undistorted and sharply defined footprints with finest anatomical details. A short sequence of high fidelity undertracks may be expected. Tracks left in sand, show a superficial penetration of the claws in the substrate and a shallow impression both of the manual and the pedal prints (Fig. 9A, E). Displacement rims are well recognisable on the mesial-posterior margin of the prints (Fig. 9A).

## Measurements

All the turtles involved in the experimental ichnology tests were small to middle sized specimens (morphometric indexes are summarised in Table 2) that produced regular trackways about 1 m long (20 paces) (measurements in Table 3). Because their strict similarity with the fossil material, a more detailed description of trackway differences and the relationship with the morphometric indexes of *Rhinoclemmys pulcherrima*, *Cuora amboinensis*, and *Emys orbicularis* is presented in the following chapters.

## Stance and gait

In the terrestrial species (i.e., *T. maginata* and *T. hermanni*, Fig. 10A, B), the hand is positioned strongly digitigrade, in contrast to the aquatic or semiaquatic species, which walk half-plantigrade (i.e., *E. orbicularis*, Fig. 10D) or fully plantigrade (i.e., *C. amboinensis*, *R. pulcherrima*, Fig. 10C, F).

Manual prints both terrestrial and aquatic turtles are generally characterised by exhibiting four or five strong claws. These are always imprinted in the tracks of the semi-aquatic

Table 2. Morphometric indices of the extant turtles involved in experimental ichnology (in centimetres).

| Species | Shell length | Plastron length | Plastron width anterior | Plastron width posterior | Max. shell width | Limbs insertion distance | forelimb | tibia | foot | hand |
|---|---|---|---|---|---|---|---|---|---|---|
| *Rhinoclemmys pulcherrima* | 15.6 | 14.7 | 8.3 | 10.0 | 13.0 | 6.6 | 3.9 | 4.5 | 3.0 | 1.6 |
| *Cuora amboinensis* | 15.9 | 15.5 | 8.1 | 9.2 | 13.2 | 6.5 | | 2.8 | | |
| *Emys orbicularis* | 16.1 | 14.9 | 8.5 | 8.8 | 11.6 | 4.5 | 2.8 | 3.8 | 3.3 | 1.2 |

Table 3. Footprints and trackways data of the extant turtles involved in ichnological experiments (in centimetres and degrees) (M, manus; P, pes).

| Species | pace | | stride | | pace angulation | | length | | width | | trackway width | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M | P | M | P | M | P | M | P | M | P | int | ext |
| *Cuora amboinensis* | 14.5 | 13.5 | 16 | 16.3 | 69 | 74 | 2.5 | 3.5 | 3 | 2.2 | 8 | 16.5 |
| *Rhinoclemmys pulcherrima* | 12.5 | 12.5 | 12.5 | 13 | 65 | 62 | 1.5 | 3.2 | 5 | 2.5 | 5 | 14 |
| *Rhinoclemmys pulcherrima* bottom walking | 11.5 | 11 | 11 | 10 | ?55 | 55 | 2 | ?4 | 1.5 | 2 | 6 | 16.5 |
| *Emys orbicularis* | 11.2 | 11.4 | 12.7 | 12 | 68 | 62 | 0.8 | 3.0 | 1.5 | 1.8 | 5 | 11.5 |
| *Emys orbicularis* bottom walking | 9.5 | 11 | 11 | 11.2 | 60 | 56 | 0.6 | 2.2 | 2.3 | 2 | 6 | 13.5 |

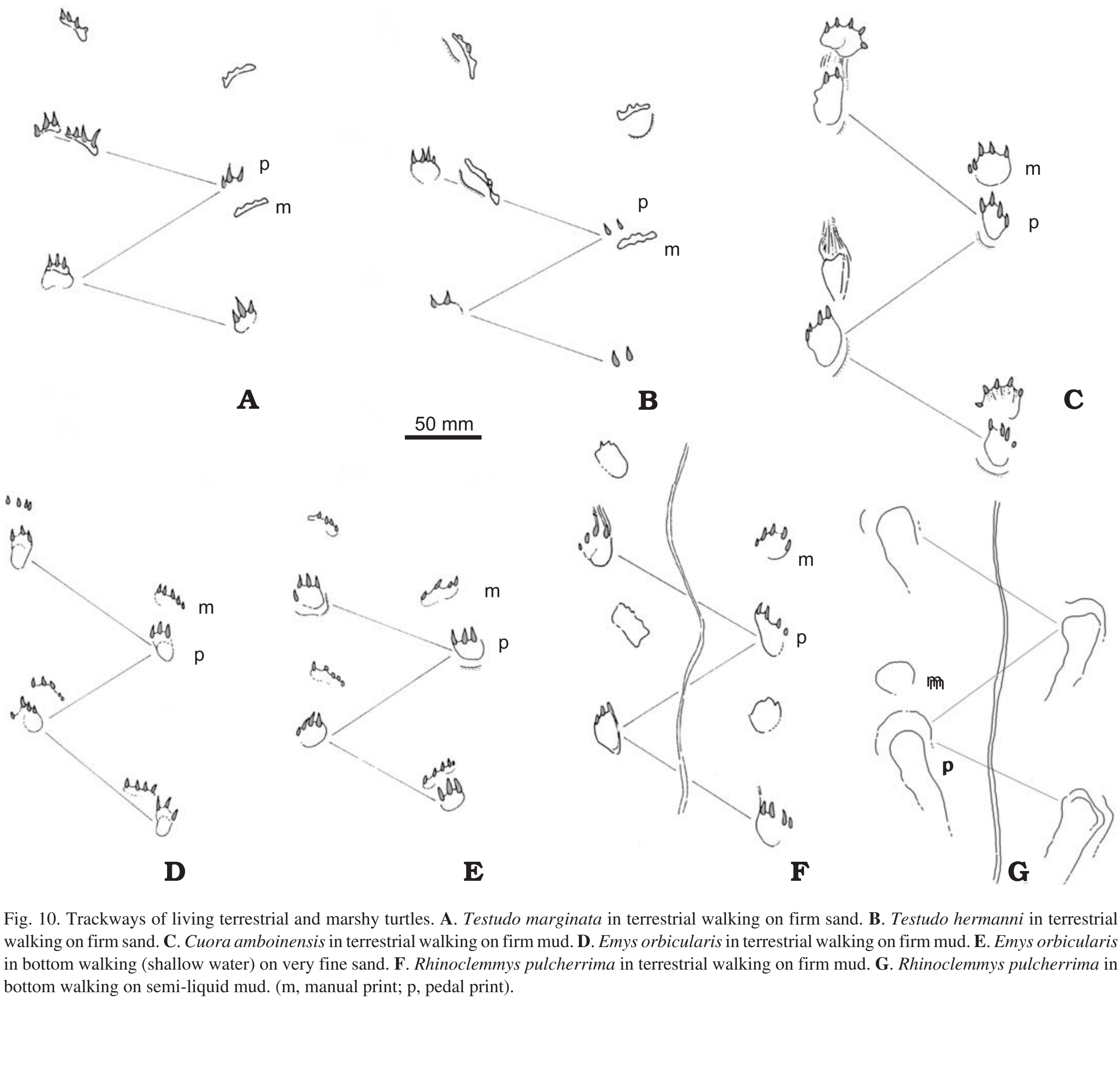


Fig. 10. Trackways of living terrestrial and marshy turtles. **A**. *Testudo marginata* in terrestrial walking on firm sand. **B**. *Testudo hermanni* in terrestrial walking on firm sand. **C**. *Cuora amboinensis* in terrestrial walking on firm mud. **D**. *Emys orbicularis* in terrestrial walking on firm mud. **E**. *Emys orbicularis* in bottom walking (shallow water) on very fine sand. **F**. *Rhinoclemmys pulcherrima* in terrestrial walking on firm mud. **G**. *Rhinoclemmys pulcherrima* in bottom walking on semi-liquid mud. (m, manual print; p, pedal print).

or fully aquatic turtles (Fig. 10C, D, F), but are commonly missing or have been replaced by discrete pits connected by an arched impression in the tracks of the terrestrial turtles (Fig. 10A, B).

In terrestrial locomotion of aquatic or semi-aquatic turtles, the foot is always positioned plantigrade and is recognisable by the impression of the semi-parallel claws I–III, which are sometimes connected to the smaller claw IV (Figs. 9I, 10C, D, F). In bottom walking pedal and manual prints are more spaced and sometimes missing. Three or four elongate and parallel ungual scratch marks characterised the bottom walking tracks in shallow water on fine sand substrate (Figs. 9C, 10E) while undefined rounded or slightly elongated prints are recognisable in bottom walking on mud (Figs. 9B, 10G). The trackways are always very wide (13–16 cm) with a low pace angle (50–70°).

In terrestrial walking of *Testudo hermanni* and *T. marginata* the pes pace angle is about 45–50°, while it is 62° in *Rhinoclemmys pulcherrima* and 72° in *Cuora amboinensis*.

The hands are slightly internal to the trackway and positioned under the body, often with an inward rotation in respect to the trackway midline. The claw impressions show distinct movement traces, indicating that the manus was placed in front and then pushed backward and slightly outwards as the animal propelled forward. The foot impressions form the outer part of the trackway, with digits nearly parallel to the trackway midline.

In bottom walking the body was partially sustained by the water and the walk pass gradually into a progressive sprawling attitude (swim) of both fore- and hind limbs.

In *Emys* bottom walking the trackway width increases from 11.5 to 13.5 cm (plastron width 8.8 cm) (Fig. 10D, E; Table 3) and the pedal pace angle decreases from 62 to 56°. In *Rhynoclemmys* also there are an augment of the trackway width (from 14 to 16.5) and a diminution of the pedal pace angle (62 to 55°) (Fig. 10F, G; Table 3). In *Rhynoclemmys* the bottom walking is characterised by an incomplete impression of the forefoot (only on a side of the tracks some manual prints are recognisable) (Figs. 9B, 10G) and both in *Emys* and in *Rhynoclemmys* the distance between manus and pes increases from about 0.5 to 3 cm. In shallow water (up to 5 cm deep) the pedal prints are shorter and wider than those measured in terrestrial walking (Fig. 10D, E).

# Discussion

Despite the number of the species involved, very little of the whole diversity of living turtles was sampled, because all species used herein are testudinoids. However, the traces, imprinted on wet sand or very wet mud, show some surprising similarities with the fossil material.

The tracks produced by the two terrestrial turtles are interesting because the limb morphology of modern land turtles (particularly the almost unguligrade forelimb posture) is unique to the clade. The forefeet of the terrestrial turtles *Testudo marginata* and *T. hermanni* imprinted on damp sand (Figs. 9A, 10A, B) result in traces comparable to those traces found in the main ichnoassembage (Fig. 3D, G). Given that the Testudinidae do not appear in the fossil record until the Palaeocene, tracks of this morphology would not be expected before this time. Numerous terrestrial turtles existed in the Mesozoic, such as meiolaniids, nanhsiungchelyids, mongolochelyids, and proganochelyids, but none of these are characterised by unguligrade forelimb posture. So, the apparent digitigrady of some of the described specimens could relate more probably to a preservation mode than to an anatomic attitude. In terrestrial walking on wet sand substrate of plantigrade extant turtles only the digit tips are frequently imprinted (sometimes connected by an arched structure). The possibility of some of the tracks being undertracks should also be considered—this could explain their apparent unguligrady.

The prints of the aquatic turtles *Emys* and *Rhynoclemmys* in different substrate but mainly in wet mud (Fig. 9C, D, F, G), are very similar to the manus-pes sets imprinted on the grey siltstone of Oles (Fig. 5), Tazones, and Luces suggesting a similar substrate and general trackmaker morphology.

The tracks from Asturias most closely resemble purported turtle tracks from the Lower Cretaceous Enciso Group of the Cameros Basin, Spain (Moratalla 1993) (Fig. 6D), from the Lower Cretaceous of Las Hoyas (Cuenca), Spain (Moratalla et al. 1995), the Late Jurassic Morrison Formation of Utah (Foster et al. 1999), the Upper Cretaceous of Colorado (Wright and Lockley 2001), and morphotypes Cvi and Cvii from the Middle Jurassic of the Cleveland Basin, England (Romano and Whyte 2003). The specimens presented herein also resemble the alleged Triassic chelonian tracks from Domeño, Valencia, Spain (Márquez-Aliaga et al. 1999), the small tracks on LIVCM slab form Storeton Quarry, England (Treasise and Sarjeant 1997), and from the Buntsandstein (Lower Triassic) of Germany (Haubold 1971b). The swimming traces described by McAllister (1989) are also very close to our sample from Oles and Tazones.

The chelonian traces described by Bernier et al. (1982) as *Chelonichnium cerinense* (recte *Emydhipus cerinensis*) from the Upper Jurassic of Cerin (France) show substantial similarities with the Asturian material, but they are not fully comparable. These tracks seem generally less defined than our material and with pronounced scratch marks. Bernier et al. (1982) consider *E. cerinensis* tracks to have been made by "walking turtles" along a slope with a very damp mud. In our opinion, such traces are compatible also to a movement underwater (bottom walking) in a shallow water environment.

The characteristics of all our material compare closely to the ichnogenus *Emydhipus* Fuentes Vidarte et al., 2003. The main trackway of Quintueles (Fig. 2) show comparable trackways parameters with manual prints medial to those of the pedes and without apparent overpass. The scratch marks on the prints suggest a relative moisture content of the substrate. The possible second trackway on the same slab seems manus-dominated. These manual prints are closer to *Chelonipus* than *Emydhipus* in their general morphology (e.g., Fig. 3G). The ungual marks are short, pointed and connected by an arched depression (digitigrady). Such characteristics are probably related to a firmer trackbed and therefore to a trampling in a moment in that the substrate has moderate moisture content. We therefore suppose, that the tracks on the slab of Quintueles are related probably to the same ichnogenus *Emydhipus* but that they were imprinted at different times and under different environmental conditions.

The isolated prints from Luces and the scratch marks from Tazones and Oles (Figs. 3A, B, 4, 5E) suggest a bottom walking on mud or very fine sand and are too incomplete or poorly preserved for an ichnotaxonomic classification.

The two manus-pes sets from Oles (Figs. 3J, 5B) related to a terrestrial walking on soft mud with high moisture content, appear interesting for the differences in the pedal prints. The semiplantigrade manual prints (Figs. 3I, J, 5A), with their long ungual marks are both well comparable with *Emydhipus*. A first pedal print instead, shows four parallel ungual marks (Fig. 5B) while a second one shows only three anteriorly oriented digits (Fig. 3J). The first one (Fig. 5B) is very similar to *Emydhipus* in general outline, digits II and III of similar length, digit I and IV slightly shorter and a divergent and rounded heel. Second specimen (Fig. 3J) instead, with the three robust and little divaricated digits and their rounded pad does not show similarities with any of the previously described ichnogenera.

# Conclusions

The Asturian tracks show in their morphologic characters a high degree of similarity to other specimens previously described as possible turtle tracks (Bernier et al. 1982; Lockley 1991; Moratalla 1993; Moratalla et al. 1995; Lockley and Hunt 1995; Foster et al. 1999; Romano and Whyte 2003). Comparison with tracks of extant turtles confirms this affinity and allows us to recognise differences between manual and pedal prints in several of our well preserved specimens.

The Asturian tracks, referable mainly to the ichnogenus *Emydhipus*, are here interpreted as having been made by turtles partially buoyed by water (Figs. 3A, B, 4, 5F) and by turtles walking in wet or firm mud in subaerial environment (Figs. 2, 3A–D).

The skeletal remains from the Lastres Formation are still under study and the relative length of the manual digits of the Upper Jurassic turtles is currently unknown (only in the eurysternids the fourth digit tends to be the longest in the hand) (Joyce 2000). For this reason it is not possible to infer what types of turtles could have made the tracks. The dimensions of the trackmakers inferred by their trackways varied probably from 15 to 40 cm of plastron width and from 20 to 60 cm of maximum length.

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