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NEW MATERIAL OF THE CHELONIAN ICHNOTAXON *EMYDHIPUS CAMEROI* FUENTES VIDARTE *ET AL.*, 2003 FROM THE BERRIASIAN (LOWERMOST CRETACEOUS) OF NORTHERN GERMANY

[Nuevo material del ichnotaxon de quelonio* Emydhipus cameroi *Fuentes Vidarte* et al., *2003 del Berriasiense (Cretácico Inferior) del Norte de Alemania]

Hans-Volker KARL[1,2], Diana VALDISERRI[3] & Gottfried TICHY[3]

[1] Thüringisches Landesamt für Denkmalpflege und Archäologie. Humboldtstraße 11. D-99423 Weimar, Germany. Email: hvkarl@web.de
[2] Geoscience Center of the University of Göttingen. Department of Geobiology. Goldschmidtstrasse 3. D-37077 Göttingen, Germany
[3] University of Salzburg. Department of Geography and Geology. Hellbrunner Strasse 32. A-5020 Salzburg. Email: gottfried.tichy@sbg.ac.at

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ABSTRACT: New turtle-tracking material from *Emydhipus cameroi* Fuentes Vidarte *et al.*, 2003 from the Berriasian of Northern Germany is described. An overview of the known ichnospecies of turtle-trackings is presented and relevant material is discussed.

Key words: Berrasian, Lower Cretaceous, Bückeberg, Lower Saxony, Northwestern Germany, *Emydhipus cameroi* Fuentes Vidarte *et al.*, 2003, description.

RESUMEN: Se describe material nuevo de huellas de quelonio, *Emydhipus cameroi* Fuentes Vidarte *et al.*, 2003, del Berriasiense del Norte de Alemania. Se supervisan y discuten las ichnoespecies conocidas de huellas de quelonios.

Palabras clave: Berriasiense, Cretácico Inferior, Bückeberg, Sajoniense inferior, Noroeste de Alemania, *Emydhipus cameroi* Fuentes Vidarte *et al.*, 2003, descripción.

INTRODUCTION

Turtle tracks are relatively rare but widespread components of Mesozoic aquatic ichnoassociation. The morphology of these tracks are strongly controlled by the gait of the trackmaker, the environment and the substrate (AVANZINI *et al.*, 2005). Terrestrial turtles show a typical unguligrade gait while semiaquatic and aquatic species are semiplantigrade. Terrestrial and subaquatic bottom-walking led to a wide range of preservation, further diversified by the substrate quality. Most fossil examples show only more or less pronounced claw-marks (occasionaly scratch-marks), which may be completed by a connecting arc-shaped structure. This preservation quality does not allow any reconstruction of autopodial anatomy but the determination of the number of digits and the general presence of ungual claws.

In this paper we describe an isolated turtle manus print (preserved as hypichnial cast) which shows an excellent grade of anatomical detail. The specimen is preserved on a slab of fine-grained sandstone from the Berriasian Bückeberg Formation (Obernkirchen Member, ?Hauptsandstein unit) of the area of Bückeburg near Minden, Lower Saxony, NW Germany. This specimen is part of the Max Ballerstedt collection, housed at the Geoscience Centre, University of Göttingen and was first described with abstract and poster in the Annual Meeting 2008 of the German Palaeontological society in Erlangen HORNUNG *et al.* (2008).

SYSTEMATIC ICHNOLOGY

Ichnia Testudinarum fossilium

Ichnosubclassis Chelonomorphipedii Vialov, 1966

Ichnoorder Testudipedia Vialov, 1966

Ichnofamily Chelonipedidae Sarjeant & Lockley, 1994

Ichnogenus *Chelonipus* Rühle von Lilienstern, 1939

(Genus typicus)

Chelonipus torquatus Rühle von Lilienstern, 1939

– *Chelonipus torquatus* n. sp. Rühle von Lilienstern, 1939

– *Chelonipus torquatus* Rühle von Lilienstern, 1939, HAUBOLD, 1971a, 1971b, KARL, 1993, KARL & TICHY, 2000, KUHN, 1958, 1963 (syn. *Chelonipus cuneiformis* n. sp. RÜHLE VON LILIENSTERN, 1939, KUHN, 1958, 1963, syn. HAUBOLD, 1971a) [Lower Triassic].

***Chelonipus triunguis* Karl & Tichy, 2000**

– "Fährten schildkrötenartiger Tiere", SOERGEL, 1925

– *Chelonipus torquatus* Rühle von Lilienstern, 1939 (in part), KARL, 1993

– *Chelonipus triunguis* n. sp. KARL & TICHY, 2000 [Lower Triassic]

***Chelonipus plieningeri* Haubold, 1971a**

– *Chelonipus plieningeri* n. sp. HAUBOLD, 1971a

– *Chelonipus plieningeri* Haubold, 1971a, HAUBOLD, 1971b; KARL, 1993a; KARL & TICHY 2000 [Upper Triassic]

Ichnogenus *Emydichnium* Nopsca, 1923

According to ABEL (1930) it is a floating track of *Eurysternum*, though no diagnostic features are available referring to HAUBOLD (1971). In this paper is provided a brief summary of all scratch- and grinding marks of turtles from the Upper Jurassic.

***Emydichnium megapodium* (Walther, 1904)**

– *Ichnium megapodium* n. sp. Walther, 1904

– *Emydichnium megapodium* (Walther, 1904), NOPSCA, 1923; ABEL, 1930; HAUBOLD, 1971b; KUHN, 1958, 1963

– *Chelonichnium ceriniense* n. isp., DEMATHIEU & GAILLARD, 1982, refer to Ichnia Non-Testudinata below

– *Saltosauropus latus* n. isp., BERNIER *et al.*, 1984

– "A giant Upper Jurassic turtle revealed by its trackways", Kimmeridgium (Oberjura) from the fossil Lagerstätte Cirin in France, GAILLARD *et al.*, 2003 [Upper Jurassic]

REMARKS: The use of the generic name *Chelonichnium* is not correct (HAUBOLD, 1971; LOCKLEY & FOSTER, 2006). The scratch-marks are the same as those of *Emydichnium megapodium*, which just show greater dimensions, similar appear to be with the material described by GAILLARD *et al.* (2003). Discussion on *Saltoposaurus* refer to LOCKLEY & MEYER (2000).

Ichnogenus *Emydhipus* Fuentes Vidarte, Meijide Calvo, Meijide Fuentes & Meijide Fuentes, 2003

Regarding single, well preserved turtle tracks and trackways from the lower Cretaceous a brief summary is provided:

Emydhipus cameroi Fuentes Vidarte, Meijide Calvo, Meijide Fuentes & Meijide Fuentes, 2003

– *Emydhipus cameroi* n. isp., FUENTES VIDARTE *et al.*, 2003

– "An exquisitely preserved turtle footprint from the Berriasian (lowermost Cretaceous) of northwestern Germany", HORNUNG, KARL & REICH, 2008 [Lower Cretaceous]

MATERIAL: GZG. BA. 0116 (Ballerstedt-Collection), imprint of a right turtle manus or pes (plate 1, 2-2).

Plate 1. Emydhipus cameroi *Fuentes Vidarte* et al.*, 2003, GZG. BA. 0116, imprint of a rigth turtles manus or pes from Bückeberg, Lower Saxony, NW-Germany. Ballerstedt-collection. Photo H.-V. Karl. Scale bar = 10 cm.*

DESCRIPTION: The large track is interpreted as a right manus or pes impression, it shows clearly the print of four digits in decreasing length, probably in medial direction. Digit III is slightly deflected ventrally and appears shortened in the imprint. The digits are thin and interphalangeal joints can be recognized at least on digit IV. All digits are merged in an extensive skin web, only the claws are free. This skin shows clear folding especially between digits III and IV but no distinctive superficial texture or traces of osteoderms. The distal metapodial region is present as a lunate depression (hypichnial rise) with a posteromedial rim of displaced sediment (HORNUNG *et al.*, 2008).

Measurements in mm:

TINGER/TOE	I	II	III	IV
Length	60	33	46	49
Wide	11	7	8	8
Total wide	119			

Gen. et spec. indet.

(Non *Chelonipus* RÜHLE VON LILIENSTERN, 1939)

- *Chelonipus sp.*, from the Eocen of Texas, USA, SARJEANT & LANGSTON, 1994; MUSTOE, 1993
- *Chelonipus sp.*, Chuckanut Formation (Eocen) of Nordwest Washington, USA, MUSTOE, 1993
- "Turtle tracks" from the Laramie/Arapahoe Formation (Upper Cretaceous), near Denver, Colorado, USA, WRIGHT & LOCKLEY, 2001
- *Trionyx* from the Eocen of the Paris Basin in Mont-Morency, DESNOYERS, 1859 (upper Figure), Genus *Trionyx* GEOFFROY, 1809 (Morphogenus)
- *Trionyx* from the tertiary Carpathian sandstones of Northern Romania (Bajutz)/Flysch of Oláblaposbánya (Ungary), HAIDINGER, 1841, 1848, ABEL, 1904, HAUBOLD, 1971; referring to NOPSCA (1926) trackways of *Chelonia mydas* LINNAEUS, 1758.

REMARKS: There are just a limited number of fossil turtle footprint reports in the literature. Fossil tracks have been closely compared with modern turtle tracks already by RÜHLE VON LILIENSTERN (1939), current base-line studies are published by EARHART & STEIN (2000) and RENOUS *et al.* (2008). FOSTER *et al.* (1999) assigned a series of 29 small (20 to 30 mm) tracks found in the Jurassic Morrison Formation to an unidentified vertebrate, probably a turtle. Those tracks were preserved in a sandstone unit with a series of scratch marks, the single scratches were associated with the digits of each manus or pes. Single claw marks, as far as defined like a nearly point-like depression, are not preserved in any of the 29 tracks described and illustrated by FOSTER *et al.* (1999). The scrapes left by the Morrison turtles are very similar to the tracks made by the Galapagos tortoises at the Philadelphia Zoo walking across a relatively dry, sandy substrate. The zoo tracks confirm the suggestion by FOSTER *et al.* (1999) that the Morrison tracks were indeed made by a turtle. WRIGHT & LOCKLEY (2001) described a series of short, wide tracks with well-defined claw marks from the Cretaceous Laramie Formation of Colorado. These tracks were referred to a turtle maker, and emphasis was placed on the presence of claw marks providing a means to investigate the interaction between animal

and substrate. They further suggested that the animal was partially buoyed by water as it walked across the substrate. Although the claws in the tracks from the Laramie Formation are prominent, the footprints illustrated by WRIGHT & LOCKLEY (2001) are in a reasonable relation with the clawed tracks left by the zoo turtles examined in the same work. The relations between tetrapod nonmarine biotaxonichnofacies and ethoichnofacies are discussed in HUNT & LUCAS (2007).

Ichnia Non-Testudinata

Another taxa former described as turtle trace fossils according HAUBOLD (1971b):

– *Agostropus* Gilmore, 1926 [*Agostropus falcatus* Rühle von Lilienstern, 1939] syn. of *Laoporus*, Lull, 1918: Ichnofamily Sphenacodontia Romer & Price, 1940 or Bauriamorpha Watson, 1917; Therapsida Broom, 1905; Kuhn, 1958; 1963; Haubold, 1971a, 1971b

– *Chelichnus* Jardine, 1850 [*Chelichnus ambiguus* Jardine, 1853 (*Chelichnus ambiguus* Hickling *Chelichnus megachirus* Huxley referring to Kuhn, 1958); *Chelichnus bucklandi* Haubold, Lockley, Hunt & Lucas, 1995; *Chelichnus duncani* (Owen, 1842); Ichnotypus pro *Testudo ducani* Owen, 1842 (*Testudo* Linnaeus, 1758= Morphogenus); ?*Chelichnus kablikae* Kuhn, 1963]: Incertae sedis or Bauriamorpha Watson, 1917; Therapsida Broom, 1905; Kuhn, 1958, 1963; Haubold, 1971a, 1971b

– *Chelonoides* Hitchkock, 1858 [*Chelonoides incedens* Hitchcock, 1858], Nomen praeoccupatum pro *Chelonoidis* Fitzinger, 1836: Testudines; syn. von *Batrachopus* Hitchkock, 1845: Batrachopodidae emend. Lull, 1904; Kuhn, 1958, 1963; Haubold, 1971a, 1971b

– *Chelonichnium* Schimper, 1850 [*Chelonichnium vogesiacum* Schimper, 1850, *Chelonichnium cerinense* Bernier, Barale, Boureau, Buffetaut, Demathieu, Gaillard & Gall, 1982]: Incertae sedis, Kuhn, 1958, 1963; Haubold, 1971a, 1971b

– *Herpetichnus* Jardine, 1850 [*Herpetichnus bucklandi* Jardine, 1850; *Herpetichnus sauroplasius* Jardine, 1850; *Herpetichnus loxodactylus* Dudgeon; Cotylosauria or turtles according to KUHN (1958, 1963)

– *Onkichnium* Nopsca, 1923: Bauriamorpha Watson, 1917, Therapsida Broom, 1905; Kuhn, 1958, 1963; Haubold, 1971a, 1971b

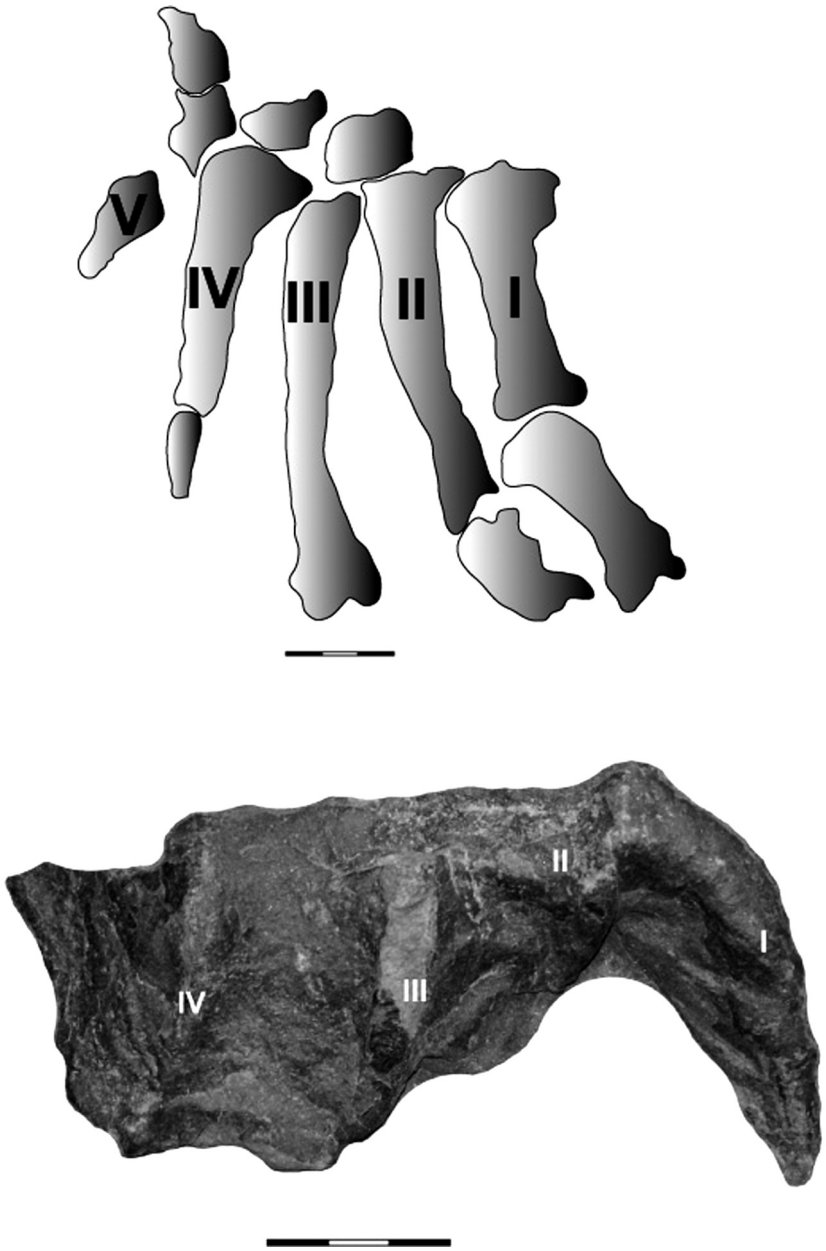

Plate 2. Partial pentadactyle pes with reduced fifth toe of Pleurosternon bullock *(I-IV = metatarsals), the Bremen-specimen adapted from* KARL et al.*, 2007 directly compared to* Emydhipus cameroi *from Bückeberg (I-IV = toe imprints). Scale bars 3 cm. Design Enrico Paust M.A., TLDA.*

DISCUSSION

FUENTES VIDARTE *et al.* (2003) named the trackway found in Valduérteles (Wealden facies, Spain) *Emydhipus*. AVANZINI *et al.* (2005) described related turtle tracks from the Late Jurassic of Asturias, Spain. One imprint at figure 5a may similar to the track described here. *Emydhipus* differs from *Chelonipus* in having the manual prints with evident clearly 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 (FUENTES VIDARTE *et al.*, 2003; AVANZINI *et al.*, 2005).

According to KARL *et al.* (2007a,b) are known at least five species of turtles from the Bückeberg Formation. Among all these species just the abundant *Hylaeochelys menkei* (Roemer, 1836) and *Pleurosternon bullocki* (Owen, 1842) with carapace length up to 70 cm, show a size comparable to the dimensions of the described footprint (HORNUNG *et al.*, 2008). Unfortunately the appendicular skeleton of these taxa, as for most of the Berriasian turtles, is unknown. Only for *Pleurosternon bullocki* is known a partial pentadactyle pes with reduced fifth toe (KARL *et al.*, 2007a,b). Therefore is to assume a strong similarity in the morphology of the footprint presented in this study, with *Pleurosternon bullocki* (plate 2). The autopodial morphology exhibited by the track is peculiar as it shows clearly the aquatic adaption of the turtle and several derived features from the plesiomorphic turtles manus. It shows an intermediate morphotype between those of less specialized semiaquatic turtles (e.g. Emydidae, including semiplantigrade gait and considerably short and broad manus) and of highly specialized aquatic turtles (e.g. Trionychoidea, including gracile phalanges, extensive webbing, reduced ungual claws, and smooth skin surface). For this reason it sheds light on the poorly known modifications in the appendicular morphology of Early Cretaceous limnic turtles. GZG. BA. 0116 is the most similar to an unnamed turtles track from the Leydon Gulch locality referring to WRIGHT & LOCKLEY (2001). See also figure 7b in MORATALLA & HERNÁN (2009). Some turtle tracks described by AVANZINI *et al.* (2005) from the Upper Jurassic of Asturias region (north Spain), show several similarities with the Los Cayos tracks described by MORATALLA & HERNÁN (2009). These similarities are based on the general tridactyl tracks morphology, the presence of parallel digit marks, and the relative curved shape of the external digital impressions. Beside these, the Asturian tracks are bigger, about 5-8 cm in length. The turtle trackway discovered in the Valduérteles locality (Soria province) provides good material for a comparison (figure 7d) (FUENTES *et al.*, 2003). The trackway is made up by a series of 14 manus-pes sets. While the pes prints are tetradactyl with a heel-like rear area, the manus tracks are formed by three or four isolated digital impressions. These digital marks show a sub-parallel disposition without a clearly impressed heel zone. The shape, size, and general disposition of these manual prints show some similarities to those of the Los Cayos C turtle tracks

described herein. MORATALLA & HERNÁN (2009) remarks that FUENTES *et al.* (2003b) named the Valduérteles trackway *Emydhipus*, altough no consistent comparison has been made with similar fossil prints or with the osteological record. Most of the diagnostic features proposed for *Emydhipus* are based on general trackway pattern and track morphology. The authors identified this trackway as an "aquatic turtle"; but gave no precise explanation about the "aquatic" term or taxa comparison. Because on the high similarity between the Los Cayos C prints and the Valduérteles trackway, MORATALLA & HERNÁN (2009) is assumed that both print association were made by a similar trackmaker and therefore the turtle tracks from Los Cayos locality can be ascribed to the ichnotaxon *Emydhipus*. All the turtles species mentioned in this study are well known from the upper Jurassic altough we considered only species that passed trough the Jurassic-Cretaceous boundary.

BIBLIOGRAPHY

ABEL, O. (1904): Wibeltierfährten aus den Ostalpen. Verh. k.k. geol. Reichs-Anst.; **1904**, p. 340.

ABEL, O. (1930): Fährtenstudien I: Über Schwimmfährten von Fischen und Schildkröten aus dem lithographischen Schiefer Bayerns. *Palaeobiologica*, **3**: 372-412.

AVANZINI, M.; GARCÍA-RAMOS, J. C.; LIRES, J.; MENEGON, M.; PIÑUELA, L. & FERNÁNDEZ, L. A. (2005): Turtle Tracks from the Late Jurassic of Asturias, Spain. *Acta Palaeontologica Polonica*, **50**: 743-755.

BERNIER, P. (1985): *Une lagune tropicale au temps des dinosaures*. Centre National de la Recherche Scientifique, Musée de Lyon, Lyon, France, 136 pp.

BERNIER, P.; BARALE, G.; BOURSEAU, J.-P.; BUFFETAUT, E.; DEMATHIEU, G.; GAILLARD, C. & GALL, J.-C. (1982): Trace nouvelle de locomotion de Chelonien et figures d'emersion associees dans les calcaires Lithographiques de Cerin (Kimmeridgien Superieur, Ain, France). *Geobios*, **15 (4)**, 447-467.

BERNIER, P.; BARALE, G.; BOURSEAU, J.-P.; BUFFETAUT, E.; DEMATHIEU, G.; GAILLARD, C.; GALL, J.-C. & WENZ, S. (1984): Découverte des pistes der dinosaures sauteurs dans les calcaires lithographiques de Cerin (Kimmeridgien superior, Ain, France)-implications paléoecologiques. *Géobios Mémoire Spécial*, **8**: 177-185.

DEMATHIEU, G. & GAILLARD, C. (1982): *In* BERNIER, P. *et al.*

DESNOYERS, J. (1859): Sur de empreintes de pas d'animaux dans le gypse des environs de Paris, et particulièrement de la vallée de Mont-Morency. *Bull. Soc. Géol. France*, **16**: 936-944.

EARHART, G. M. & STEIN, P. S. G. (2000): Step, Swim, and Scratch Motor Patterns in the Turtle. *J. Neurophysiol.*, **84**: 2181-2190.

FIORILLO, A. R. (2005): Turtle Tracks in the Judith River Formation (Upper Cretaceous) of South-Central Montana. *Palaeontologia Electronica*, **8** (1, 9A): 11 p, 1MB; <http://palaeo-electronica.org/paleo/2005_1/fiorillo9/issue1_05.htm>.

FITZINGER, L. J. (1836): Entwurf einer systematischen Anordnung der Schildkröten nach Grundsätzen der natürlichen Methode. *Ann. Wiener Mus. Naturgesch.*, **1**: 105-128. Wien.

FOSTER, J. R.; LOCKLEY, M. G. & BROCKETT, J. (1999): Possible turtle tracks from the Morrison Formation of southern Utah. *In*: GILLETTE, D. D. (Ed.): *Vertebrate Paleontology in Utah*. *Utah Geological Survey*. Miscellaneous Publication, **99-1**: 185-191.

FUENTES VIDARTE, C.; MEIJIDE CALVO, M.; MEIJIDE FUENTES, F. & MEIJIDE FUENTES, M. (2003): Rastro de un pequeño tetrápodo de pequeño tamaño en el Weald de Cameros (Sierra de Oncala, Soria, España) nov. icnogen. nov. icnosp: *Emydhipus cameroi*. *In*: *Dinosaurios y otros Reptiles Mesozoicos en España*. *Ciencias de la Tierra*. Instituto de Estudios Riojanos, **26**: 119-128.

GAILLARD, C.; BERNIER, P.; BARALE, G.; BOURSEAU, J.-P.; BUFFETAUT, E.; EZQUERRA, R.; GALL, J.-C.; LAPPARENT DE BROIN, F. de; RENOUS, S. & WENZ, S. (2003): A giant Upper Jurassic turtle revealed by its trackways. *Lethaia*, **6**: 315-322.

GILMORE, C. W. (1926): Fossil footprints from the Grand Canyon. *Smithsonian Miscellaneous Collection*, **77 (9)**: 41 pp.

HAIDINGER, W. von (1841): Über eine neue Art von vorweltlichen Thierfährten. N. Jb. Geol. etc. 1841: 546-548.

HAIDINGER, W. von (1848): Thierfährten aus dem Wiener- oder Karpathensandsteine. Ber. Mitt. Freunde Naturkd. Wien, **3**: 284-288. 1841: 546-548.

HAUBOLD, H. (1971a): Die Tetrapodenfährten des Buntsandsteins in der DDR und in Westdeutschland und ihre Äquivalente in der gesamten Trias. Paläontologische Abhandlungen, Abt. A, *Paläozoologie*, **IV** (3): 395-660, 114 Abb., 29 Tabs., 35 Taf. Berlin.

HAUBOLD, H. (1971b): Ichnia Amphibiorum et Reptiliorum fossilium. *In*: KUHN, O. (Hsg.): *Encyclopaedia of Palaeoherpetology*, **18**: 1-123, 65 figs., 2 tabs. Jena.

HAUBOLD, H.; LOCKELY, M. G.; HUNT, A. P. & LUCAS, S. G. (1995): Lacertoid Footprints from Permian Duen Sandstones, Cornberg and De Chelly Sandstones. *In*: LUCAS, S. G. & HECKERT, A. B. (Eds.): *Early Permian footprints and facies, New Mexico Museum of Natural History and Science Bulletin*, **6**: 235-244.

HITCHCOCK, E. (1858): Ichnology. A report on the sandstone of the Connecticut Valley, especially its fossil footmarks. *Bosont*, **1858**, 220 pp.

HORNUNG, J.; KARL, H.-V. & REICH, M. (2008): An exquisitely preserved turtle footprint from the Berriasian (lowermost Cretaceous) of northwestern Germany. *Abstract and poster to Annual meeting 2008 of the German Palaeontological Society in Erlangen*. Erlanger geol. Abh., Sonderband, **6**: 91-92.

HUNT, A. P. & LUCAS, S. G. (2007): Tetrapod Ichnofacies: A New Paradigm. *Ichnos*, **14 (1)**: 59-68.

JARDINE, W. (1850): Note to Mr. Harkness's paper "on the position of the impressions of footsteps in the Bunter sandstones of Dumfriesshire". *Annals and Magazine of Natural History*, **6**: 208-209.

KARL, H.-V. (1993): Über *Chelonipus torquatus* Rühle von Lilienstern 1939 aus der Trias von Bad Berka (Thüringen, Deutschland). *Mauritiana (Altenburg)*, **14 (2)**: 107-113.

KARL, H.-V.; GEHLER, A.; RODEN, V. J. & REICH, M. (2007a): Die Schildkröten des nordwestdeutschen "Wealden" (Unter-Kreide: Berriasium) und ihre Palökologie. *Wissenschaftliche Mitteilungen*, **36**: 64-65. Technische Universität Bergakademie Freiberg, Geologisches Institut.

KARL, H.-V.; STAESCHE, U.; TICHY, G.; LEHMANN, J. & PEITZ, S. (2007b): Systematik der Schildkröten (Anapsida: Chelonii) aus Oberjura und Unterkreide von Nordwestdeutschland. *Geologisches Jahrbuch*, **B 98**: 5-90.

KARL, H.-V. & TICHY, G. (2000): Eine neue Schildkröten-Fährtenspezies aus der Unteren Trias Thüringens. *Mauritiana (Altenburg)*, **17 (3)**: 421-423.

KUHN, O. (1958): *Die Fährten der vorzeitlichen Amphibien und Reptilien*. 64 S., 13 Taf. Meisenbach, Bamberg.

KUHN, O. (1963): Ichnia Tetrapodorum. *Fossilium Catalagous I: Animalia*, **101**: 1-175.

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 swimtracks. *Pal. and Geol. of the Upper Jurassic Morrison Formation. New Mexico Mus. Nat. Hist. and Science Bull.*, **36**: 193-198.

LOCKLEY, M. & MEYER, Ch. (2000): *Dinosaur Tracks and other Fossil Footprints of Europe*. Columbia University Press, New York, 323 pp.

LULL, R. S. (1904): Fossil footprints of the Jura-Trias of North America. *Memoires of the Boston Society of Natural History*, **5 (11)**: 461-557.

LULL, R. S. (1918): Fossil footprints from the Grand Canyon of the Colorado. *Am. J. Sc.*, 4 **(45)**: 337-346.

MORATALLA, J. J. & HERNÁN, J. (2009): Turtle and pterosaur tracks from the Los Cayos dinosaur tracksite, Cameros Basin (Cornago, La Rioja, Spain): tracking the Lower Cretaceous bio-diversity. *Revista Española de Paleontología*, **24 (1)**: 59-77.

MUSTOE, G. E. (1993): Eocene bird tracks from the Chuckanut Formation, northwest Washington. *Can. J. Earth Sci.*, **30**: 1205-1208.

NOPSCA, F. (1923): Die Familien der Reptilien. *In*: SOERGEL, W.: *Fortschritte der Geologie und Paläontologie*, **2**: 1-210. Berlin.

NOPCSA, F. VON (1926): Osteologia Reptiliorum fossilium et recentium. *In*: DIENER, C. (ed.): *Fossilium Catalogus, 1. Animalia*, Pars **27**: 391 pp.

OWEN, R. (1842): Report on British Fossil reptiles, Part II: Report of the Meeting of the British Association for the Advancement of Science, 1841, **11**: 60-124.

RENOUS, S.; DE LAPPARENT DE BROIN, F. J.; DEPECKER, M.; DAVENPORT, J. & BELS, V. (2008): Evolution of Locomotion in Aquatic Turtles. *In*: WYNEKEN, J.; GODFREY, M. H. & BELS, V. (Eds.): *Biology of Turtles*. CRC Press, Taylor & Francis, pp. 97-138.

ROMER, A. S. & PRICE, L. I. (1940): Review of the Pelycosauria. *Geol. Soc. Am. Spec. Pap.*, **28**: 1-538.

RÜHLE VON LILIENSTER, H. (1939): Fährten und Spuren im Chirotheriumsandstein von Südthüringen. *Fortschr. Geol. Paläont.*, **XII (40)**: 329-341.

SARJEANT, W. A. S. & LANGSTON, W. Jr. (1994): Vertebrate footprints and invertebrate traces from the Chadronian (Late Eocene) of West Texas. *Texas Memorial Museum, Bulletin*, **36**: v + 86 pp.

SOERGEL, W. (1925): *Die Fährten der Chirotheria-eine paläobiologische Studie*. Fischer Jena, 92 pp.

VIALOV, O. S. (1966): On the classification of dinosaurian traces. *Annual of the All-Union Paleontological Society*, **31**: 322-325.

WALTHER, J. (1904): Die Fauna der Solenhofener Plattenkalke bionomisch betrachtet. *Jenaische Denkschriften der Medizinischen und Naturwissenschaftlichen Gesellschaft (Ernst-Haeckel-Festschrift)*, **11**: 135-214.

WRIGHT, J. & LOCKLEY, M. (2001): Dinosaur and turtle tracks from the Laramie/Arapahoe formations (Upper Cretaceous), near Denver, Colorado, USA. *Cretaceous Research*, **22**: 365-376.

