

Footprints of marine reptiles from the Middle Triassic (Anisian-Ladinian) Guanling Formation of Guizhou Province, southwestern China: The earliest evidence of synchronous style of swimming



Lida Xing^{a,b}, Hendrik Klein^{c,*}, Martin G. Lockley^d, Xiao-chun Wu^e, Michael J. Benton^f, Rong Zeng^g, Anthony Romilio^h

^a State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Beijing 100083, China,

^b Shandong Key Laboratory of Depositional Mineralization and Sedimentary Minerals, Shandong University of Science and Technology, Qiaodiao 266590, China

^c Saurierwelt Paläontologisches Museum, Alte Richt 7, Neumarkt D-92318, Germany

^d Dinosaur Trackers Research Group, CB 172, University of Colorado at Denver, PO Box 173364, Denver, CO 80217-3364, USA

^e Canadian Museum of Nature, P.O. Box 3443, Station 'D', Ottawa, ON K1P 6P4, Canada

^f School of Earth Sciences, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TQ, UK

^g Guizhou Provincial Museum, Guiyang 550001, China

^h School of Chemistry and Molecular Biosciences, The University of Queensland, Brisbane, Queensland 4072, Australia

ARTICLE INFO

Keywords:

Tetrapod tracks
Dikoposichnus
Anshunpes
 Nothosaurs
 Placodonts
 Saurosphargids

ABSTRACT

Subaqueously-registered trackways of marine tetrapods are only rarely preserved; some of the best examples so far come from the Shizishan Member (Member II) of the Guanling Formation (Middle Triassic, Anisian-Ladinian) of Yunnan Province in southwestern China. The unit is well-known for the Luoping Biota including abundant skeletons of marine reptiles. The described footprints consist of impressions of fin-like autopodia comprising numerous broad trackways that have been named *Dikoposichnus luopingensis* and interpreted as having been made by foraging nothosaurs. Morphologically identical tracks and trackways have now been discovered near the city of Anshun in Guizhou Province, in slightly older strata and on a large surface of argillaceous dolostone belonging to the Songzikang Member (Member I) of the Guanling Formation. Additionally, a second morphotype is abundant on the same surface, with long trackways that show semi-plantigrade to plantigrade foot imprints with four distinct digit impressions. All tracks are similar in shape and positioned symmetrically, in broad trackways on either side of the trackway midline. Based on several unique features this morphotype is assigned here to the new ichnotaxon *Anshunpes aquacursor* ichnogen. nov. ichnosp. nov. It is interpreted as the trackway of a buoyant and punting tetrapod, using its forefeet only. The trackmaker is inferred to be similar to some diapsid placodonts and saurosphargids whose skeletons have been found in the Guanling Formation (Middle Triassic, Anisian-Ladinian) and in the overlying Falang Formation (Middle–Upper Triassic, Ladinian–Carnian). Comparative measurements of trackways and skeletons support this. Additional associated ichnofossils are enigmatic traces such as isolated large oval impressions and cord-like knobby structures. The palaeoenvironment was a shallow near-coast marine habitat, possibly a lagoon. The ichnofauna from Anshun is important, because it is the first record of subaqueous progression activity by marine diapsid placodonts and/or saurosphargids, and also indicates the early adoption of a synchronous style of swimming by marine reptiles.

1. Introduction

At the invitation of Guizhou Provincial Museum, the lead author (LX) discovered more than 200 footprints attributable to marine reptiles near Qingyuan Village (formerly Qingtaobao Village), Yaopu Town, Anshun Development Zone, Guizhou Province (GPS: 26°10'20.14 N,

105°49'22.26 E) in July 2017 (Fig. 1A). In February 2018, the footprint surface was mapped and photogrammetrically documented by LX and RZ (Supplementary Materials 1–2). In November 2018, the authors LX, HK and RZ revisited the locality, taking further measurements and photographs.

The assemblage is important because the Guanling Formation

* Corresponding author.

E-mail addresses: xinglida@gmail.com (L. Xing), Hendrik.Klein@combyphone.eu (H. Klein), martin.lockley@ucdenver.edu (M.G. Lockley), xcwu@nature.ca (X.-c. Wu), Mike.Benton@bristol.ac.uk (M.J. Benton), a.romilio@uq.edu.au (A. Romilio).

<https://doi.org/10.1016/j.palaeo.2020.109943>

Received 15 April 2020; Received in revised form 13 June 2020; Accepted 16 June 2020

Available online 06 August 2020

0031-0182/ © 2020 Elsevier B.V. All rights reserved.

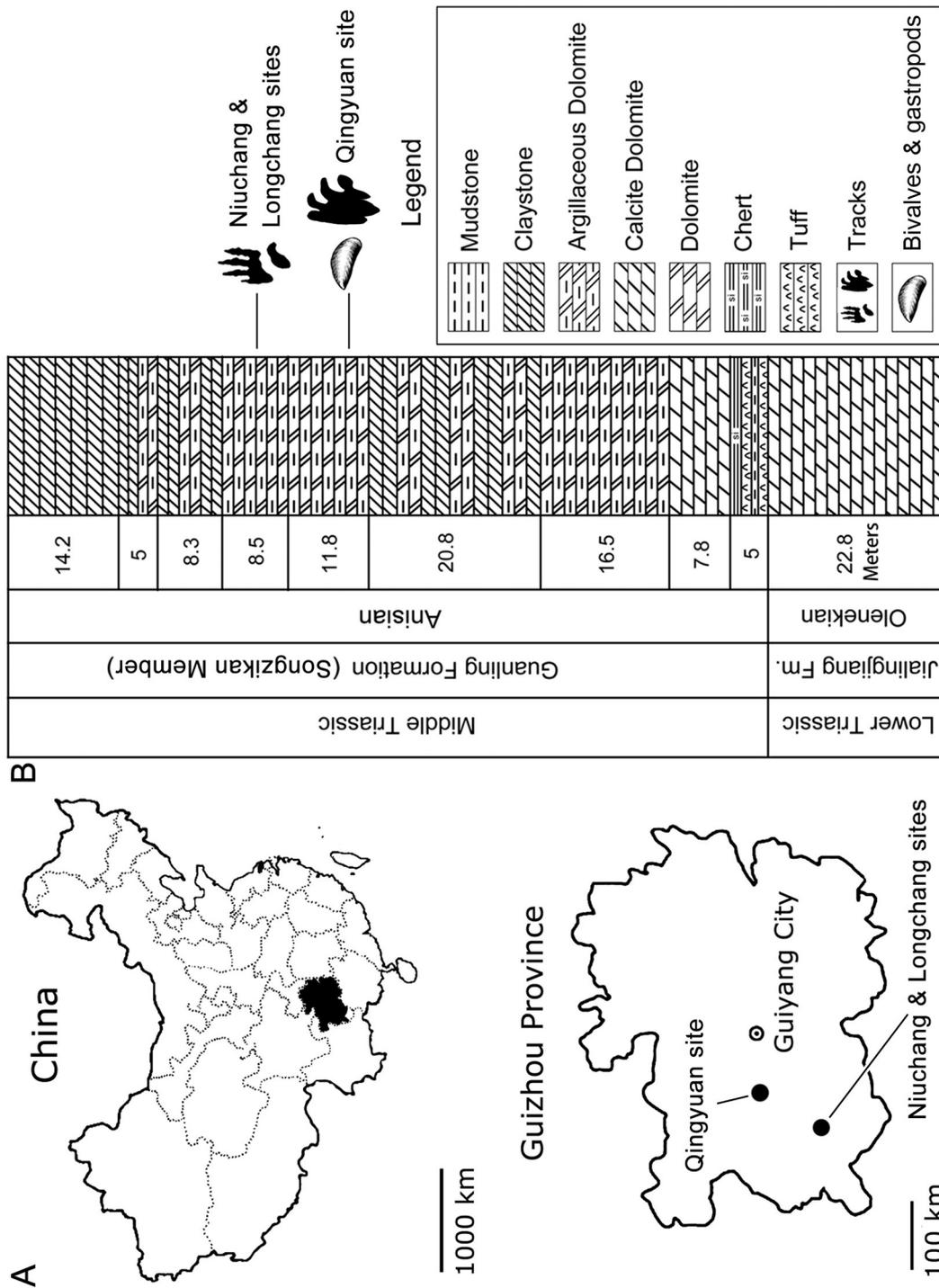


Fig. 1. A. Geographic position of study area in China. B. Section of the Lower-Middle Triassic of Guizhou Province with the Songzikian Member (Member I) of the Guanling Formation (Middle Triassic, Anisian) and position of footprints and invertebrate body fossils; the lower level contains the track surface described in this paper, the upper level assemblages described by Xing et al. (2013).

(Middle Triassic, Anisian-Ladinian) and the overlying Falang Formation (Middle–Upper Triassic, Ladinian–Carnian) have yielded abundant skeletons of marine reptiles (Yin et al., 2000; Benton et al., 2013; Hu et al., 2011), some of them being candidates for the trackmakers. The diverse vertebrate fauna consists of conodonts, fish and tetrapods. Among the tetrapod skeletons are saurosphargids, thalattosaurians, ichthyosaurs and sauropterygians such as placodonts and nothosaurs, tanystropheids (archosauromorphs) and archosaurs. The accompanying invertebrate fauna comprises ammonoids, belemnoids, crinoids, echinoids, bivalves, gastropods, brachiopods, crustaceans and other arthropods, and foraminifers. Also common are plant remains (Wang et al., 2008; Hu et al., 2011). Members of the vertebrate groups are also known worldwide, in particular from Europe (western Tethys and Germanic Basin, e.g. Italy, Switzerland, Germany, The Netherlands) and North America (California, Nevada) (e.g. Wild et al., 1973; Motani, 2009; Scheyer et al., 2017). The fauna and flora of the Middle Triassic (Anisian) Guanling Formation has been termed as the Luoping Biota, named after Luoping County in Yunnan Province where abundant fossils were found. This Biota is also present with rich assemblages in southwestern Guizhou Province. The fauna of the Carnian Wayao Member (= Xiaowa Formation by different terminology) of the overlying Falang Formation is known as the Guanling Biota, because of its geographic location (note that the Guanling Formation is older than, and distinct from, the Guanling Biota). Marginal marine deposits from the Triassic are frequently characterized by the intercalation of marine and terrestrially influenced deposits. While the former mostly contain bones of marine reptiles, the latter often show footprints of terrestrial tetrapods. This is the case for example in the Germanic Basin, in the Vossenveld Formation (Lower Muschelkalk Anisian) of Winterswijk, The Netherlands (Demathieu and Oosterink, 1983).

From the Lower (Songzikian) Member of the Guanling Formation *Chirotherium barthii*, the trackways of terrestrial archosaurs have been described (Lü et al., 2004; Xing et al., 2013a). In Yunnan Province, the same unit yielded numerous *C. barthii* trackways co-occurring with those of small lacertoid *Rhynchosauroides* (Xing and Klein, 2019). Footprints of marine and semi-aquatic reptiles are rarely preserved due to their formation under shallow water conditions with low preservation potential. Sometimes swimming or buoyant tetrapods leave imprints of their autopodia when touching the bottom. These can be preserved occasionally if the area subsequently dried out after areal exposure due to drop of the water level, or the sediment underwent other favourable diagenetic processes. For the described surface the former can be excluded because no mudcracks have been observed. Therefore diagenetic peculiarities of the calcareous sediment might be responsible, but this has to be examined in a detailed sedimentological analysis.

In 2014, Zhang et al. described footprints of marine reptiles from the Guanling Formation of Yunnan Province. These authors attributed them to foraging nothosaurs. The new surface from Guanling, Guizhou has similar tracks and trackways, but additionally has abundant footprints representing a different morphotype that shows distinct impressions of digits and occasionally of the sole (Klein et al., 2019). In the following, we give a detailed description of these footprints and discuss potential producers, comparing them to known foot skeletons of tetrapods from the Guanling and Falang formations. The ichno-assemblage is important because it gives insight into the behavior and movement of marine reptiles along the bottom of Middle Triassic shallow waters, possibly lagoons. Furthermore, it enriches our limited knowledge of the footprints of marine reptiles.

Institutional and ichnological abbreviations

QY = Qingyuan tracksite near Qingyuan Village (formerly Qingtaobao Village), Yaopu Town, Anshun Development Zone, Guizhou Province, China; T = trackway; L = length of footprint; W = width of footprint; “PL” = “pace” length; “SL” = “stride” length (see definitions below); D = distance between successive imprints of the same side of the trackway; Tw = trackway width.

2. Geological setting

2.1. Lithostratigraphy

The Guanling Formation forms the lower part of the Middle Triassic succession in Guizhou Province and mainly comprises limestone, dolostone, and minor claystone strata; its total thickness ranges from 440 m to 810 m (Fig. 1B). The Guanling Formation is divided into two members: the Songzikian Member (Lower Member/Member I) and the Shizishan Member (Upper Member/Member II) (Guizhou Bureau of Geology and Mineral Resources, 1987; Dong, 1997). The Songzikian Member is formed of purple red, greyish-green and yellow green varicoloured calcareous clay and arenaceous and dolomitic clay interbedded with argillaceous dolomite and marlstone and is rich in bivalve body fossils. The Shizishan Member is formed of grey, dark grey thin-to-medium thick bedded limestone, argillaceous limestone and vermicular limestone interbedded with bioclastic limestone and argillaceous dolomite and contains bivalves and ammonites (Dong, 1997).

According to the regional geological map (No. 108 Geological Team, Guizhou Bureau of Geological and Mineral Resource, 1971) and field measurement data by the authors, rocks exposed in Anshun area are more than 470 m thick and are Middle Triassic marine strata deposited on the platform, platform margin and slopes. In this area, the covering Quaternary strata are loose continental deposits, which are often thinner than 2 m. The area of interest comprises grey and light grey thin-to-medium thick-bedded dolomite, limestone interbedded with dolomitic limestone and argillaceous limestone within the Songzikian Member of the Guanling Formation, covered by Quaternary yellowish brown and ash-black clay, silty clay and gravels. The trackways are preserved on the bedding surface of the thin-to-medium thick argillaceous dolostone of the Songzikian Member. The sedimentary environment can be characterized as lagoon to neritic deposits (No. 108 Geological Team, Guizhou Bureau of Geological and Mineral Resource, 1971).

The Qingyuan site (26°10'20.14"N, 105°49'22.26"E) and the Niuchang-Longchang sites (25°34'28.26"N, 105°39'4.50"E; 25°28'14.58"N, 105°30'53.82"E) of Zhenfeng County are about 80 km apart. Both of them belong to the Songzikian Member of the Guanling Formation (Xing et al., 2013a), but the former is slightly older than the latter.

2.2. Biostratigraphy and age of track-bearing strata

The Middle Triassic (Anisian) age of the Guanling Formation is widely accepted (Zhang et al., 2008). It is supported by an invertebrate fauna with gastropods (*Neritaria*) and foraminifers (*Trochammina*, *Eerlandinita*, *Diptoretmina*, *Turritella*, *Aciculella*) found at Luosishan Mountain close to the study area (He, 1984). Additionally, characteristic conodonts and bivalves of the early Anisian are known from the lower Guanling Formation (Songzikian Member) (Wang et al., 2005; Zhang et al., 2009). The known marine reptiles from these strata, however, are less useful for biostratigraphy. Ichnostratigraphically the occurrence of the chirotheriid ichnospecies *Chirotherium barthii*, a few metres above the ichnofauna described here points to an early Anisian age for this unit (Klein and Lucas, 2010; Xing and Klein, 2019; Xing et al., 2013a). Dating of volcanic ashes from the base of the Guanling Formation by the ⁴⁰Ar/³⁹Ar method gives an age of 238–239 Ma, which after radioisotopic data of Mundil et al. (2010) corresponds to a younger (Ladinian) age. Presently this discrepancy with the biostratigraphic data cannot be explained satisfyingly.

3. Materials and methods

The track surface has been protected under a roof built up by local people. Footprints were photographed under natural light conditions using Canon digital camera (5D Mark III EF 24-105 mm F4L) and Nikon

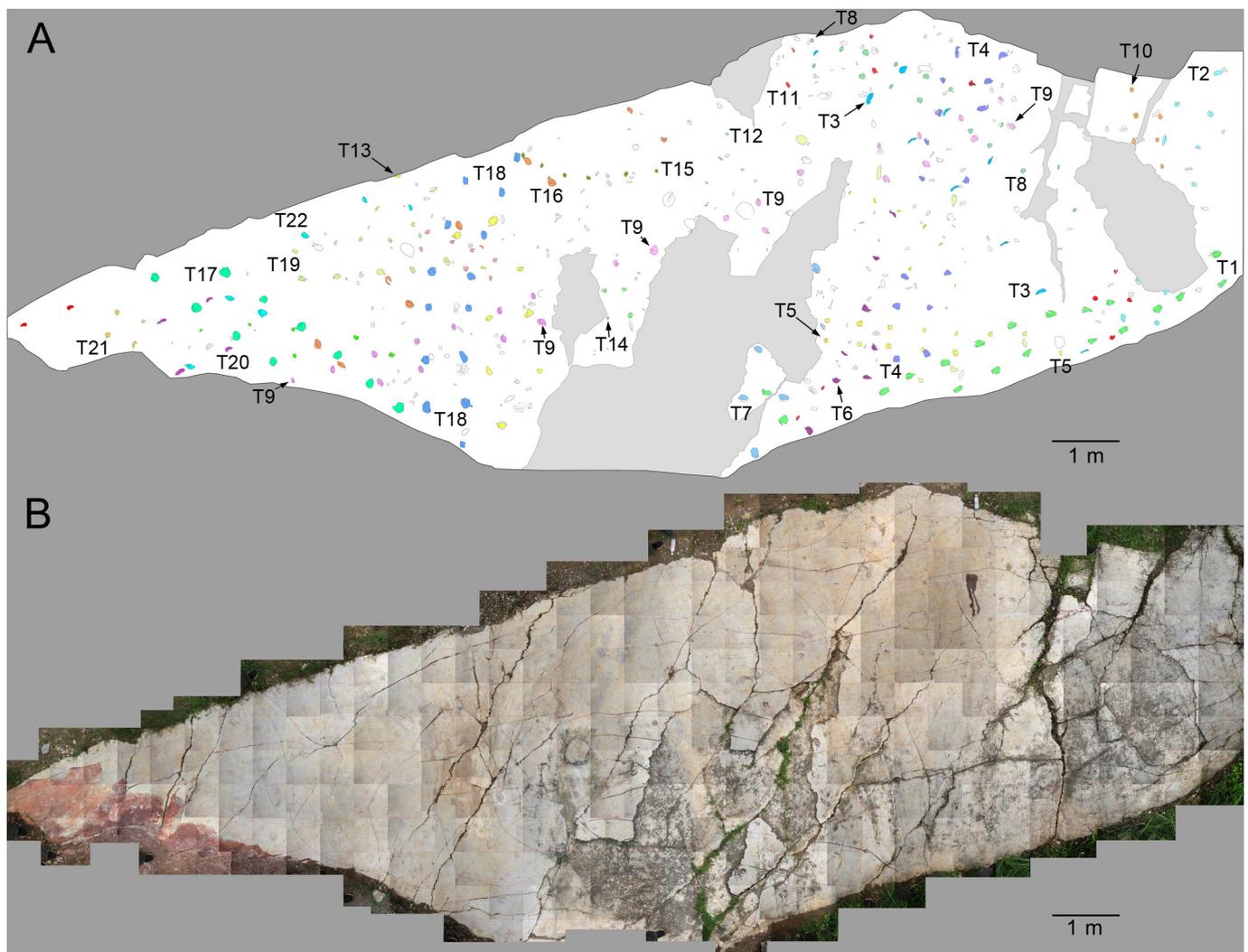


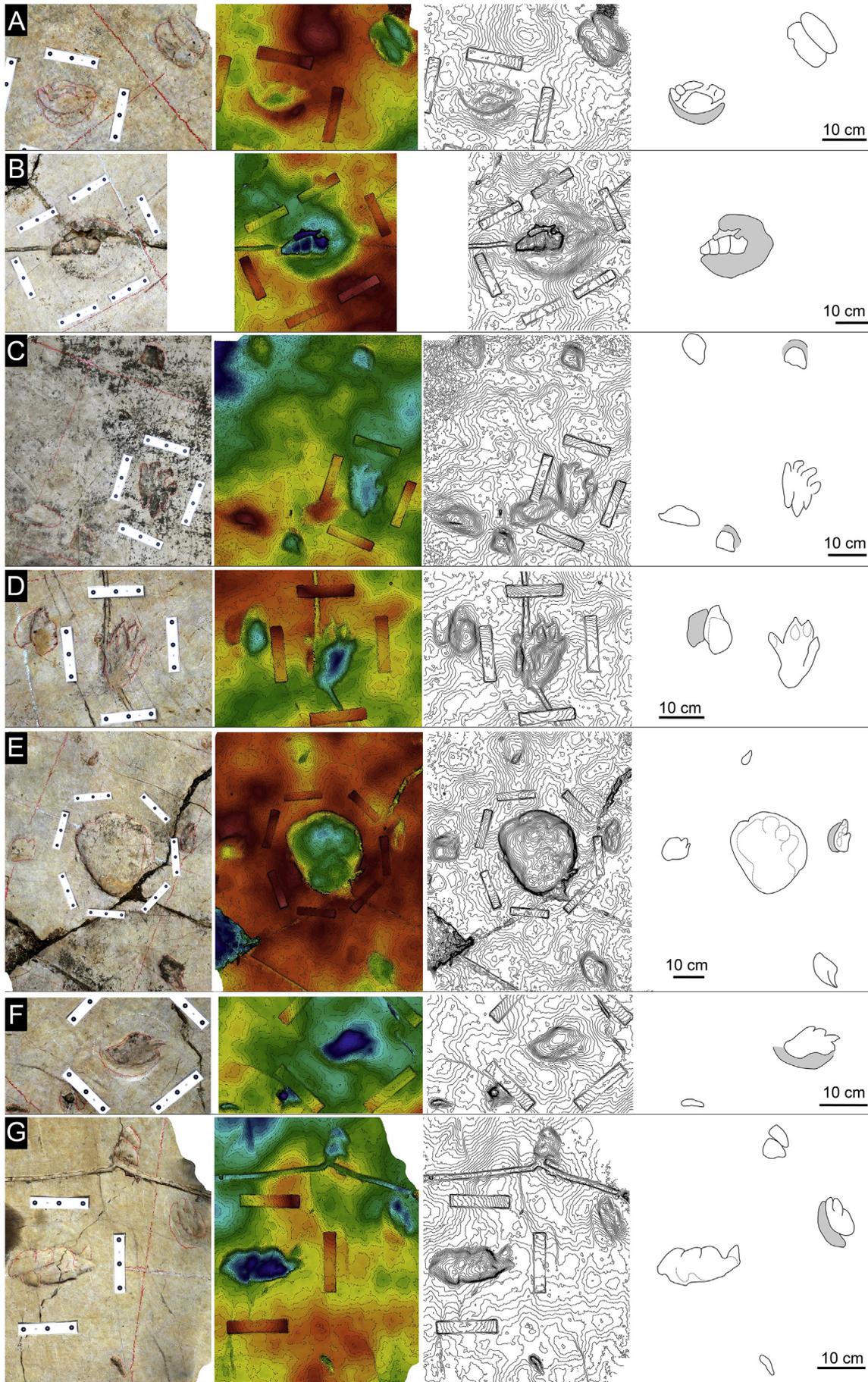
Fig. 2. Overview of the track surface at the Qingyuan locality. A. Map showing distribution of tracks and trackways. Labels are indicated for trackways only. Numbers for isolated tracks are added in the map in Supplementary materials. B. Photogrammetric overview of the site.

D5200 (24 Megapixel) camera equipment. Mapping of the track surface (Fig. 2A) is based on outline tracings on transparency film that were digitized with vector-based drawing software. Photogrammetry data (Figs. 2B, 3) of the in situ track surface was photographed in a series of overlapping images using a Canon digital camera (5D Mark III) under natural lighting conditions. Photographs were added to AgisoftMetaShape Professional Edition (version 1.5) to generate scale-corrected digital surface models (DSM). The 3D virtual model was centred on the centre of the cartesian coordinate system using Meshlab (64bit_fp v2016.12; Cignoni et al., 2008), and the surface topography visualised using filters in the software Paraview (version 5.0.0 64 bit; Ahrens et al., 2005) and CloudCompare (v2.6.1 64 bit; www.cloudcompare.org) following procedures adapted from Xing et al. (2018). Measurements were taken based on standard methods recommended by Leonardi (1987).

Because of the different patterns of progression in trackmakers that were buoyant, we modified the descriptive terms used. Swimming tetrapods, or at least those such as described here that were using their limbs to push along on the sea bed, generally use their limbs synchronously in pairs instead of alternating “left-right-left” as in terrestrially walking forms. “PL” and “SL” (“pace” and “stride” length) were set in quotation marks to indicate that they were not applied in their original definition (Leonardi, 1987; Fig. 4). The term “punting” has also been used for this type of buoyant swimming while also touching the bottom

to help with progression (Martinez et al., 1998; Mustoe, 2019; Lee et al., 2019).

Pace length (sensu stricto) is the distance between successive right-left or left-right autopodial imprints in a trackway of a terrestrially walking tetrapod, while the stride length defines the distance of successive imprints of the same side (right or left) in a trackway. In some buoyant tetrapods, fore- or hindlimbs are moved in concert, meaning their impressions are organised in a symmetric, mirror image pattern on either side of the midline of the trackway (but see extant crocodiles in Farlow et al., 2018, moving in an alternating fashion). In this study, we measure these parameters as if animals were walking on land. Additionally, we introduce the measurement D = the distance between successive imprints on the same side of the trackway. Further, we measured the trackway width T_w between the imprints positioned opposite each other, along a line connecting the centres or digit IV bases, perpendicular to “SL” (see Fig. 4 for explanations). Average measurement data of trackways are in Table 1. All other measurements, including those of isolated tracks are in the Supplementary Materials 3–4. Preservation of footprints was determined based on the classification proposed by Marchetti et al. (2019).



(caption on next page)

Fig. 3. Overview of characteristic morphotypes present at the Qingyuan tracksite as photographs, colour depth maps, contour maps and outline drawings (from left to right). A. Crossing of QY-T16 (left) with QY-T18 (right). B. QY-I220. C. QY-T1 (R5). D. QY-I109. E. QY-I119 (center) with QY-T9 crossing. F. QY-T9 (R9). G. Crossing of QY-T9 (right), QY-T4 (left), with QY-I57 (top).

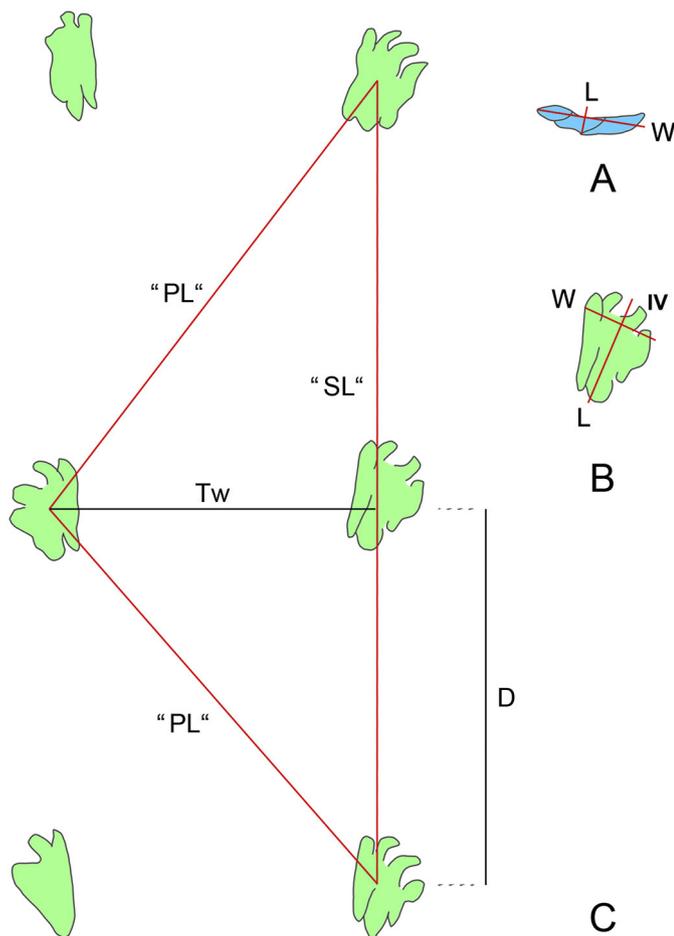


Fig. 4. Sketch explaining measuring methods applied in this study.

Table 1

Measurements being calculated average values for each trackway at Qingyuan tracksite, Anshun, Guizhou Province, China. For detailed measurements see Supplementary Materials 4–5.

Trackway	L	W	L/W	“PL”	“SL”	D	Tw
QY-T1	15.2	9.4	1.6	70.5	106.3	53.2	45.8
QY-T2	8.8	8.3	1.2	74.6	109.1	55.8	50.3
QY-T3	4.3	14.7	0.3	114.8	196.5	98.4	65.9
QY-T4	9.6	9.9	1.5	80.0	103.2	51.2	60.6
QY-T5	6.2	7.5	0.8	57.0	96.5	48.8	28.7
QY-T6	6.0	10.7	0.6	61.2	136.3	61.7	45.9
QY-T7	9.6	14.0	0.7	89.2	133.6	84.1	59.6
QY-T8	6.4	8.0	0.8	49.7	77.3	43.4	35.5
QY-T9	7.6	9.8	1.0	78.1	129.0	63.9	42.6
QY-T10	7.1	5.9	1.2	67.8	76.3	37.9	35.5
QY-T11	8.7	8.0	1.1	163.5	278.4	130.6	51.1
QY-T12	1.8	5.4	0.3	57.6	76.9	37.7	36.5
QY-T13	8.5	10.5	0.8	93.2	145.5	74.5	60.7
QY-T14	6.0	5.6	1.1	51.6	–	30.7	40.4
QY-T15	5.7	5.8	1.0	–	83.2	40.9	–
QY-T16	10.1	13.8	0.8	156.6	280.5	146.9	50.9
QY-T17	12.7	13.5	0.9	96.2	135.1	67.8	67.3
QY-T18	13.0	10.3	1.3	87.7	130.6	65.4	57.5
QY-T19	8.1	8.3	1.0	70.6	99.9	50.7	51.2
QY-T20	13.5	5.5	2.5	109.8	–	78.3	79.1
QY-T21	8.8	5.8	1.5	56.3	–	36.5	40.7
QY-T22	7.9	12.6	0.6	136.5	260.9	127.3	61.5

4. Systematic palaeoichnology

4.1. *Ichnogenus Dikoposichnus* Zhang et al., 2014

4.1.1. *Dikoposichnus luopingensis* Zhang et al., 2014

Type ichnospecies

Dikoposichnus luopingensis monotypic.

Referred material

12 trackways, QY-T3, QY-T5, QY-T6, QY-T7, QY-T8, QY-T9, QY-T12, QY-T13, QY-T14, QY-T16, QY-T20, QY-T22, isolated QY-I194 on same surface as *Anshunpes aquacursor* ichnogen. nov. ichnosp. nov. (see below); all left in situ in the field (Figs. 2–3A, F, G, 5).

Horizon and locality

Songzikian Member (Member I) of the Guanling Formation (Middle Triassic, Anisian), Qingyuan Village, Yaopu Town, Anshun Development Zone, Guizhou Province, China.

Stratigraphic and geographic range

Songzikian Member (Member I) of Guanling Formation in Guanling Province and Shizishan Member (Member II, Luoping Biota) of Yunnan Province, China.

Diagnosis (from Zhang et al., 2014)

Double row of imprints, preserved as concave epireliefs (bed) or convex hyporeliefs (sole). Each imprint is a narrow V-shaped, slot-like depression, with a mound of sediment behind. Individual imprints may be elliptical to sigmoid-shaped in plan view, sometimes with an anterior sweep at the medial edge. Individual imprints are transverse to the direction of travel, spaced widely apart and with variable pace length. When preserved as trackways, prints generally occur in matching pairs, suggesting the limbs moved in concert, but they may be offset, produced by alternate left-right pacing. Overall trackway width is 30–70 cm and individual prints are 5–20 cm along their longest axis, transverse to the direction of movement. Occasionally comprises a single trackway of prints.

Description

These are half moon- to crescent-shaped, posteriorly convex imprints, sometimes showing 3–4 laterally directed sharp digit traces. Characteristically, the posterior margin is formed by a rim of backwardly pushed sediment (Fig. 5). They are generally much wider than long, their length ranging from 1 to 15.7 cm and their width from 1 to 16.5 cm (Table 1, Supplementary Materials 3–4). Trackways are very broad, about 5–6 times imprint width. Imprints are positioned symmetrically about the trackway midline and can be slightly outwardly rotated, parallel or slightly inwardly rotated about their length (L) axis relative to trackway midline or direction of movement. All are preserved as concave epireliefs. After the preservation scale recommended by Marchetti et al. (2019), the preservation values of imprints ranges from 1 to 2.

4.1.2. Discussion

The continuous trackway pattern with imprints positioned symmetrically suggests the trackways of tetrapods while swimming and touching the bottom with their front- or hindfeet/ paddles: i.e., punting (sensu Mustoe, 2019; Lee et al., 2019). The half moon- or crescent-shaped imprints, the laterally pointing digits and the posterior sediment rim supports this (Fig. 5). These trackways are morphologically identical to those described from the Shizishan Member (Member II) of the Guanling Formation of Yunnan Province (Luoping Biota) that have been attributed to the foraging activity of nothosaurs (Zhang et al., 2014; see discussion below). Size of the imprints and the broad trackway pattern (Table 1) corresponds to the trackways described by these authors and for which they introduced the new ichnogenus and -species

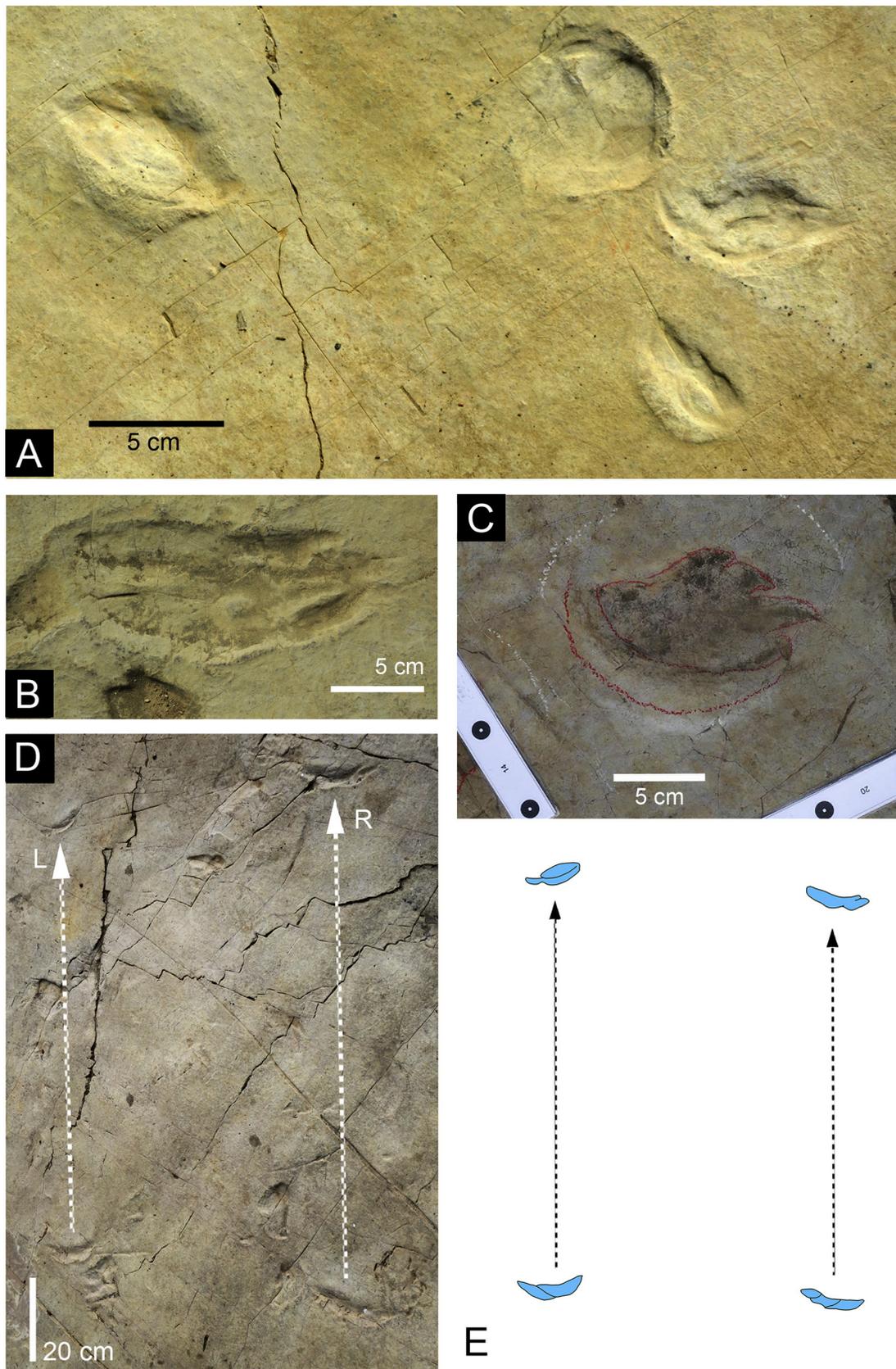


Fig. 5. Selection of *Dikoposichnus luopingensis* tracks from the Qingyuan tracksite. A. Crossing of QT-T16 (*D. luopingensis*) with QY-T17 (*Anshunpes aquacursor*), with QY-194 (isolated *D. luopingensis*) at bottom. B. QY-T3 (R2). C. QY-T9 (R9). D–E. QY-T3 section of trackway.

Dikoposichnus luopingensis (Zhang et al., 2014). Therefore here we assign the material described from Guizhou Province to the same ichnotaxon.

A modest literature already exists on the traces made by large Mesozoic sea turtles that swam with synchronous strokes of their large anterior paddles, sometimes leaving pairs of traces situated symmetrically on either side of the trackway midline (Thulborn, 1989, 1990; Gaillard et al., 2003 and references therein). These traces, some initially misinterpreted (Bernier et al., 1984) are presently only known from the Upper Jurassic of France, but are important evidence of synchronous paddling or rowing swimming styles (Davenport et al., 1984; Renous et al., 1989) which distinguish them from those of the alternate-stroke style of swimming of freshwater turtles. Moreover they show that the taxa that registered *Dikoposichnus* and *Anshunpes* trackways had adopted such synchronous-stroke swimming styles about 90 million years before they again appeared independently among sea turtles.

4.2. Ichnogenus *Anshunpes* ichnogen. nov.

4.2.1. *Anshunpes aquacursor* ichnosp. nov.

Type ichnospecies.

Monotypic.

Holotype

QY-T1, trackway consisting of 10 right and 9 left autopodial (?manus) imprints (Figs. 2–3C, 6–7).

Referred material 9 trackways, QY-T2, QY-T4, QY-T10, QY-T11, QY-T15, QY-T17, QY-T18, QY-T19, QY-T21, and isolated track QY-I109 on same surface as the holotype [Figs. 2–3D, 8–10, 11E (center)].

Type horizon and locality.

Songzikian Member of the Guanling Formation (Middle Triassic, Anisian), Qingyuan Village, Yaopu Town, Anshun Development Zone, Guizhou Province, China.

Stratigraphic and geographic range

Type horizon and locality only.

Diagnosis

Plantigrade to semi-plantigrade tetradactyl imprints, averaging 15 cm in length and 9 cm in width, with outwardly curved, blunt or slightly tapering robust digits and broad sole area. Two medial digits II and III longest, outer digits IV and V shorter, with the lateral one being in a more posterior position relative to all others. Posterior margin of the sole often extended to a bi- or trilobed “heel”. Trackways broad, with $T_w = 45.8$ cm on average. Imprints positioned opposite to each other and outwardly rotated relative to the midline. Different from 1) *Characichnos* by complete semiplantigrade-plantigrade foot impressions with defined digits, vs. scratch-like digit traces in the latter, 2) *Chelonipus* by longer foot and blunt digit impressions vs. very short and broad foot imprints with sharp digit and claw traces in the latter, 3) *Chirotherium* by the less compact anterior digit group II–IV and the relatively long digit V.

Etymology.

After Anshun locality in Guizhou Province where the material was discovered and “*aquacursor*” = “water runner”).

Description

The holotype trackway CY-T1 (Figs. 6–7) shows five well-preserved autopodial imprint pairs (PL ~15 cm, PW ~9 cm) with the left and right track positioned symmetrically. All are rotated outward. “PL” is 70.5 cm and “SL” 106.3 cm on average. The distance D of successive imprints is 53.2 cm and the trackway width T_w 45.8 cm on average (Table 1, Supplementary Materials 3). The trackway is slightly sinuously curved. Imprints are longer than wide with mostly blunt and thick, outwardly curved digits and a broad sole. Digit proportions are two middle toe traces longest, and medial and lateral ones shorter. Some imprints show a distinct posterior shift of the lateral digit. Often digit and sole traces are posteriorly dragged and elongated into a distinct “heel” which is commonly bi- or trilobed. Some imprints show only three digits impressed with the middle one being the longest.

Tracks of the right side are generally impressed slightly more deeply. All are preserved as concave epireliefs and are partly coated by a black-coloured manganese mineral, possibly a diagenetic or post-diagenetic phenomenon. Using the scale of Marchetti et al. (2019), the preservation quality of imprints along the holotype trackway is 1–2. Numerous other trackways QY-T2, QY-T4, QY-T10, QY-T11, QY-T15, QY-T17, QY-T18, QY-T19, QY-T21 and QY-T23 show a partly different imprint shape due to the incomplete registration with only two or three digits: 1) bean-shaped impressions, 2) impressions consisting of elongated digit scratches, 3) rounded impressions with digit traces indistinct or absent (Figs. 9–10; Supplementary Materials 3).

4.2.2. Discussion

This morphotype is different from *Dikoposichnus* in the presence of a fully impressed autopodium with digit and sole traces, similar to the tracks of terrestrially walking tetrapods. However, the imprints were consistently registered symmetrically about the mid line, a pattern characteristically seen in subaqueously swimming (“punting”) or bottom-walking tetrapods (e.g., Gaillard et al., 2003). Because all imprints are identical in shape, they represent the manus or the pes only. Based on the function and characteristic movement of inferred trackmakers, mainly using their forelimbs, and based on congruence with the morphology of manus skeletons (see below), we interpret these imprints as manus tracks.

Also difficult is the interpretation of the preserved digit traces that could represent digits I–IV or digits II–V. The more posterior position of the outermost digit trace, combined with a slight lateral abduction in some imprints, however, suggests the presence of digit V and the latter option as the most likely one. Furthermore there is a slight similarity to chirotheriid archosaur tracks, but digit proportions, the sole portion and the very broad trackway pattern preclude an affinity to this group (see trackmaker discussion below).

Swim tracks of archosaurs have been described under the ichnogenus *Characichnos* from numerous localities, in particular from the Mesozoic (e.g. Whyte and Romano, 2001; Xing et al., 2013b; Thomson and Droser, 2015; see also Farman and Bell, 2020). They mostly consist of three or more parallel scratches of the claws, left when the trace-makers touched the ground with their hindlegs while swimming in a river or lake. *Characichnos* also does not represent a trackmaker that consistently registered a symmetrical trackway, as reported here. The trackways from Guizhou are quite different. While showing extramorphological variation with dragmarks and scratches in several trackways obviously left by buoyant or swimming individuals (QY-T2, QY-T4, QY-T10, QY-T11, QY-T15, QY-T17, QY-T18, QY-T19, QY-T21 and QY-T23), the holotype trackway CY-T1 reflects several fully impressed feet along a larger distance and left by swimming (“punting”) and foraging animals (Figs. 6–7).

The unique morphology of the imprints resembling “normal” terrestrial walking tracks, in combination with distinctive track morphology and a trackway pattern that suggests subaqueous progression above a submerged substrate is not known from the footprint record thus far. Therefore we assign these tracks to a new ichnogenus and ichnospecies we name *Anshunpes aquacursor*.

4.3. Isolated tracks and indeterminate traces and structures

Referred material.

The surface displays 220 isolated impressions, QY-I1–220 (Figs. 3B, E, 11). Some are specified and listed under respective ichnotaxa above (for their position on the surface and measurements see Supplementary Materials 4).

Horizon and locality

Songzikian Member of the Guanling Formation (Middle Triassic, Anisian), Qingyuan Village, Yaopu Town, Anshun Development Zone, Guizhou Province, China.

Description

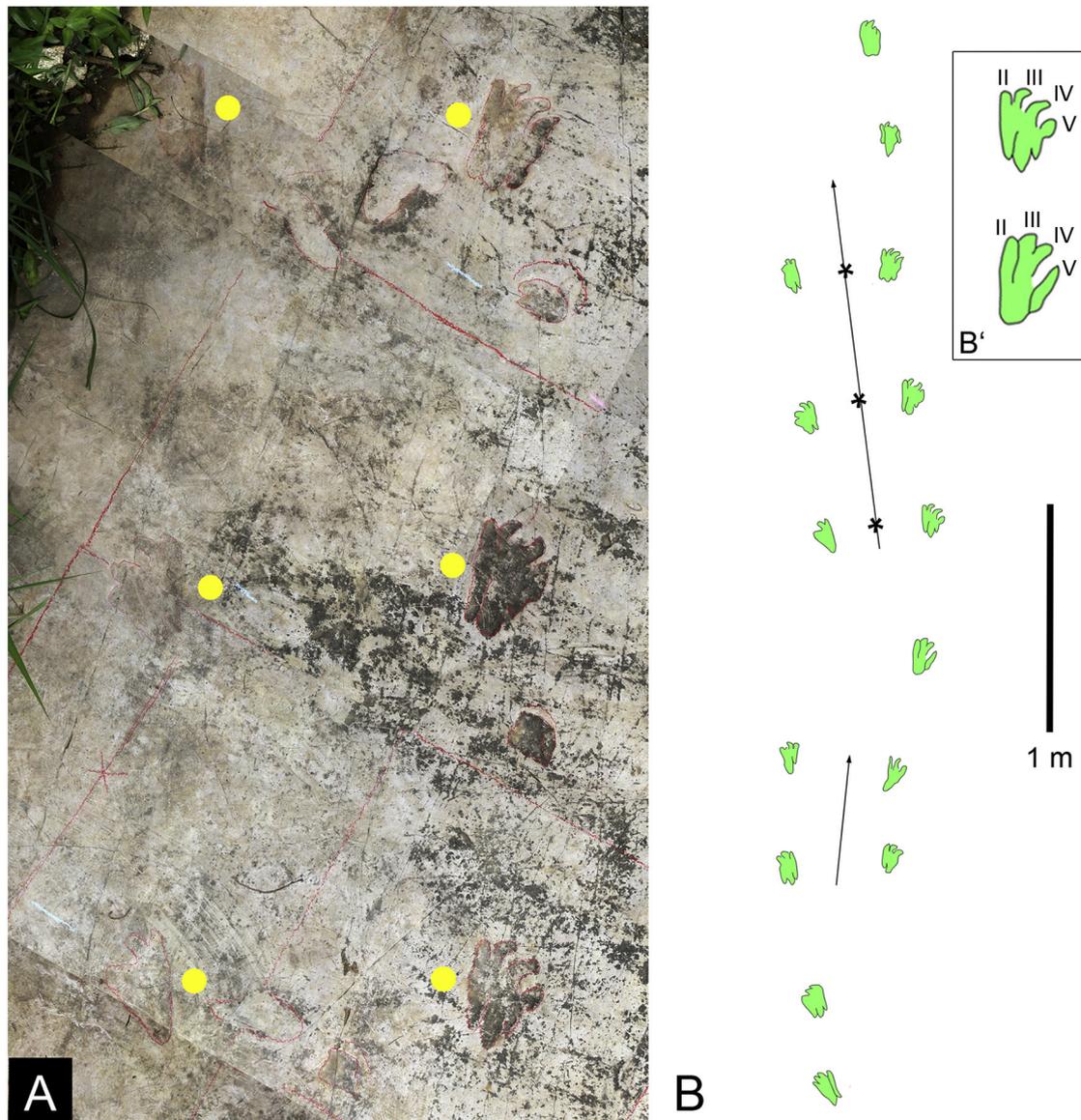


Fig. 6. *Anshunpes aquacursor* ichnogen. nov. ichnosp. nov. holotype trackway QY-T1. A. Photograph showing section of trackway with tracks R5–R7, indicated by asterisks in B. B. Sketch of holotype trackway with B' showing interpreted digit numbering.

Most of these show similarities with the ichnotaxa and morphotypes described above. Some enigmatic traces and structures are briefly described here (Fig. 11). These are: 1) QY-I220, arrangement of deep, short parallel furrows with sharp edges that increase in length from one side to the other (~13 cm by largest dimension), giving it a “gastropod-like” shape (Fig. 11A); it is placed within a large oval impression, similar to that shown in Fig. 11B; 2) QY-I177, large oval impressions showing a series of two or three parallel rims (Figs. 11B, E right); 3) accumulations of “knobby” cords (Fig. 11C); 4) convex hourglass-shaped epirelief of ~34 cm by largest dimension (Fig. 11D).

4.3.1. Discussion

QY-I220 (Fig. 11A) is probably an autopodial impression, similar to some imprints assigned here to *Anshunpes aquacursor* (see above), but with unusually sharp edges, a preservation possibly related to the peculiar substrate that should be further examined. The position within a large oval impression could be just by accident and a kind of overlap of non-related traces. QY-I177 (Fig. 11B) and similar depressions scattered over the track surface are not involved in any trackway pattern. It is presently unclear whether they have anything to do with tetrapods and

the makers of *Dikoposichnus* or *Anshunpes aquacursor*. There is some similarity with fish nests or fish feeding traces, but this cannot be confirmed. The same is true for the accumulations of “knobby” cords (Fig. 11C), that could be the feces of fishes. The organic origin of the hourglass-shaped structure (Fig. 11D) is not sure. It could also represent a sedimentary feature in this calcareous material.

5. Potential trackmakers

5.1. Marine reptiles from Guanling and Falang formations

The Guanling (Anisian) and Falang (Ladinian–Carnian) formations of Guizhou and Yunnan provinces have yielded abundant skeletons of marine reptiles that are considered here as potential producers of the Guanling footprints. In particular neodiapsids are common. Representatives of the turtle stem lineage come from the Carnian Wayao Member (= Xiaowa Formation) of the Falang Formation in Guizhou Province, namely *Odontochelys semitestacea* and *Eorhynchochelys sinensis* (Li et al., 2008, 2018). Ichthyopterygia are present in the Guanling Formation of Guizhou Province with

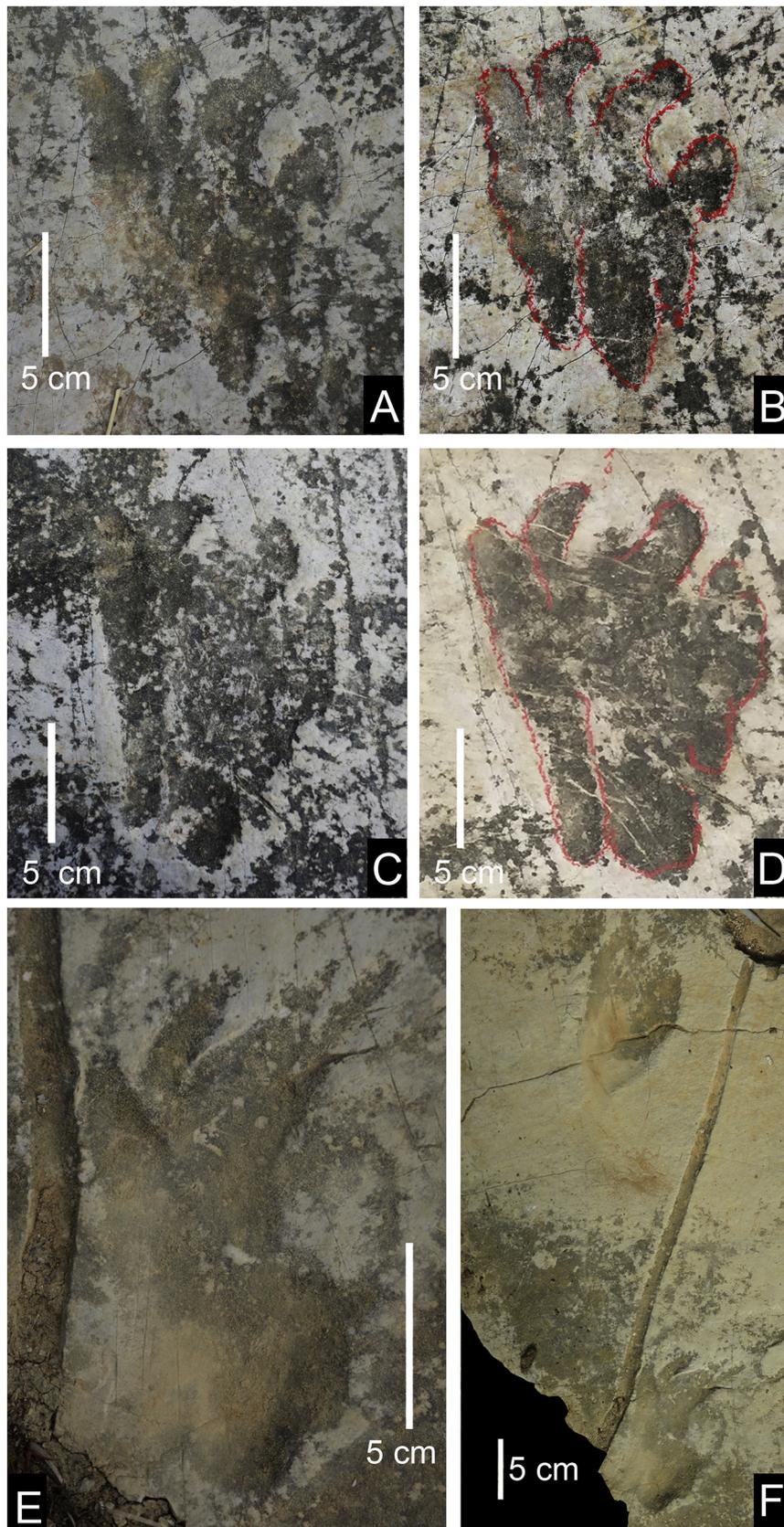


Fig. 7. *Anshunpes aquacursor* ichnogen. nov. ichnosp. nov. Details of tracks from holotype trackway QY-T1. A–B. R5 (with red pen outline in B). C–D (with red pen outline in D). R6. E. R10. F. R10 with L1 of QY-T7. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

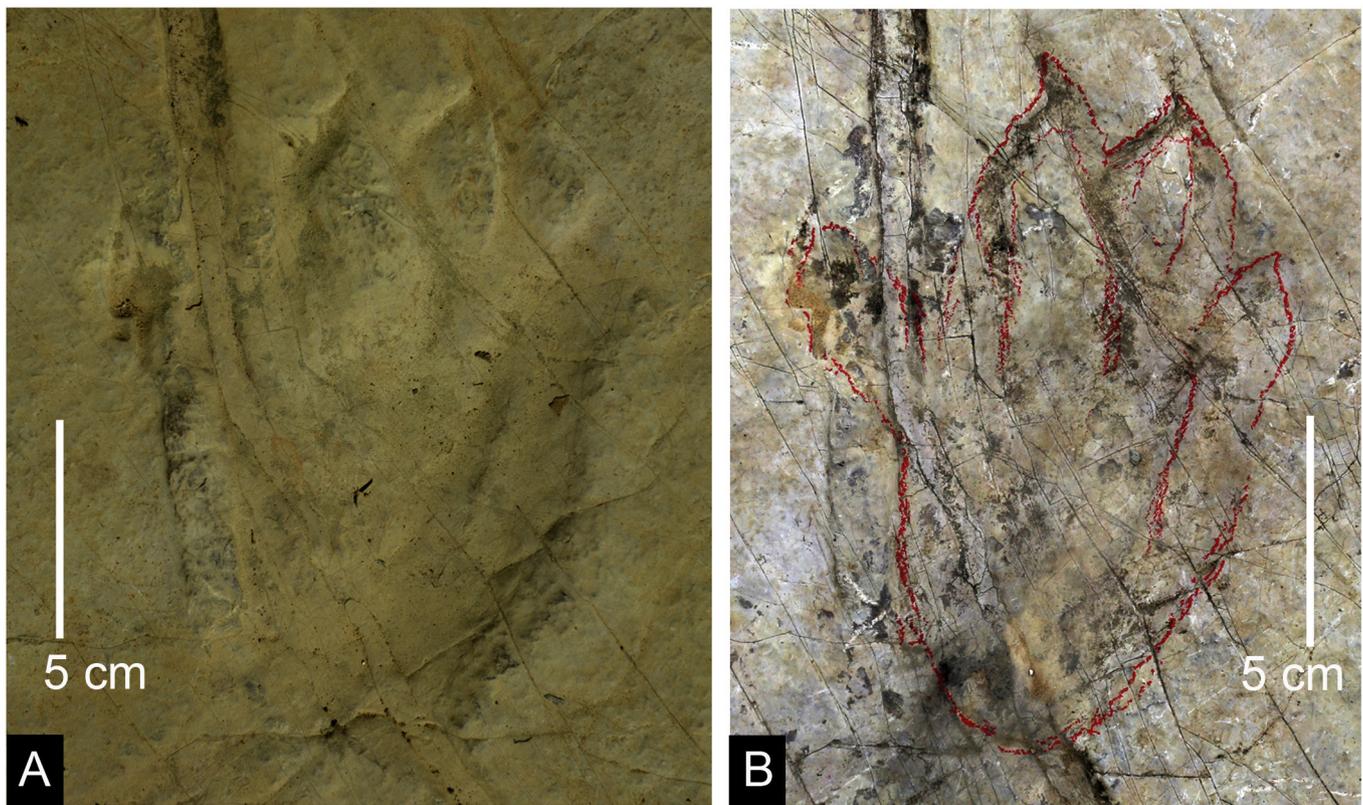


Fig. 8. *Anshupes aquacursor*. A–B. Isolated track QY-1109. B. With red pen outline. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Barracudasauroides panxianensis and *Xinminosaurus catactes*, and in the Wayao Member of the Falang Formation of Guizhou Province with *Qianichthysaurus zhoui*, *Ghuizhouichthysaurus tangae* and *Guanlingichthysaurus liangae* (Li, 1999; Jiang et al., 2006b, 2008b; Maisch, 2010). Thalattosauria are extremely diverse with *Anshunsaurus huangshuensis*, *A. wushaensis*, *Miodentosaurus brevis*, *Xinpusaurus suni*, *X. bamaolinensis*, *X. kohi*, *Concavispina biseridens* (Cheng, 2003; Cheng et al., 2014; Jiang et al., 2004; Liu and Rieppel, 2005; Rieppel et al., 2000, 2006; Cheng et al., 2007; Wu et al., 2007; Zhao et al., 2010, 2013; Liu, 2013; Liu et al., 2013; Maisch, 2014, 2015; Li et al., 2016b). All are from the Wayao Member of the Falang Formation (Carnian) of Guizhou Province. Saurosphargids, well known from European Triassic assemblages are represented in the Guanling Formation by *Sinosauropsphargis yunguiensis* from Yunnan and Guizhou provinces (Li et al., 2011), *Largocephalosaurus polycarpon* from Luoping, Yunnan Province (Cheng et al., 2012) and *L. qianensis* from Guizhou Province (Li et al., 2014). Several genera and species of placodonts come from the Ladinian-Carnian Falang Formation of Guizhou and Yunnan provinces, namely *Sinocyamodus xinpuensis*, *Psephochelys polyosteoderma* and *Glyphoderma kangi* (Li, 2000; Li and Rieppel, 2002; Zhao et al. 2008a, b). The Guanling Formation (Anisian) of Guizhou and Yunnan provinces yielded the eosauroptrygian *Wumengosaurus delicatmandibularis* (Jiang et al., 2008a; Wu et al., 2011), and other members of this group are present in the Guanling and Falang formations with *Sanchiaosaurus dengi*, *Chinchenia sungi*, *Lariosaurus hongguoensis*, *Diandongosaurus acutidentatus*, *Dianopachysaurus dingi*, *Nothosaurus zhang* and *Keichousaurus hui*, *Keichousaurus yuananensis*, *Shingyisaurus unexpectus* (Young, 1965; Rieppel, 1999; Cheng et al., 2004; Jiang et al., 2006a; Shang et al., 2011; Liu et al., 2011, 2014). Only *Sanchiaosaurus* and *Chinchenia* are from the Lower Member of the Guanling Formation while others are from the Upper Member of the Guanling Formation.

Semiaquatic-aquatic archosauromorphs are rare, but occur as the protorosaurs *Dinocephalosaurus orientalis* and *Pectodens zhenyuensis* from

the Guanling Formation of Guizhou and Yunnan provinces (Li, 2003; Li et al., 2004, 2017; Rieppel et al., 2008). Archosauriformes are present in the lower Falang Formation (Zhuganpo Member, Ladinian) of Yunnan Province with *Litorosuchus somnii* (closely related to *Vancleavea* from the Chinle Formation of North America) (Li et al., 2016a). *Diandongosuchus fuyuanensis* from the lower Falang Formation (Zhuganpo Member, Ladinian) of Yunnan Province (Li et al., 2012) has recently been re-assigned to phytosaurian archosaurs (Stocker et al., 2017). *Qianosuchus mixtus* (Li et al., 2006) from the Guanling Formation (Anisian) of Guizhou belongs to Paracrocodylomorpha (Archosauria, Pseudosuchia). *Atopodentatus unicus* from the Guanling Formation of Yunnan Province (Cheng et al., 2014) is a neodiapsid of uncertain affinity.

5.2. Footprints vs foot skeletons - comparison

5.2.1. Stem-turtles

Most skeletons of stem-turtles from the Middle-Late Triassic of China, North America, Greenland and Europe are smaller than the trackmakers of the described Guanling tracks. However, *Eorhynchochelys sinensis* from the Falang Formation (Wayao Member, Carnian) of Guizhou Province (Li et al., 2018) is relatively large, with an estimated width of 58 cm between forelimb autopodia if held in a feasible (extended antero-laterally) position for bottom walking, while the manus was approximately 15.5 cm in length. In the smaller *Odon-tochelys semitestacea* (Li et al., 2008) from the same unit, the estimated width of forelimb autopodia in walking position is only 17 cm, and the comparable length of the forefoot is only 3.5 cm. In comparison the mean trackway width of the holotype of *Anshupes aquacursor* QY-T1 is 45.8 cm, while the mean pes length PL is 15.2 cm (Table 1). Known turtle tracks from the Triassic are all small and show a characteristic broad and short arch in the manus (*Chelonipus torquatus*; Lichtig et al., 2017). The latter feature is typical for turtles and can also be observed

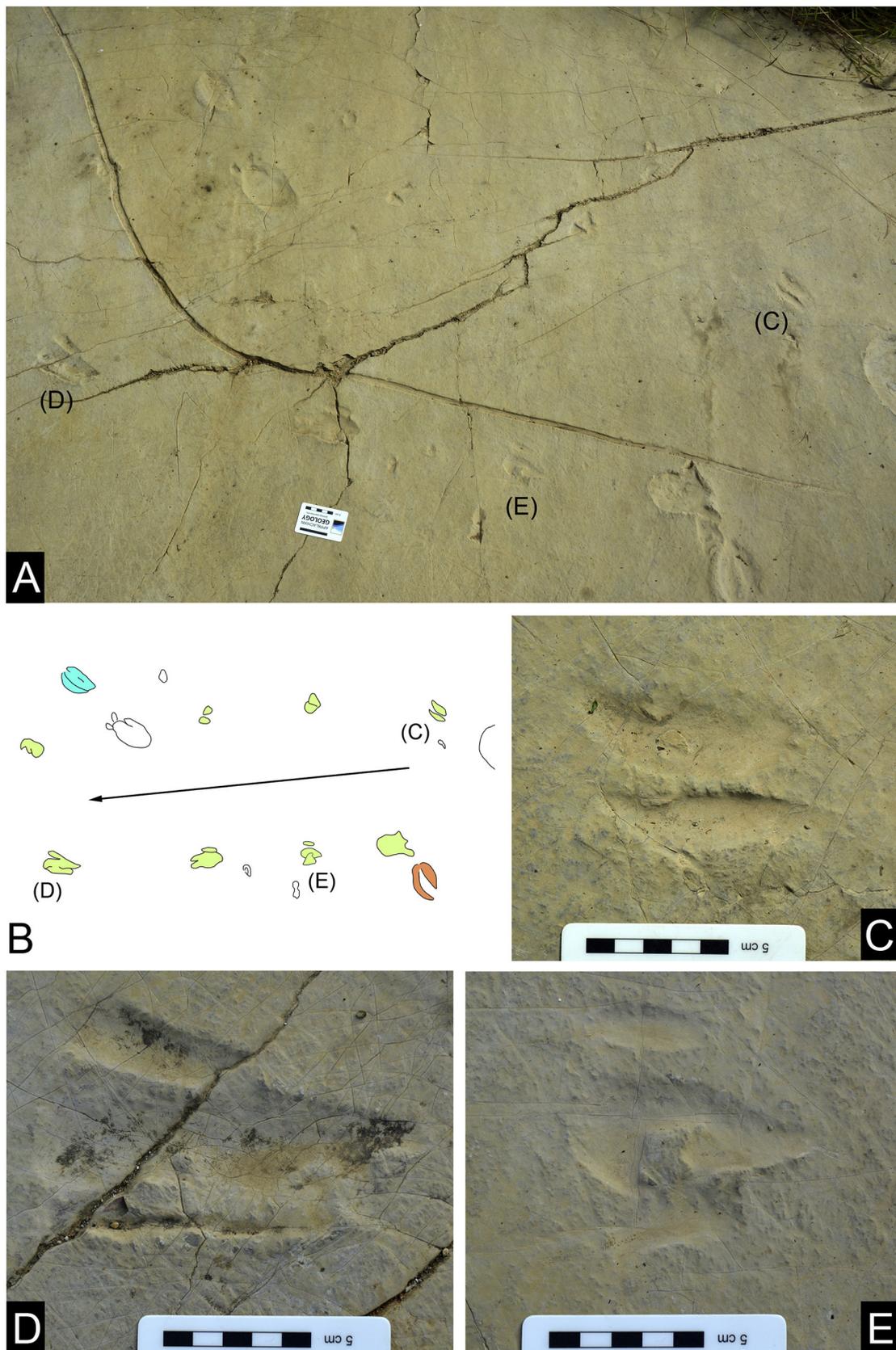


Fig. 9. *Anshunpes aquacursor* trackway QY-T19 showing extramorphological variation. A. Overview photograph indicating position of tracks in C–E. B. Sketch of trackway QY-T19, with tracks from *Dikoposichnus luopingensis* trackways QY-T16 and QY-T22 (orange, turquoise). C–E. Details of QY-T19 as photographs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

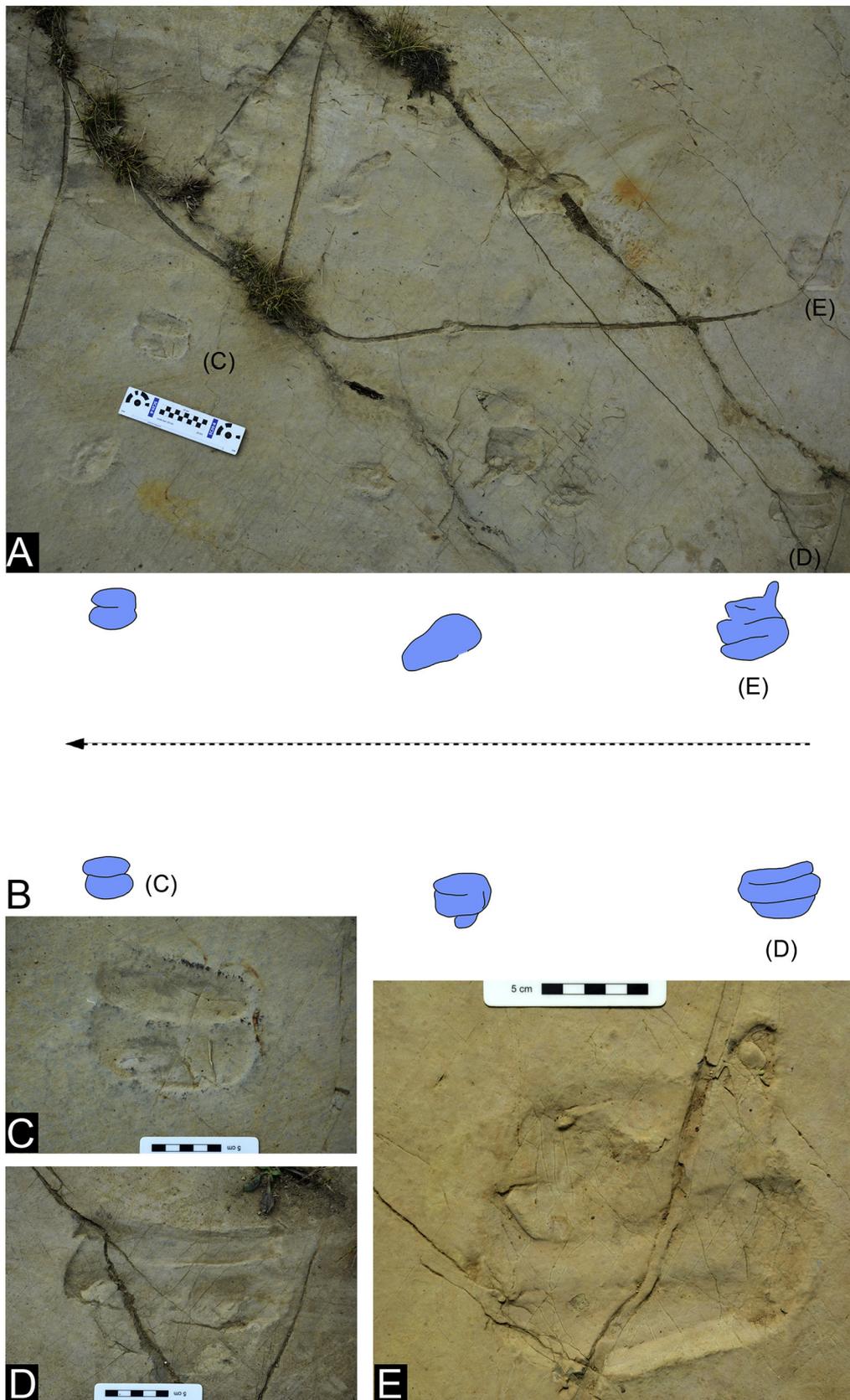


Fig. 10. *Anshumpes aquacursor* trackway QY-T18 showing extramorphological variation. A. Overview photograph indicating position of tracks in C–E. B. Sketch of trackway with C–E indicated. C–E. Photographs with details of trackway QY-T18.

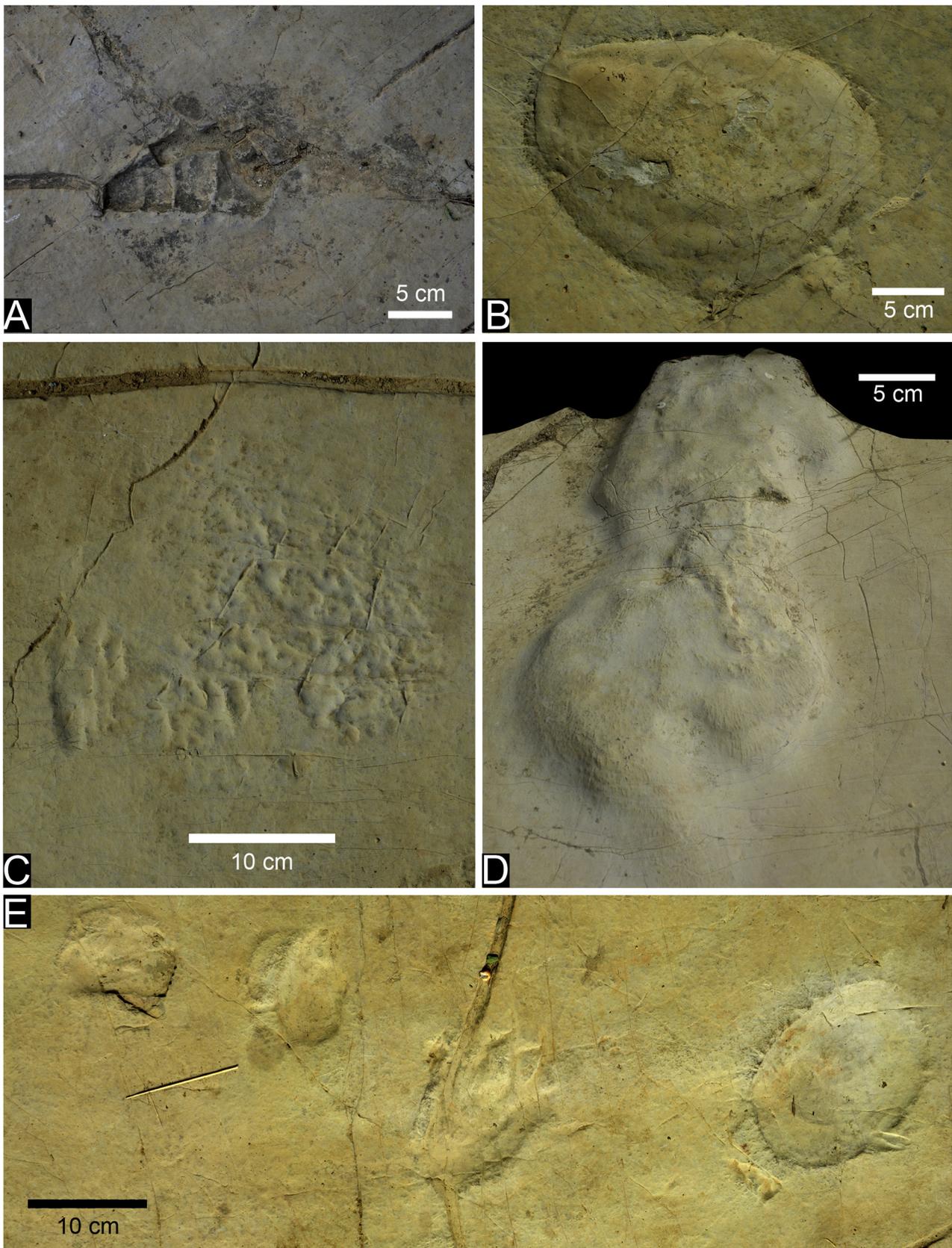


Fig. 11. Indeterminate traces and structures from the Qingyuan surface. A. Furrows with sharp edges, possibly digit traces; notice oval depression surrounding it. B. QY-I177; notice several rims along the margin. C. “Knobby” structures, ?faecal cords; notice *Anshunpes aquacursor* impression QY-I161 at left. D. “Hourglass-shape” structure as convex epirelief. E. Photograph with QY-I109, *Anshunpes aquacursor* (centre), track from QY-T9 and QY-I110, *Dikoposichnus luopingensis* (left) and QY-I107 enigmatic oval impression (right).

in the manus skeletons from the Falang Formation, but this feature is missing in the tracks described here. Digit traces of typical turtle tracks are rather scratch-like, resulting from sharp claws seen also in the skeletons, whereas the Guanling tracks have broad digits with well-rounded, sometimes hoof-like distal ends. Digit proportions of the Guanling tracks, however, could possibly match the skeletons, depending on the correct interpretation of the tetradactyl tracks showing digits II–V. The trackway pattern of *Anshunpes aquacursor* is difficult to compare with that of Triassic turtles (*Chelonipus*), because trackways of the latter are known from terrestrially walking, not from swimming individuals (Lichtig et al., 2018). They show both pes and manus imprints in a broad alternating arrangement with short strides. Trackways of swimming, fully marine turtles are known from the Late Jurassic (Gaillard et al., 2003). They indicate synchronous rowing of fore and hindlimbs, not alternating movement, but with traces of both pes and manus. Digit traces are rather scratch-like as in *Dikoposichnus luopingensis* and not well-defined as in *Anshunpes aquacursor*.

5.2.2. Ichthyopterygia

Ichthyosaurs can be excluded as the trackmakers of the *Anshunpes* tracks that show distinct digit impressions. Their extremities were well-developed as paddles that left no digit impressions at all, or at best scratch-like traces that might look similar to those in the suggested nothosaur foraging tracks (Zhang et al., 2014; see above).

5.2.3. Thalattosauria

Thalattosaurs were well-adapted for swimming. During swimming thalattosaurs held their extremities and autopodia laterally or posteriorly, parallel to the body in order to have a more streamlined shape. “Punting” with anteriorly directed feet or even bottom walking similar to the inferred behavior of placodonts and the known behavior of some turtles (Avanzini et al., 2005) is less likely as is the synchronous rowing of extremities such as in sauropterygians. The laterally compressed tail of thalattosaurs was probably used for strong propulsion while swimming, as in ichthyosaurs. This moving pattern is different from that seen in the trackways where footprints are positioned opposite to each other and point antero-laterally. Furthermore, the pes skeleton of thalattosaurs shows digit IV being the longest, whereas in the manus digit IV is subequal with digit III. This corresponds to the footprints, where digits III and IV are subequal in length, but in the skeletons, claws are moderately sharp whereas in the footprints no sharp claws or scratches are observed and the distal ends of digits are well-rounded.

5.2.4. Saurosphargidae

Sinosauropsphargis yunguiensis comes from the Guanling Formation of Yunnan and Guizhou provinces (Li et al., 2011). One of the Yunnan specimens has a partly preserved autopodium (manus) (Fig. 12A–B). While phalangeal parts are incomplete except for digits IV and V, metatarsals are complete and MC IV is longest. So, digit IV seems to be longest in *Sinosauropsphargis yunguiensis*. *Largocephalosaurus polycarpon* originally considered to be an eosauroptrygian (Cheng et al., 2012), but subsequently referred to Saurosphargidae (Li et al., 2014) has a well-preserved manus, where digit IV is distinctly longest. If our interpretation of digits representing II–V is correct, this does not correspond to the footprints in which digit IV is subequal in length with III. Another point is the thin digit V in the preserved manus of *Sinosauropsphargis* (Fig. 12A–B), whereas digit I seems to be more robust. This could indicate that the former did not leave any trace and the latter is more likely to have been impressed. But this is also dependent on the different load with possible emphasis on outer digits. Nevertheless, uncertainties about the correct digit numbering in the imprints makes this statement about correlation tentative. Unfortunately, no pes is preserved in the skeletons, but most likely digit IV was longest here as well. In the holotype of *Sinosauropsphargis yunguiensis* (Li et al., 2011, Fig. 1A), the total length of the missing anterior autopodium can be estimated at 9 cm, based on proportions in the single preserved

autopodium of a different specimen (Li et al., 2011, Fig. 1B). Based on the suggested position of the forelimbs during progression, while touching the bottom with the forefeet, the width between anterior autopodia might have been 50–65 cm. Compared to the ichnological data these values are larger ($Tw = 45.8$ cm), while the skeletal autopodium is shorter than the imprints ($PL = 15.2$ cm). However, the skeletal data are only estimates of suggested life position from figures and not exact. Further, they reflect a distinct size of the individual. Nevertheless, it seems clear that *Sinosauropsphargis* was able to leave broad symmetrical trackways, possibly similar to those seen in *Anshunpes aquacursor*.

5.2.5. Placodontia

While searching for food such as the shells of marine invertebrates, buoyant or swimming placodonts might have touched the bottom mostly with their forelimbs, with the centre of mass being shifted anteriorly. This corresponds to our interpretation of *Anshunpes aquacursor* as most likely to represent imprints of the manus rather than the pes. All trackways lack imprints of the hindlimbs. During swimming or “punting” placodonts may have held their hindlimbs in a horizontal position aligned to the body. Known skeletons from China are more or less complete, partly showing well-preserved autopodia. These are *Placodus inexpectatus* from the upper Guanling Formation of Guizhou Province (Jiang et al., 2008c), *Sinocyamodus xinpuensis* (Li, 2000), *Psephochelys polyosteoderma* (Li and Rieppel, 2002) and *Cyamodus orientalis* (Wang et al., 2008) from the upper Falang Formation (Wayao Member, Carnian) of Guizhou Province, and *Glyphoderma kangii* (Zhao et al., 2008a, b) from the lower Falang Formation (Zhuganpo Member, Ladinian) of Yunnan Province.

An important feature of *Anshunpes aquacursor* tracks is that the digits show broad rounded or transversely expanded, not tapering distal ends. In particular this matches the autopodial skeletons of the placodonts *Sinocyamodus xinpuensis* (Li, 2000) and *Glyphoderma kangii* (Zhao et al., 2008; Fig. 12C–D). In these taxa the broad, disk-like terminal phalanges indicate that they were either clawless or broadly hoof-shaped. In the manus skeleton digit proportions of *Sinocyamodus* are $I < V < II < IV < III$ (Li, 2000). If the digit numbering is correctly interpreted, the imprints of *Anshunpes aquacursor* display digits III and IV subequal in length and digits II and V shorter. A problem for matching the footprints with *Sinocyamodus* and placodonts is the lack of digit I in the tracks, but in buoyant animals a short digit I might not have left an impression. Furthermore, the manus might have been held more laterally and supinated with pronounced load on outer digits. In the adult specimen of *Sinocyamodus xinpuensis* from the Wayao Member of the Falang Formation (Carnian) described by Wang et al. (2018), the estimated distance between forefeet in supposed progression position (length of foreleg = length of humerus + ulna + metacarpal; data taken from Wang et al., 2018) is 30 cm compared to the trackway width $Tw = 45.8$ cm measured in *Anshunpes aquacursor*. Unfortunately most of the forefoot is missing. The lengths of autopodial skeletons in *Glyphoderma kangii* (Zhao et al., 2008b) compared with the lengths of footprints, are 6 cm and 15.2 cm, respectively. The distance between skeletal forelimb autopodia in supposed progression position is approximately 35 cm, while the mean trackway width (Tw) in *Anshunpes aquacursor* is 45.8 cm. It appears that the placodont skeletons from China are smaller than the trackmaker of *Anshunpes aquacursor*. However, it has to be emphasized that the limb position during progression was only estimated. So these kinds of comparisons and correlation efforts have to be treated with caution. Furthermore measurements can reflect individual or growth related sizes, and of course different placodont species or genera.

After Klein et al. (2015), *Cyamodus* has long and massive humeri that permitted limb rowing with strong strokes and some “wriggling with the rear and tail.” *Sinocyamodus* had at least moderate swimming abilities and furthermore might have performed bottom walking similar to some semi-aquatic turtles. Thus far there is no evidence for webbing in the feet of placodonts (N. Klein et al., 2015), and the footprints also

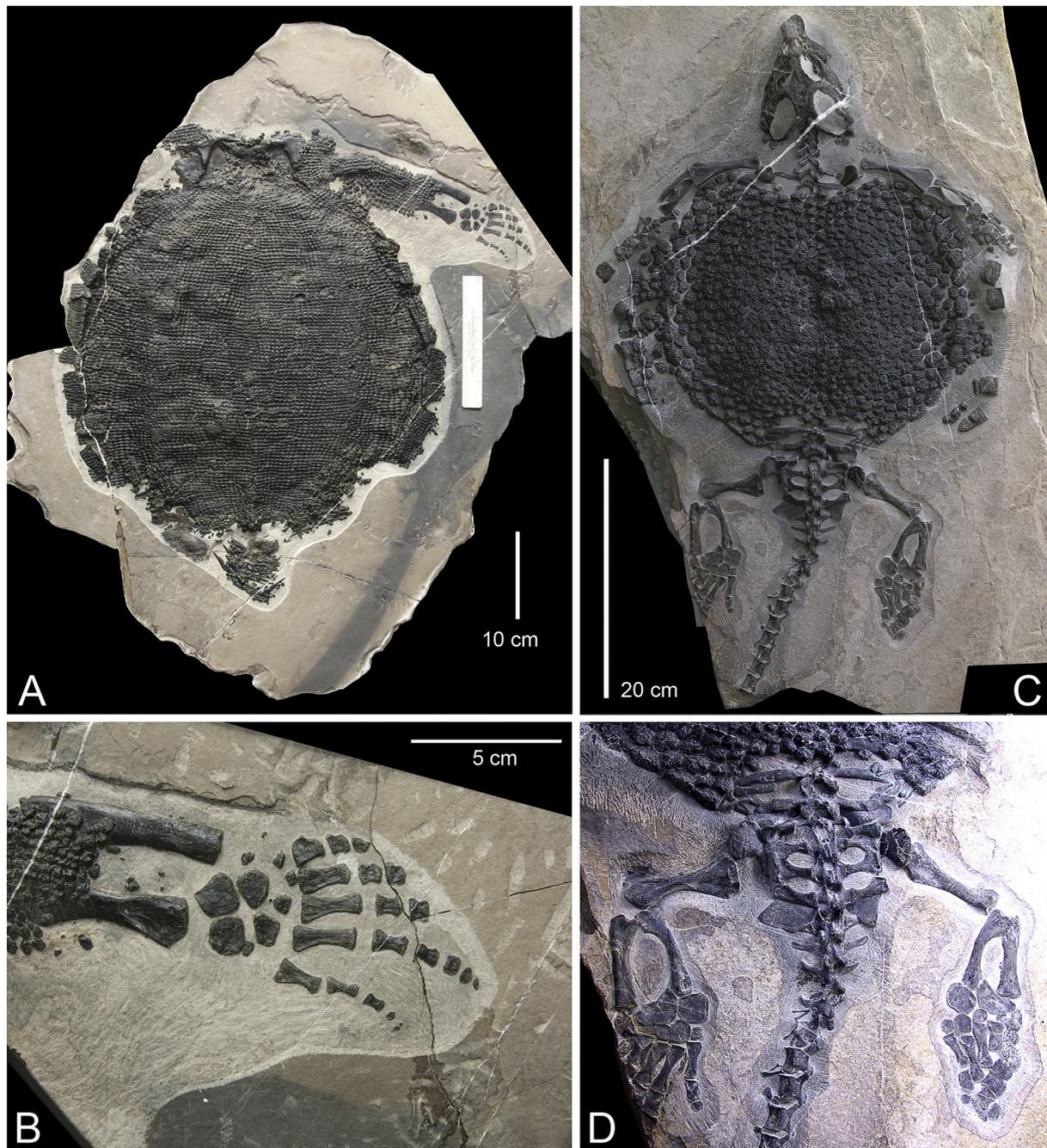


Fig. 12. Skeletons of some potential trackmakers of *Anshunpes aquacursor* ichnogen. nov. ichnosp. nov. from Triassic deposits of southwestern China. A.–B. *Sinosaurosphargis yunguiensis* from the Guanling Formation (Middle Triassic, Anisian) of Yunnan Province. A. Overview of skeleton ZMNH M 8797. B. Detail of A with right forelimb. C–D. *Glyphoderma kangi* (Diapsida: Placodontia). C. Holotype ZMNH M 8729 from the Zhuganpo Member of the Falang Formation (Upper Triassic, Carnian) of Yunnan Province. D. Detail of C with hindlimbs. Photographs from Li et al., 2011 (A–B) and from Zhao et al., 2008b (C–D).

show no impressions of webbing. In summary, placodonts would have left broad trackways with imprints of the forefeet showing robust digit traces with blunt terminations, similar to *Anshunpes aquacursor*. We stress that there is a chronostratigraphic conflict between the skeletal and the ichnological record. While the footprints described here are Anisian in age, the skeletons of *Glyphoderma kangi* are slightly younger (Ladinian), and those of *Sinocyamodus xinpuensis* are Late Triassic (Carnian) in age. *Placodus inexpectatus* is Anisian in age, but in this taxon manual and pedal digits IV are longest. However, it is possible that *Anshunpes aquacursor* trackways belong to placodont taxa whose skeletons have not been found in the Guanling Formation thus far. While oldest placodonts come from the Germanic Basin (Neenan et al.,

2013) and are Anisian in age, “turtle-shaped” cyamodontoid placodonts were present in the Western Tethys region from the Anisian-Ladinian (Scheyer, 2010). An early exchange with the Eastern Tethys and today’s China cannot be excluded. Currently placodonts are widely considered to belong to the turtle-stem (Pan-Testudines or their sister group) (Schoch and Sues, 2015). Middle Triassic *Anshunpes aquacursor* trackways and imprint morphology match the placodont anatomy, but are different from ichnites of the same age attributed to stem-turtles (*Chelonipus*; see above). The latter support terrestrial movement and habitats for early turtles (see Lichtig et al., 2018), whereas most placodonts were fully aquatic or semi-aquatic.

5.2.6. *Eosauropterygia*

Nothosaurs developed paddle-like extremities that might have left wide trackways with digits preserved as scratches of the distal parts only, similar to *Dikoposichnus lopingiensis*, as has been

demonstrated by Zhang et al. (2014).

5.2.7. *Protorosauria*

Protorosaurs are potential trackmakers. In a functional analysis of *Tanystropheus* Renesto and Saller (2018) stress that this tetrapod was a “shoreline dweller rather than a fully aquatic animal” and “it was able to swim for by rowing with symmetrical strokes of the hindlimbs.” However, in the skeletons of protorosaurs from China, for example in *Dinocephalosaurus orientalis* (Li, 2003; Li et al., 2004; Rieppel et al., 2008) and *Pectodens zhenyuensis* (Li et al., 2017) from the Guanling Formation of Yunnan Province, digit IV in both pes and manus are longest. In *Tanystropheus* digit IV in the pes is longest, whereas in the manus it is subequal to digit III. If the hindlimb dominated in progression of these animals and potentially left subaqueous traces, the proportions of the hindfeet do not correspond to the footprints where digit IV is subequal with digit III. Also, in the skeletons digits are slender and claws are acuminate, while the footprints show robust digits with broad and rounded distal ends. Footprints of protorosaurs such as *Tanytrachelos* have been described for example by Lucas et al. (2014) and have been assigned to the ichnogenus *Gwyneddichnium*. It is also significant that two trackways attributed to *Gwyneddichnium*, and hence to a *Tanytrachelos* like form, indicate swimming progression with synchronous registration of the hind feet leaving highly distinctive symmetrical trackways (Lockley, 2006).

5.2.8. *Archosauriformes*

Litorosuchus somnii was adapted to swimming and similar to *Vancleavea* from the Chinle Formation (Upper Triassic) of North America (Li et al., 2016a; Nesbitt et al., 2009). The laterally compressed long tail was obviously used in undulatory movement and forward propulsion. The manus skeleton is nearly complete. Digit III was slightly longer than digit IV and longest, digit II shorter, followed by digit V and I. In the incomplete pes skeleton, according to relative lengths of the metatarsals, digit III was slightly longer than digit IV. These proportions roughly match the relative lengths seen in the footprints of *Anshunpes aquacursor*, but digits in the skeletons are very slender with sharp claws, whereas digit traces in the latter are robust with rounded distal ends.

Based on Stocker et al. (2017) *Dianlongosuchus fuyuanensis* from the Zhuganpo Member of the Falang Formation (Ladinian) of Yunnan Province is a phytosaur, stratigraphically the oldest representative of the group. Pes and manus skeletons of the single specimen are fragmentary. In the pes, digit IV might have been the longest, while in the manus digits III and IV might have been subequal in length if metatarsals/metacarpals are used as a proxy (Stocker et al., 2017). As in other archosaurs, the limb performance during swimming probably did not match the rowing pattern seen in the trackways described here. Skeletons of the paracrocodylomorph *Qianosuchus mixtus* from the Guanling Formation (Anisian) of Guizhou Province show only a fragmentary pes (Li et al., 2006). Therefore, the relative length of digits is uncertain. From the length of the metatarsals digit III might have been longest in the pes, whereas the manus is missing. *Qianosuchus* appears to have been adapted to swimming, but it is doubtful whether it could have performed synchronous rowing movements of left and right hind limbs, while the forefeet did not touch the bottom. Rather swimming and bottom-walking archosaurs, such as living crocodylians, move their legs as in normal walking, with alternating left-right-left paddling, which can be seen for example in extant crocodylians (Farlow et al., 2018). The long flattened tail of *Qianosuchus* suggests undulating power strokes during swimming, in contrast to the straight pattern of the trackways. Further, the claws appear to have been acuminate, not blunt as in the digit terminations in the tracks.

5.3. Early evolution of synchronous style of swimming

Synchronous limb movement or rowing and “punting,” the latter describing subaqueous progression with the fore- or hindfeet contacting the bottom, is scarcely documented from swimming aquatic tetrapods by the trackways of marine turtles, protorosaurs and nothosaurs (Gaillard et al., 2003; Lucas et al., 2014; Zhang et al., 2014; see above). Early aquatic or semi-aquatic amniotes such as the parareptile *Mesosaurus* or the stem-diapsid *Hovasaurus* from the Early Permian-Early Triassic (Núñez Demarco et al., 2018), could have had a similar limb performance, in combination with undulatory movement of the tail, but based exclusively on their skeletons, this cannot be proven, and alternate movement of the limbs not be excluded. For example extant crocodiles move their limbs asynchronously (left-right-left) during bottom walking as do some aquatic turtles (Farlow et al., 2018).

Trackways of buoyant and swimming tetrapods unequivocally document the movement of their producers and can serve as an indicator of peculiarities in the evolution of functional adaptations of the locomotor apparatus. Biostratigraphically *Anshunpes aquacursor* and *Dikoposichnus luopingensis* demarcate the earliest occurrence of the synchronous swimming style in the Middle Triassic (Anisian), probably performed by diapsid marine reptiles such as placodonts, saurosphargids and nothosaurs. For *Anshunpes aquacursor* a placodont similar to *Sinocyamodus* is proposed as a potential trackmaker in Fig. 13. The massive head and robust forelimbs of placodonts suggest an anterior shift of the center of mass (COM) that may have supported punting progression of placodonts along the bottom of the shallow coastal lagoons along the eastern Tethys.

6. Conclusions

The Guanling Formation of southwestern China shows assemblages with abundant trackways, documenting subaqueous activities of swimming and bottom-walking marine diapsids. At the newly described site near Anshun, Guizhou Province, the two ichnotaxa, *Dikoposichnus luopingensis* and *Anshunpes aquacursor* ichnogen. nov. ichnosp. nov. suggest the co-occurrence of nothosaurian sauropterygians, placodonts and/or saurosphargids foraging in shallow marine habitats that possibly were lagoons along the coast of the eastern Tethys. Potential food were cephalopods, bivalves, crustaceans, echinoderms and other invertebrates as well as fish, all abundantly known from body fossils in the Guanling and overlying Falang formations.

In China and the eastern Tethys, the stratigraphically oldest skeletal remains of placodonts and saurosphargids are known from the Anisian Guanling Formation. This time frame corresponds to the occurrence of the footprints attributed to these groups and described here from the same unit. The new ichnotaxon *Anshunpes aquacursor* appears to be the first ichnological documentation of the swimming and “punting” movement of marine diapsid placodonts and/or saurosphargids, supporting the supposed lifestyle of these animals foraging in shallow near-coast habitats of the Tethys Ocean. Based on the new findings, future prospecting of marginal marine settings of other Triassic localities around the globe might provide similar trackways, providing potential for palaeobiological palaeobiogeographical, and palaeoenvironmental studies.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2020.109943>.

Declaration of Competing Interest

None.

Acknowledgements

James O. Farlow and Spencer G. Lucas are thanked for their

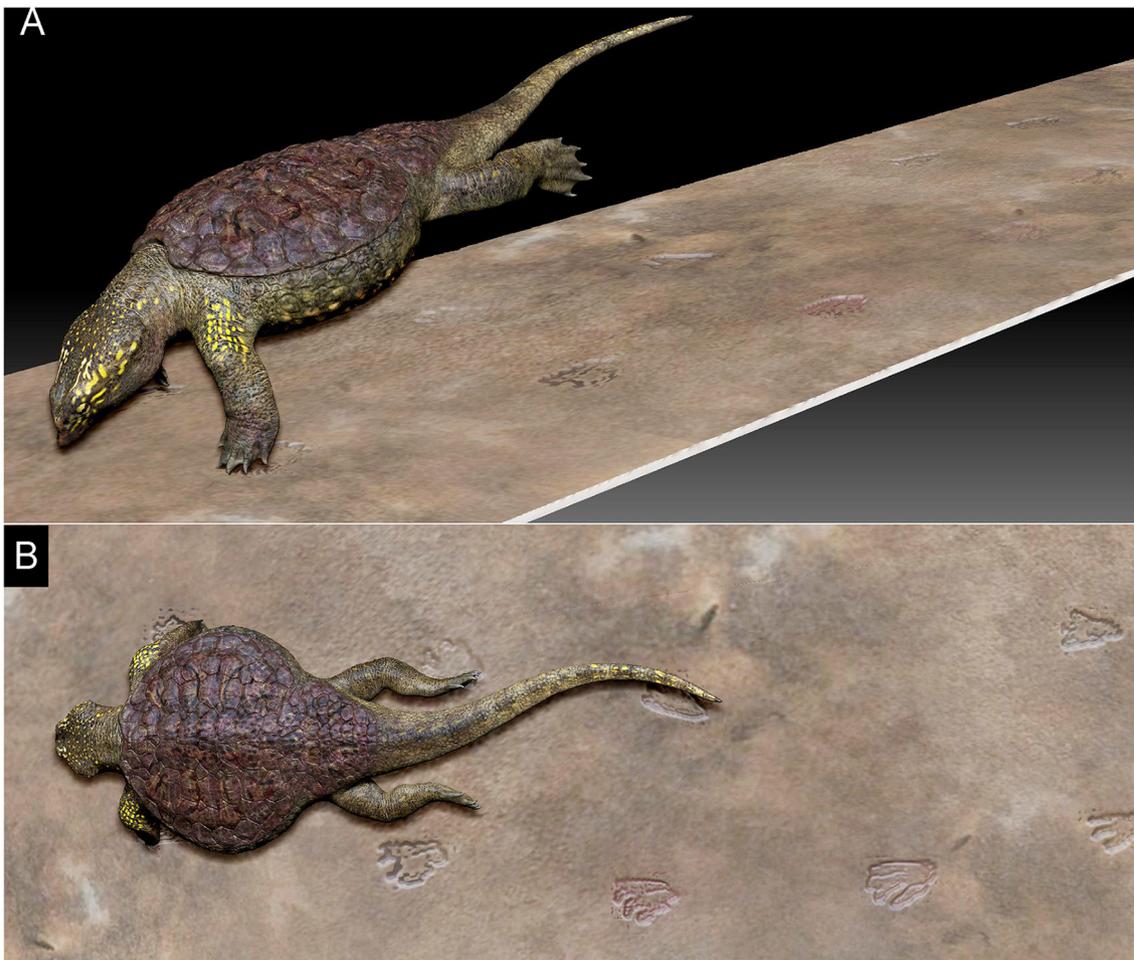


Fig. 13. A swimming (“punting”) placodont similar to *Sinocyamodus* leaving a trackway (*Anshunpes aquacursor*) along the eastern Tethys coast near today's Anshun, Guizhou Province, China. A. Antero-lateral view. B. Dorsal view. Note synchronous style use of forelimbs in progression, while hindlimbs are not involved. Artwork by Cheung Chung Tat.

constructive reviews and comments. The authors appreciate Sifu Cai and Xiuchun Luo (Guizhou Provincial Museum, China), Huiling Yu and Youyue Wang (Friends of Xing Dinosaur Lab, China) who helped in field work. This research was funded by the Shandong Key Laboratory of Depositional Mineralization and Sedimentary Minerals, Shandong University of Science and Technology (No. DMSMX2019008), National Natural Science Foundation of China (No. 41772008).

References

- Ahrens, J., Geveci, B., Law, C., 2005. Paraview: An End-User Tool for Large-Data Visualization. Academic Press, Cambridge, pp. 18.
- 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 Palaeontol. Pol.* 50 (4), 743–755.
- Benton, M.J., Zhang, Q., Hu, S., Chen, Z.Q., Wen, W., Liu, J., Huang, J., Zhou, C., Xie, T., Tong, J., Choo, B., 2013. Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. *Earth Sci. Rev.* 123, 199–243.
- Bernier, P., Barale, G., Bouriseau, J.P., Buffetaut, E., Demathieu, G., Gaillard, C., Gall, J.C., Wenz, S., 1984. Découverte de pistes de dinosaures sauteurs dans les calcaires lithographiques de Cerin (Kimméridgien supérieur, Ain, France): implications paléocologiques. *Geobios* 8, 177–185.
- Cheng, L., 2003. A new species of Triassic Thalattosauria from Guanling, Guizhou. *Geol. Bull. China* 22 (4), 274–277.
- Cheng, Y.-N., Wu, X.-C., Ji, Q., 2004. Triassic marine reptiles gave birth to live young. *Nature (Lett. Nat.)* 432, 383–386.
- Cheng, Y.-N., Wu, X.-C., Sato, T., 2007. A new thalattosaurian (Reptilia: Diapsida) from the Upper Triassic of Guizhou, China. *Vet. Palaeontol.* 45 (3), 246–260.
- Cheng, L., Chen, X.H., Zeng, X.W., Cai, Y.J., 2012. A new eosauroptrygian (Diapsida: Saurapterygia) from the Middle Triassic of Luoping, Yunnan Province. *J. Earth Sci.* 23 (1), 33–40.
- Cheng, L., Chen, X.-H., Shang, Q.-H., Wu, X.-C., 2014. A new marine reptile from the Triassic of China, with a highly specialized feeding adaptation. *Naturwiss.* 101, 251–259.
- Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F., Ranzuglia, G., 2008. In: Scarano, V., De Chiara, R., Erra, U. (Eds.), *MeshLab: An Open-Source Mesh Processing Tool in Eurographics Italian Chapter Conference*, University of Catania, Italy, pp. 129–136.
- Davenport, J., Munks, J., Oxford, P.J., 1984. A comparison of swimming in marine and freshwater turtles. *Proc. R. Soc. B: Biological Sciences* 220, 447–475.
- Demathieu, G., Oosterink, H.W., 1983. Die Wirbeltier-Ichnofauna aus dem Unteren Muschelkalk von Winterswijk (Die Reptilfährten aus der Mitteltrias der Niederlande). *Staringia* 7, 1–51.
- Dong, W.P. (Ed.), 1997. *Stratigraphy (Lithostratic) of Guizhou Province*. China Univ. Geosci. Pr, Wuhan, pp. 1–306.
- Farlow, J.O., Robinson, N.J., Turner, M.L., Black, J., Gatesy, S.M., 2018. Footfall pattern of a bottom-walking crocodile (*Crocodylus acutus*). *Palaios* 33, 406–413.
- Farman, R.M., Bell, P.R., 2020. Australia's earliest tetrapod swimming traces from the Hawkesbury Sandstone (Middle Triassic) of the Sidney Basin. *J. Paleontol.* <https://doi.org/10.1017/jpa.2020.22>.
- Gaillard, C., Bernier, P., Barale, G., Bouriseau, J.-P., Buffetaut, E., Ezquerro, R., Gall, J.-C., de Lapparent, F., Renous, S., Wenz, S., 2003. A giant Upper Jurassic turtle revealed by its trackways. *Lethaia* 36, 315–322.
- Guizhou Bureau of Geology and Mineral Resources, 1987. *Regional Geology of Guizhou Province*. Geological Publishing House, Beijing, pp. 698.
- He, Y., 1984. Middle Triassic foraminifera from Central and Southern Guizhou, China. *Acta Palaeontol. Sin.* 23 (4), 420–431.
- Hu, S.-X., Zhang, Q.-Y., Chen, Z.-Q., Zhou, C.-Y., Lü, T., Xie, T., Wen, W., Huang, J.-Y., Benton, M.J., 2011. The Luoping biota: exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction. *Proc. R. Soc. Ser. B* 278, 2274–2282.
- Jiang, D.-J., Maisch, M.W., Sun, Y.-L., Matzke, A.T., Hao, W.-C., 2004. A new species of (*Xinpusaurus* Thalattosauria) from the Upper Triassic of China. *J. Vert. Paleontol.* 24 (1), 80–88.
- Jiang, D.-Y., Maisch, M.W., Sun, Z.-Y., Sun, Y.-L., Hao, W.-C., 2006a. A new species of *Lariosaurus* (Reptilia, Saurapterygia) from the Middle Anisian (Middle Triassic) of

- Guizhou, southwestern China. N. Jb. Geol. Paläontol. Abh. 242, 19–42.
- Jiang, D.-Y., Schmitz, L., Hao, W.-C., Sun, Z.-Y., 2006b. A new mixosaurid ichthyosaur from the Middle Triassic of China. *J. Vert. Paleontol.* 26 (1), 60–69.
- Jiang, D.-Y., Rieppel, O., Motani, R., Hao, W.-C., Sun, Y.L., Schmitz, L., Sun, Z.Y., 2008a. A new Middle Triassic eosauroptrygian (Reptilia, Sauroptrygia) from Southwestern China. *J. Vert. Paleontol.* 28 (4), 1055–1062.
- Jiang, D.-Y., Motani, R., Hao, W., Schmitz, L., Rieppel, O., Sun, Y., Sun, Z., 2008b. New primitive ichthyosaurian (Reptilia, Diapsida) from the Middle Triassic of Panxian, Guizhou, southwestern China and its position in the Triassic biotic recovery. *Progr. Nat. Sci.* 18 (10), 1315.
- Jiang, D.-Y., Motani, R., Hao, W.-C., Rieppel, O., Sun, Y.-L., 2008c. First record of Placodontoida (Reptilia, Sauroptrygia, Placodontia) from the eastern Tethys. *J. Vert. Paleontol.* 28 (3), 904–908.
- Klein, H., Lucas, S.G., 2010. Tetrapod footprints – their use in biostratigraphy and biochronology of the Triassic. In: Lucas, S.G. (Ed.), *The Triassic Timescale*. Geol. Soc. London Spec. Publ. 334, 419–446.
- Klein, N., Houssaye, A., Neenan, J.M., Scheyer, T.M., 2015. Long bone histology and microanatomy of Placodontia (Diapsida: Sauroptrygia). *Contrib. Zool.* 84 (1), 59–84.
- Klein, H., Xing, L., Benton, M.J., Wu, X.-C., 2019. Subaqueous tracks of marine tetrapods – indications to trackmakers based on new surfaces from the Middle Triassic of Guizhou Province, China. In: 3rd Int. Conf. Cont. Ichinol. (ICCI), Abstr. Vol. Field Trip Guide. *Hallesches Jb. Geowiss. B.* 46, pp. 42.
- Lee, Y.-N., Lee, H.-J., Kobayashi, Y., Paulina-Carabajal, A., Barsbold, R., Fiorillo, A.R., Tsogetbaatar, K., 2019. Unusual locomotion behavior preserved within a crocodyliform trackway from the Upper Cretaceous Bayanshiree Formation of Mongolia and its paleobiological implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 533, 109239.
- Leonardi, G., 1987. Glossary and manual of tetrapod palaeoichnology. *Minist. Minas Energ. Depart. Nacion. Prod. Min., Brasilia*, pp. 117.
- Li, C., 1999. Ichthyosaur from Guizhou, China. *Chin. Sci. Bull.* 44, 1318–1321 (in Chinese).
- Li, C., 2000. Placodont (Reptilia: Placodontia) from Upper Triassic of Guizhou, Southwest China. *Vert. Paläasiat.* 38 (4), 314–317.
- Li, C., 2003. First record of protosaurid reptile (Order Protosauria) from the Middle Triassic of China. *Acta Geol. Sin.* 77 (4), 419–423.
- Li, C., Rieppel, O., 2002. A new cyamodontoid placodont from Triassic of Guizhou, China. *Chin. Sci. Bull.* 47 (5), 403–407.
- Li, C., Rieppel, O., LaBarbera, M.C., 2004. A Triassic aquatic protosaur with an extremely long neck. *Science* 305 (5692), 1931.
- Li, C., Wu, X.-C., Cheng, Y.N., Sato, T., Wang, L.T., 2006. An unusual archosaurian from the marine Triassic of China. *Naturwiss.* 93 (4), 200–206.
- Li, C., Wu, X.-C., Rieppel, O., Wang, L.-T., Zhao, L.-J., 2008. An ancestral turtle from the Late Triassic of southwestern China. *Nature (Letters)* 456, 497–501.
- Li, C., Rieppel, O., Wu, X.-C., Zhao, L.-J., Wang, L.-T., 2011. A new Triassic marine reptile from southwestern China. *J. Vert. Paleontol.* 31 (2), 303–312.
- Li, C., Wu, X.-C., Zhao, L.-J., Sato, T., Wang, L.-T., 2012. A new archosaur (Diapsida, Archosauriformes) from the marine Triassic of China. *J. Vert. Paleontol.* 32 (5), 1064–1081.
- Li, C., Jiang, D.-Y., Cheng, L., Wu, X.-C., Rieppel, O., 2014. A new species of *Largocephalosaurus* (Diapsida: Saurophargidae), with implications for the morphological diversity and phylogeny of the group. *Geol. Mag.* 151 (1), 100–120.
- Li, C., Wu, X.-C., Zhao, L.-J., Nesbitt, S.J., Stocker, M.R., Wang, L.-T., 2016a. A new armored archosauriform from the marine Middle Triassic of China, with implications for the diverse life styles of archosauriforms prior to the diversification of Archosauria. *Sci. Nat.* 103, 95. <https://doi.org/10.1007/s00114-016-1418-4>.
- Li, Z.-G., Jiang, D.-Y., Rieppel, O., Motani, R., Tintori, A., 2016b. A new species of *Xinpusaurus* (Reptilia: Thalattosauria) from the Ladinian (Middle Triassic) of Xingyi, Guizhou, southwestern China. *J. Vert. Paleontol.* 36 (6), e1218340.
- Li, C., Fraser, N.C., Rieppel, O., Zhao, L.-J., Wang, L.-T., 2017. A new diapsid from the Middle Triassic of southern China. *J. Paleontol.* 91 (6), 1306–1312.
- Li, C., Fraser, N.C., Rieppel, O., Wu, X.-C., 2018. A Triassic stem-turtle with an edentulous beak. *Nature (Letter)* 560, 476–479.
- Lichtig, A.J., Lucas, S.G., Klein, H., Lovelace, M., 2018. Triassic turtle tracks and the origin of turtles. *Hist. Biol.* 30, 1112–1122.
- Liu, J., 2013. On the taxonomy of *Xinpusaurus* (Reptilia: Thalattosauria). *Vert. Paläasiat.* 51 (1), 17–23.
- Liu, J., Rieppel, O., 2005. Restudy of *Anshunsaurus huangguoshuensis* (Reptilia: Thalattosauria) from the Middle Triassic of Guizhou, China. *American Mus. Nov.* 3488, 1–34.
- Liu, J., Rieppel, O., Jiang, D.Y., Aitchison, J.C., Motani, R., Zhang, Q.Y., Zhou, C.Y., Sun, Y.Y., 2011. A new pachypleurosaur (Reptilia: Sauroptrygia) from the lower Middle Triassic of southwestern China and the phylogenetic relationships of Chinese pachypleurosaur. *J. Vert. Paleontol.* 31 (2), 292–302.
- Liu, J., Zhao, L.-J., Li, C., He, T., 2013. Osteology of *Concavispina biseridens* (Reptilia, Thalattosauria) from the Xiaowa Formation (Carnian), Guanling, Guizhou, China. *J. Paleontol.* 87 (2), 341–350.
- Liu, J., Hu, S.X., Rieppel, O., Jiang, D.-Y., Benton, M.J., Kelley, N.P., Aitchison, J.C., Zhou, C., Wen, W., Huang, J., Xie, T., Lv, T., 2014. A gigantic nothosaur (Reptilia: Sauroptrygia) from the Middle Triassic of SW China and its implication for the Triassic biotic recovery. *Sci. Rep.* 4, 7142.
- Lockley, M.G., 2006. Observations on the ichnogenus *Gwyneddichnium* and *Gwyneddichnium*-like footprints and trackways from the late Triassic of the western United States. *New Mexico Mus. Nat. Hist. Sci. Bull.* 37, 170–175.
- Lü, H.B., Zhang, Y.X., Xiao, J.F., 2004. *Chirotherium*: fossil footprints of primitive reptiles in the Middle Triassic Guanling Formation, Zhenfeng, Guizhou Province, China. *Acta Geol. Sin.* 78, 468–474.
- Lucas, S.G., Szajna, M.J., Lockley, M.G., Fillmore, D.L., Simpson, E.L., Klein, H., Boyland, J., Hartline, B.W., 2014. The Middle-Late Triassic tetrapod footprint ichnogenus *Gwyneddichnium*. *New Mexico Mus. Nat. Hist. Sci. Bull.* 62, 135–155.
- Maisch, M.W., 2010. Phylogeny, systematics, and origin of the Ichthyosauria – the state of the art. *Palaeodiversity* 3, 151–214.
- Maisch, M.W., 2014. On the morphology and taxonomic status of *Xinpusaurus kohi* Jiang et al., 2004 (Diapsida: Thalattosauria) from the Upper Triassic of China. *Palaeodiversity* 7, 47–59.
- Maisch, M.W., 2015. A juvenile specimen of *Anshunsaurus huangguoshuensis* Liu, 1999 (Diapsida: Thalattosauria) from the Upper Triassic of China. *Palaeodiversity* 8, 71–87.
- Marchetti, L., Belvedere, M., Voigt, S., Klein, H., Castanera, D., Díaz-Martínez, I., Marty, D., Xing, L., Feola, S., Melchor, R.N., Farlow, J.O., 2019. Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present. *Earth-Sci. Rev.* 193, 109–145.
- Martinez, M.M., Full, R.J., Koehl, M.A.R., 1998. Underwater punting by an intertidal crab: a novel gait revealed by the kinematics of pedestrian locomotion in air *versus* water. *J. Exp. Biol.* 201, 2609–2623.
- Motani, R., 2009. The evolution of marine reptiles. *Evo Edu Outreach* 2 (2), 224–235.
- Mundil, R., Pálffy, J., Renne, P.R., Brack, P., 2010. The Triassic timescale: New constraints and a review of geochronological data. In: Lucas, S.G. (Ed.), *The Triassic timescale*. Geol. Soc. London Spec. Publ. 334, 41–60.
- Mustoe, G.E., 2019. Lower Eocene footprints from Northwest Washington USA, Part 1: Reptile Tracks. *Geosciences* 9, 321. <https://doi.org/10.3390/geosciences9070321>.
- Neenan, J.M., Klein, N., Scheyer, T.M., 2013. European origin of placodont marine reptiles and the evolution of crushing dentition in Placodontia. *Nature Com.* 4, 1621. <https://doi.org/10.1038/ncomms2633>.
- Nesbitt, S.J., Stocker, M.R., Small, B.J., Downs, A., 2009. The osteology and relationships of *Vancleavea campi* (Reptilia: Archosauriformes). *Zool. J. Lin. Soc.* 157, 814–864. No. 108 Geological Team, Guizhou Bureau of Geological and Mineral Resource, 1971. The Geological Map of Anshun at Scale 1:200,000 (No. G-48-16). *Min. Geol. Min. Res. Guizhou*.
- Núñez Demarco, P.N., Meneghel, M., Laurin, M., Piñeiro, G., 2018. Was *Mesosaurus* a fully aquatic reptile? *Front. Ecol. Evol.* 6, 109. <https://doi.org/10.3389/fevo.2018.00109>.
- Renosto, S., Saller, F., 2018. Evidences for a semi aquatic life style in the Triassic diapsid reptile *Tanystropheus*. *Riv. Italiana Paleontol. Strat.* 124 (1), 23–34.
- Renous, S., Bels, V., Davenport, J., 1989. Locomotion in Marine Chelonian: adaptation to the aquatic habitat. *Hist. Biol.* 14, 1–13.
- Rieppel, O., 1999. The sauropterygian genera *Chinchenia*, *Kwangisaurus*, and *Sanchiasaurus* from the Lower and Middle Triassic of China. *J. Vert. Paleontol.* 19 (2), 321–337.
- Rieppel, O., Liu, J., Bucher, H., 2000. The first record of a thalattosaur reptile from the Late Triassic of southern China (Guizhou Province, PR China). *J. Vert. Paleontol.* 20 (3), 507–514.
- Rieppel, O., Liu, J., Li, C., 2006. A new species of the thalattosaur genus *Anshunsaurus* (Reptilia: Thalattosauria) from the Middle Triassic of Guizhou Province, southwestern China. *Vert. Paläasiat.* 44 (4), 285–296.
- Rieppel, O., Li, C., Fraser, N.C., 2008. The Skeletal Anatomy of the Triassic protosaur *Dinocephalosaurus orientalis* Li, from the Middle Triassic of Guizhou Province, Southern China. *J. Vert. Paleontol.* 28 (1), 95–110.
- Scheyer, T.M., 2010. New interpretation of the postcranial skeleton and overall body shape of the placodont *Cyamodus hildegardis* Peyer, 1931 (Reptilia, Sauroptrygia). *Palaeontol. Electr.* 13 (2), 15A.
- Scheyer, T.M., Neenan, J.M., Bodogan, T., Furrer, H., Obrist, C., Plamondon, M., 2017. A new, exceptionally preserved juvenile specimen of *Eurosphargis dalsassoi* (Diapsida) and implications for Mesozoic marine diapsid phylogeny. *Sci. Rep.* 7, 4406. <https://doi.org/10.1038/s41598-017-04514-x>.
- Schoch, R., Sues, H.-D., 2015. A Middle Triassic stem-turtle and the evolution of the turtle body plan. *Nature* 523, 584–587.
- Shang, Q.-H., Wu, X.-C., Li, C., 2011. A new eosauroptrygian from Middle Triassic of eastern Yunnan Province, southwestern China. *Vert. Paläasiat.* 49 (2), 155–171.
- Stocker, M.R., Zhao, L.-J., Nesbitt, S.J., Wu, X.-C., Li, C., 2017. A short-snouted Middle Triassic phytosaur and its implications for the morphological evolution and biogeography of phytosauria. *Sci. Rep.* 7, 46028. <https://doi.org/10.1038/srep46028>.
- Thomson, T.J., Droser, M.L., 2015. Swimming reptiles make their mark in the Early Triassic: delayed ecologic recovery increased the preservation potential of vertebrate swim tracks. *Geology* 43 (3), 215–218.
- Thulborn, R.A., 1989. The gaits of dinosaurs. In: Gillette, D.D., Lockley, M.G. (Eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, pp. 39–50.
- Thulborn, R.A., 1990. *Dinosaur Tracks*. Chapman Hall, London.
- Wang, W., Li, C., Wu, X.-C., 2018. An adult specimen of *Sinocyamodus xinpuensis* (Sauroptrygia: Placodontia) from Guanling, Guizhou, China. *Zool. J. Lin. Soc.* 185 (3), 910–924. <https://doi.org/10.1093/zoolnean/zly080>.
- Wang, H.M., Wang, X.L., Li, R.X., Wei, J.Y., 2005. Triassic conodont succession and stage subdivision of the Guandao section, Bianyang, Luodian, Guizhou. *Acta Palaeontol. Sin.* 44, 611–626.
- Wang, X.F., Bachmann, G.H., Hagdorn, H., Sander, P.M., Cuny, G., Chen, X.H., Wang, C.S., Chen, L.D., Cheng, L., Meng, F.S., Xu, G.G., 2008. The Late Triassic black shales of the Guanling area, Guizhou Province, south-West China: a unique marine reptile and pelagic crinoid fossil Lagerstätte. *Palaeontology* 51, 27–61.
- Whyte, M.A., Romano, M., 2001. A dinosaur ichnocoenosis from the Middle Jurassic of Yorkshire, UK. *Ichnos* 8, 233–234.
- Wild, R., Kuhn-Schwyder, E., Peyer, B., 1973. Die Triasfauna der Tessiner Kalkalpen. In: XXIII. *Tanystropheus longobardicus* (Bassani) (Neue Ergebnisse). *Schweiz. Paläontol. Abh.* 95, pp. 1–162.
- Wu, X.-C., Cheng, Y.-N., Sato, T., Shan, H.-Y., 2007. *Miodontosaurus brevis* Cheng et al.,

- 2007 (Diapsida: Thalattosauria): its postcranial skeleton and phylogenetic relationships. *Vert. PalAsiat.* 47, 1), 1–20.
- Wu, X.-C., Cheng, Y.-N., Li, C., Zhao, L.-J., Sato, T., 2011. New information on *Wumengosaurus delicatmandibularis* Jiang et al., 2008 (Diapsida: Sauropterygia), with a revision of the osteology and phylogeny of the taxon. *J. Vert. Paleontol.* 31 (1), 70–83.
- Xing, L.D., Klein, H., 2019. *Chirotherium* and first Asian *Rhynchosauroidea* tetrapod trackways from the Middle Triassic of Yunnan, China. *Hist. Biol.* <https://doi.org/10.1080/08912963.2019.1661409>.
- Xing, L.D., Klein, H., Lockley, M.G., Li, J.J., Matsukawa, M., Xiao, J.F., 2013a. *Chirotherium* trackways from the Middle Triassic of Guizhou, China. *Ichnos* 20 (2), 99–107.
- Xing, L.D., Lockley, M.G., Zhang, J.P., Milner, A.R.C., Klein, H., Li, D.Q., Persons, W.S.I.V., Ebi, J.F., 2013b. A new Early Cretaceous dinosaur track assemblage and the first definite noneavian theropod swim trackway from China. *Chinese Science Bulletin (English version)* 58, 2370–2378.
- Xing, L.D., Lockley, M.G., Guo, Y., Klein, H., Zhang, J.Q., Zhang, L., Persons, W.S., Romilio, A., Tang, Y.G., Wang, X.L., 2018. Multiple parallel deinonychosaurian trackways from a diverse dinosaur track assemblage of the Lower Cretaceous Dasheng Group of Shandong Province, China. *Cret. Res.* 90, 40–55.
- Yin, G., Zhou, X., Cao, Z., Yu, Y., Luo, R., 2000. A preliminary study of the early Late Triassic marine reptiles from Guanling, Guizhou. *Geol. Geochem.* 28 (3), 1–22 (in Chinese with English summary).
- Young, C.C., 1965. On the new nothosaurs from Hupeh and Kweichow, China. *Vert. PalAsiat.* 9 (4), 337–356.
- Zhang, Q.Y., Zhou, C.Y., Lü, T., 2008. Discovery and significance of the Middle Triassic Anisian biota from Luoping, Yunnan Province. *Geol. Rev.* 54, 523–526.
- Zhang, Q.Y., Zhou, C.Y., Lu, T., Xie, T., Lou, X.Y., Liu, W., Sun, Y.Y., Huang, J.Y., Zhao, L.S., 2009. A conodont-based Middle Triassic age assignment for the Luoping Biota of Yunnan, China. *Sci. China Ser. D Earth Sci.* 52 (10), 1673–1678.
- Zhang, Q., Wen, W., Hu, S., Benton, M.J., Zhou, C., Xie, T., Lü, T., Huang, J., Choo, B., Chen, Z.Q., Liu, J., Zhang, Q., 2014. Nothosaur foraging tracks from the Middle Triassic of southwestern China. *Nat. Com.* 11 (5), 3973. <https://doi.org/10.1038/ncomms4973>.
- Zhao, L.-J., Sato, T., Liu, J., Li, C., Wu, X.-C., 2010. A new skeleton of *Miodentosaurus brevis* (Diapsida: Thalattosauria) with a further study of the taxon. *Vert. PalAsiat.* 48, 1), 1–10.
- Zhao, L.-J., He, T., Li, C., 2008a. A brief review on the placodonts from southwestern China. *Proc. Eleventh Ann. Meet. Chinese Soc. Vert. Paleontol.* 243–248.
- Zhao, L.-J., Li, C., Liu, J., He, T., 2008b. A new armored placodont from the Middle Triassic of Yunnan Province, southwestern China. *Vert. PalAsiat.* 46, 171–177.
- Zhao, L.-J., Liu, J., Li, C., He, T., 2013. A new thalattosaur *Concavispina biseridens* gen. et sp. nov. from Guanling, Guizhou, China. *Vert. PalAsiat.* 51 (1), 24–28.