Trackway of Procolophonichnium *isp., convex hyporelief. Photo by Hans van der Donck*

Leaving only trace fossils – the unknown visitors of Winterswijk

U vindt een samenvatting aan het eind van de tekst.

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Abstract | **The tetrapod tracks from Winterswijk receive global attention for their abundance and preservation quality, including long trackways and skin- and claw impressions. The footprint association is consistent with a Middle Triassic age. It includes four ichnotaxa: *Brachychirotherium paraparvum, Rhynchosauroides peabodyi, Procolophonichnium haarmuehlensis* and *Coelurosaurichnus ratumensis*. Their terrestrial producers probably include: archosauriforms, archosauromorphs/lepidosauromophs and both small and large therocephalian therapsids, respectively. These groups are almost completely unknown from the fossil (bone) record of the Vossenveld Formation, which includes mostly aquatic life-forms. The occurrence of vertebrate swimming traces and invertebrate tracks and burrows indicates a marginal marine palaeoenvironment, subject to frequent flooding and rapid drying (tidal flat).**

What is a trace fossil?

Any animal walking on the ground may leave traces, we see it every day. Usually, to produce a trace we need a relatively soft substrate, which can be deformed. This often happens nearby water bodies such as on the muddy coast of the sea (such as the Winterswijk palaeoenvironment, Figure 1), a lake margin, or a river margin etc. But how is it fossilised and what do we mean with 'trace fossil'? A trace fossil is the result of the interaction between a living organism and the substrate, which has been lithified and later exhumed. It is the same process that forms sedimentary rocks. The science which studies the trace fossils is called palaeoichnology. A tetrapod track is originally registered as a depression, usually in a wet substrate that can be dried, superimposed and cracked subsequently. The foot may have been heavy enough to deform the underlying layers as well, in which case an undertrack or underprint will be produced in the underlying layers. The substrate is later filled in with

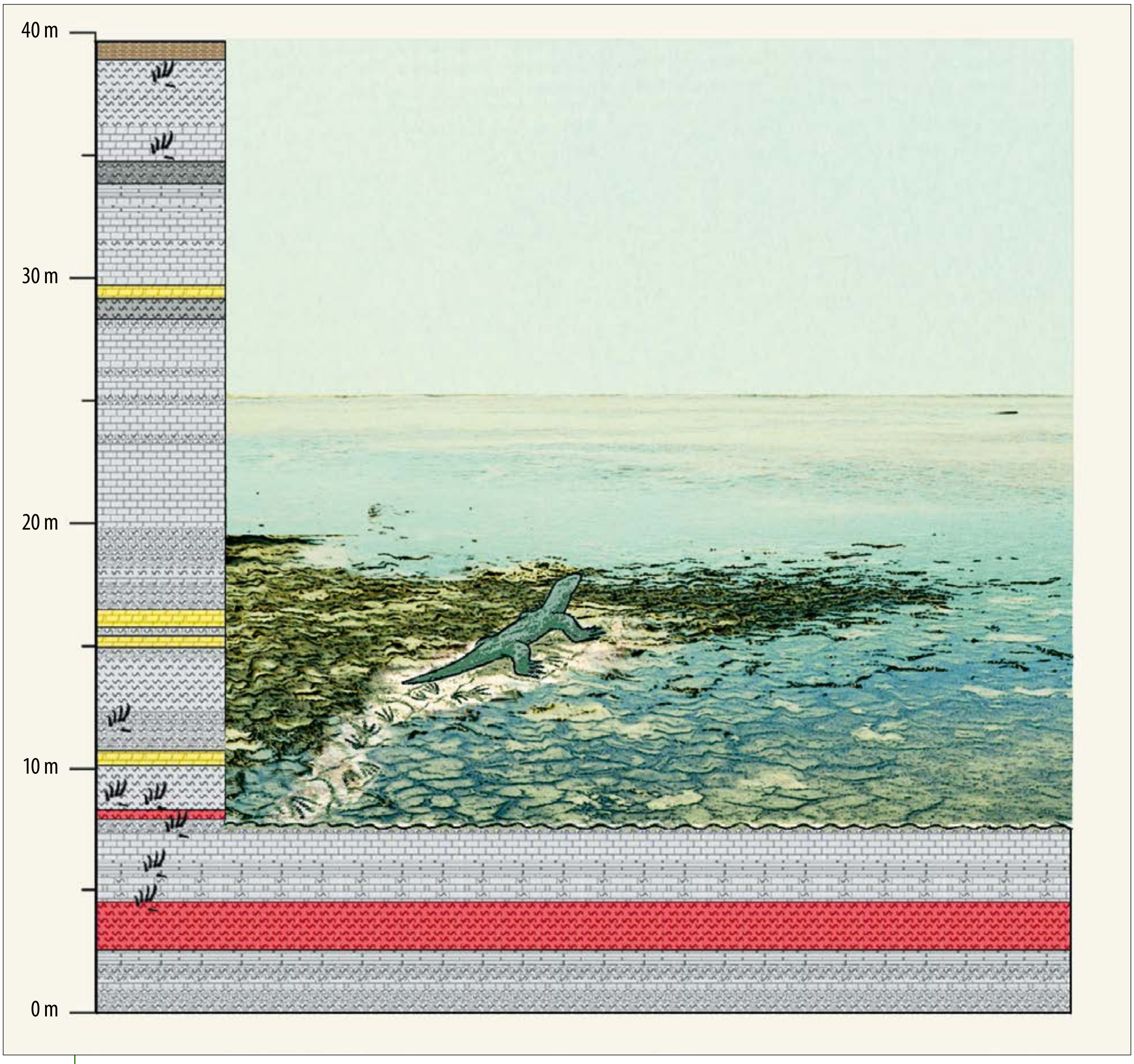


FIGURE 1. | *The stratigraphy of Winterswijk (See During* et al., *in this volume page 168 - Fig. 1, for the legend) with the most well-known track layers indicated. In the foreground is a reconstruction of an unknown trackmaker walking the tidal flats. Preservation of footprints require a rapid alternation of flooding (which makes the substrate soft allowing to leave a footprint) and drying (quickly turning the footprint into a cast) and non-erosive flooding (burying the footprint with a new layer of sediment, which generates a mould).*

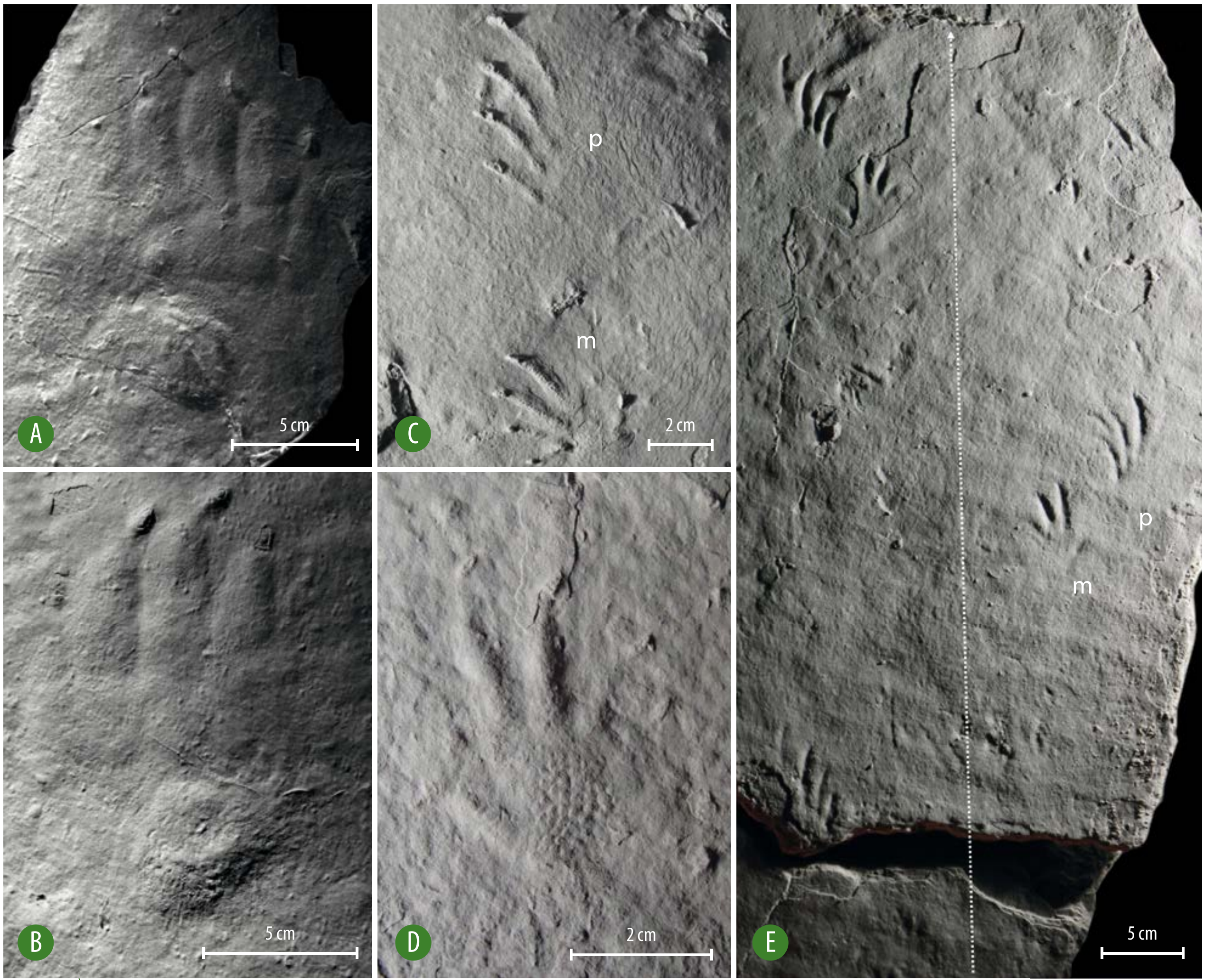


FIGURE 2. | *The tetrapod ichnotaxa from Winterswijk. Archosauromorph neodiapsid tracks. p=pes, m=manus, arrow=trackway direction. A-B)* Brachychirotherium paraparvum*; A) Right pes and invertebrate traces, convex hyporelief; B) Left pes, convex hyporelief. Jos Lankamp private collection. C-E)* Rhynchosauroides peabodyi*; C) Left pes-manus couple with scale skin impressions, convex hyporelief. Naturkunde Museum of Berlin; D) Right manus with scale skin impression, convex hyporelief. Mathias Schab private collection; E) Trackway, concave epirelief. Natural History Museum of Rotterdam.*

new sediment that is gently deposited all over it, with or without minor erosion. It is in this moment that the overlying layer creates the shape of the footprint as a natural cast, made with the trace infilling. In some cases, layers further above the trace level may still be deformed by the trace, creating overtracks in these overlying layers. The strata including the natural trace, the underprint, the undertrack, the natural cast and the overtrack are buried by more sediment and lithified during the process of rock diagenesis. After the diagenesis, the rock with the trace fossils is exhumed by tectonic processes and brought to the surface, ready to be found! Note that several terms used in palaeontology, such as: genus, species, taxon, association, and fauna, have the prefix ichno- in palaeoichnology. Footprints may be preserved as natural moulds (in concave epirelief) or natural casts (in convex hyporelief). For footprints of quadrupeds, the hindfoot impression is named pes and the front foot impression is named manus, and the associated pes and manus form a pes-manus couple. Three or more consecutive pes-manus couples form a trackway. Medial refers to the side of the footprint from the center of the trackway. Lateral refers to the side of the footprint to the outside (left or right) of the trackway. Proximal refers to the footprint hind part and distal to the footprint front part, based on the direction of locomotion. The digit impressions are numbered from I to V, from the medial to the lateral side of the footprint. The distance between two consecutive footprints on the same trackway side is named stride length, the distance between two consecutive footprints on two trackway sides is named pace length, and the angle between two consecutive pace length segments is named pace angulation.

The Winterswijk trace fossils

The Winterswijk locality is known for its trace fossil content since the fifties. The first scientific work is by Faber (1958), who introduced the new ichnotaxon *Chirotherium peabodyi* (later renamed *Rhynchosauroides peabodyi*) based on material from this site. But it is with the research of private collector Henk Oosterink that Winterswijk became one of the most famous tetrapod trace fossil localities of the Triassic. He built a new extensive collection and published the scientific results in two classic works of tetrapod palaeoichnology of the Triassic, in collaboration with

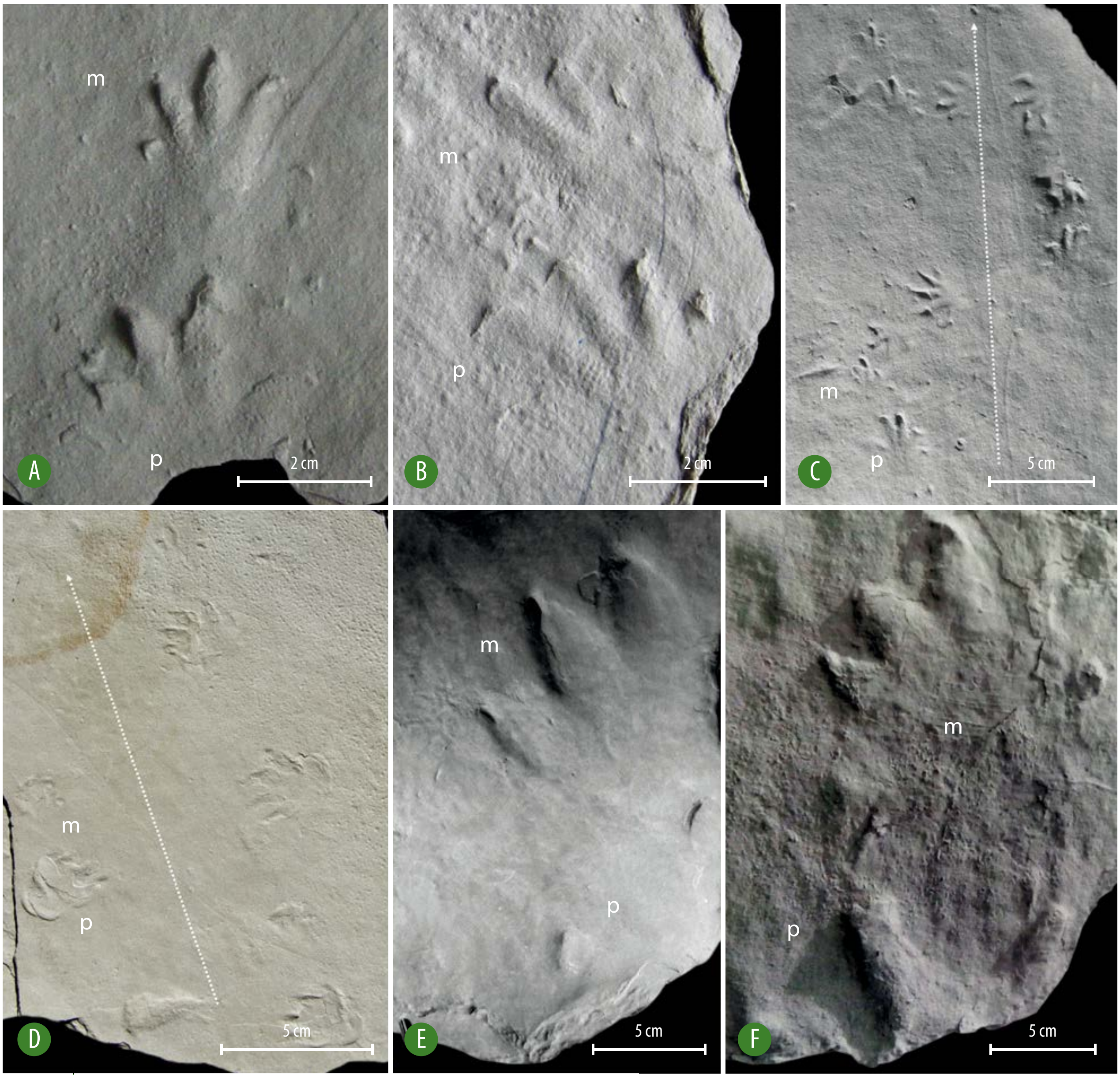


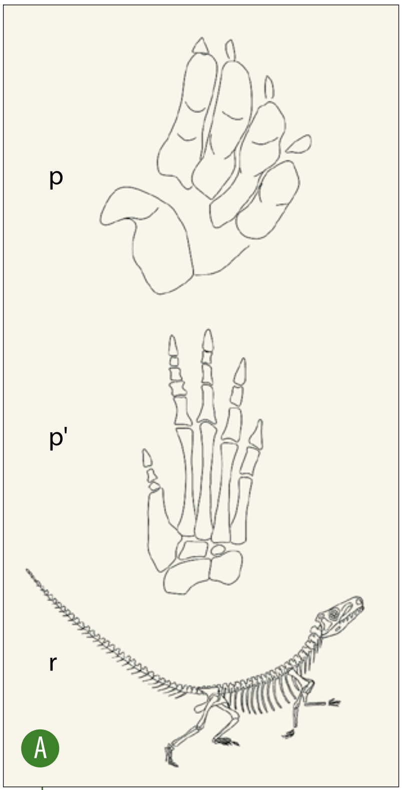
FIGURE 3. | *The tetrapod ichnotaxa from Winterswijk. Therocephalian therapsid tracks. p=pes, m=manus, arrow=trackway direction. A-C)* Procolophonichnium haarmuehlensis*; A) Left pes-manus couple, convex hyporelief; B) Right pes-manus couple with scale skin impression, convex hyporelief. A-B) Hans van der Donck private collection; C) Trackway with thin continuous tail impression and other tracks, convex hyporelief. Naturkunde Museum of Berlin. D) cf.* Procolophonichnium isp. *Trackway, concave epirelief. Hans van der Donck private collection. E-F)* Coelurosaurichnus ratumensis*; E) Right pes-manus couple, convex hyporelief. Jos Lankamp private collection, plaster cast. The original is in the Henk Oosterink private collection; F) Left pes-manus couple, convex hyporelief. Henk Oosterink private collection, photograph from Oosterink* et al. *(2003), modified.*

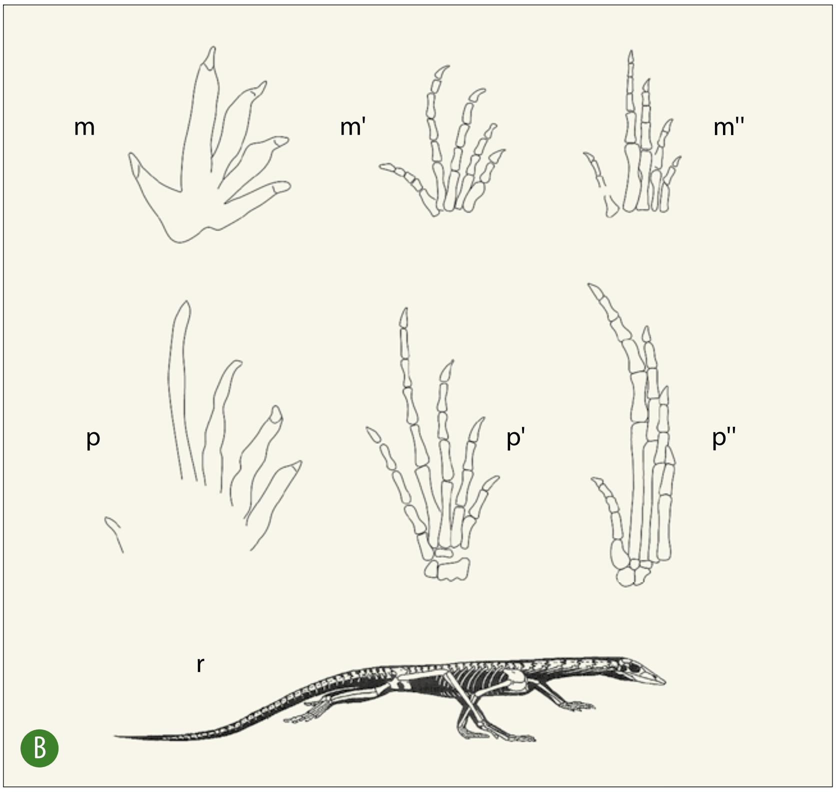
the French ichnologist Georges R. Demathieu (Demathieu & Oosterink, 1983, 1988). Based on the material from the Oosterink collection, they introduced two new tetrapod ichnogenera (*Phenacopus* and *Sustenodactylus*) and six new tetrapod ichnospecies (*Phenacopus faberi, Phenacopus agilis, Procolophonichnium winterswijkense, Brachychirotherium paraparvum, Coelurosaurichnus ratumensis,* and *Sustenodactylus hollandicus*). This extensive collection includes: complete pes-manus couples, trackways, and skin- and claw impressions. More recent work highlights the occurrence of long trackways (Diedrich & Oosterink, 2000) and tetrapod swimming traces (Oosterink, 2009; Schulp *et al.*, 2017). Additionally, fish swimming traces and invertebrate traces were described (Demathieu & Oosterink, 1983; Oosterink 2009). A palaeoenvironmental interpretation of the Winterswijk site was provided by Diedrich & Oosterink (2000), who hypothesised an intertidal setting for the footprint-bearing layers, similar to the German Muschelkalk, while vertebrate and invertebrate remains are brought in during subtidal conditions.

The tetrapod ichnotaxa

***Brachychirotherium paraparvum* (Demathieu & Oosterink, 1988)**
(fig. 2A & 2B)

This ichnotaxon is relatively rare in the Winterswijk quarry (about 20 footprints discovered; Demathieu & Oosterink, 1988). It is characterised by pentadactyl footprints of quadrupeds of intermediate size (foot length of about 13 cm). The pes is longer than it is wide, digits I-IV are relatively thick, parallel and closely grouped together,





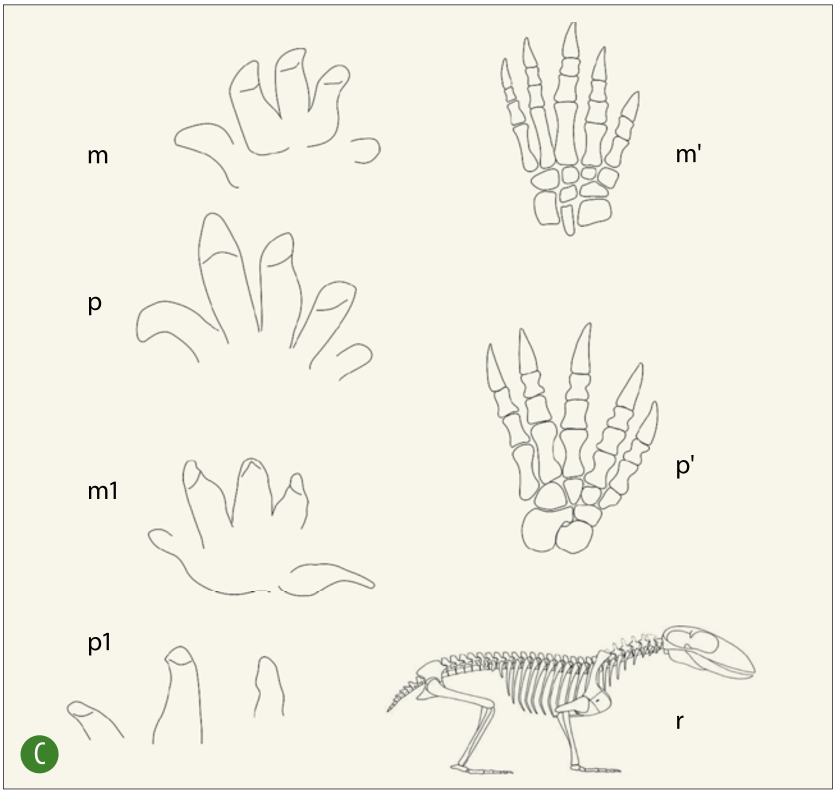


FIGURE 4. | *Tracks and possible trackmakers. A) Archosauriform diapsids. P=*Brachychirotherium paraparvum *left pes. P′=*Euparkeria *left pes. R=skeleton reconstruction of* Euparkeria. *B) Lepidosauromorphs/ archosauriforms. P and M=*Rhynchosauroides peabodyi *left pes and manus. P′ and M′=*Polysphenodon *left pes and manus. P′′and M′′=*Macrocnemus *left pes and manus. R=skeleton reconstruction of* Macrocnemus. *C) Therocephalian therapsids. P and M=* Procolophonichnium haarmuehlensis *left pes and manus. P1 and M1=* Coelurosaurichnus ratumensis *left pes and manus. P′=Whaitsia pes. M′=*Aelurosuchus *manus. R=skeleton reconstruction of a* therocephalian therapsid. *All the right pes,manus and imprints are reflected for a better comparison, as if they were all left. Footprints and skeletons are not to scale, but the proportions between pes and manus are correct. Note that the* P. haarmuehlensis *trackmaker probably had a longer tail than the figured reconstruction, because a tail drag mark is sometimes preserved in association with this ichnotaxon. Skeleton reconstructions redrawn from Huene (1941), Romer (1956), Avanzini & Renesto (2002), Kemp (2005) and Benton (2015).*

showing acuminate (tapering to a point) claw impressions. Digits III and IV are the longest. Digit V is relatively short and oriented laterally and thereby separated and positioned more proximal. Digit V also lacks a claw impression. The manus is smaller than the pes (about 1/2) and is as long as it is wide. The overall structure is similar, but the digit impressions are shorter. Small and polygonal scale skin impressions are preserved on both the pes and the manus. The trackway pattern is unknown, but the manus is placed in front of the pes. Initially, some of this material was assigned to *Brachychirotherium* cf. *circaparvum*, which is known from the Middle Triassic of France (Demathieu & Oosterink, 1983). Later, the new ichnospecies *B. paraparvum* was introduced based on material from the Oosterink collection. Different digit proportions distinguished this material from *B. circaparvum* (Demathieu & Oosterink, 1988). More recently, the ichnogenus *Brachychirotherium* was assigned strictly to Late Triassic material, leading to questions surrounding several Early and Middle Triassic ichnospecies (including *B. paraparvum*; e.g., Klein & Lucas, 2010). A more fitting candidate is possibly the ichnogenus *Synaptichnium*, showing similar digit length patterns and sub-equal lengths of digits III and IV of the pes. Nevertheless, a comprehensive revision is needed to eventually re-assign this material.

***Rhynchosauroides peabodyi* (Faber, 1958) (Fig. 2C-2E)**
This is the most common ichnotaxon found in the Winterswijk Quarry. Surfaces with hundreds of footprints have been exposed, including long trackways and well-preserved complete tracks often exhibiting scale-skin impressions (e.g. Demathieu & Oosterink, 1983). This ichnotaxon is characterised by pentadactyl footprints of quadrupeds of small to intermediate size (maximum foot length about 9 cm). The digits I-IV are long, thin, curved medially and terminate in sharp claw impressions, the digit length markedly increases between digit I and IV. Digit V is small, proximal and oriented outwards. The manus is more completely impressed (semiplantigrade) than the pes (semidigitigrade) and smaller (about 2/3) than pes. The pes is markedly longer than wide, the manus is slightly longer than wide. Along the trackways, the manus is in line or medial relative to the pes, the pace angulation is not high (about 100°), and the pes is commonly found in front of the manus. Tail impressions may occur. This ichnotaxon was introduced by Faber (1958) as *Chirotherium peabodyi*. Later, Demathieu & Oosterink (1983) proposed the combination *Rhynchosauroides peabodyi* (Faber, 1958), which is used nowadays. They considered this ichnospecies to be different from similar *Rhynchosauroides* ichnospecies because of proportions and trackway pattern, therefore suggesting to keep this ichnospecies separated. Nevertheless, a comprehensive revision of the ichnogenus is still pending (e.g., Klein *et al*., 2011).

***Procolophonichnium haarmuehlensis* (Holst, Smit & Veenstra 1970) (Fig. 3A-3D)**
This is the second-most common ichnotaxon at the Winterswijk site. It is characterised by semiplantigrade, pentadactyl footprints of a quadruped of small size (foot length of about 2-3 cm). Footprints are wider than long. The digit length increases between digits I and IV, digits III and IV have a similar length. Digit V is proximal to the other digits and shorter than digit III. All digits terminate in small, pointed and commonly curved outward claws. Digits III, IV and V are occasionally bent laterally. The angles between digits are relatively high (fingers or toes are spread wide). The proximal margin of the palm/sole imprint is concave. Scale-skin impressions may be present. The manus is smaller and less deeply impressed than the pes but of similar morphology. The trackways consist of alternate pes-manus couples with the manus in front of the pes, the pace angulation is between 80-130°. Tail impressions may occur. This material was initially assigned to *Procolophonichnium winterswijkense, Phenacopus faberi* and *Phenacopus agilis*, based on the Oosterink collection (Demathieu & Oosterink, 1983, 1988). Eventually the differences among these ichnotaxa were considered preservational variants of a single ichnospecies and therefore all this material was assigned to the oldest available ichnospecies, that is *Procolophonichnium haarmuehlensis* Holst, Smit & Veenstra, 1970 (Diedrich & Oosterink, 2000; Oosterink, 2009; Klein *et al*., 2015).

***Coelurosaurichnus ratumensis* (Demathieu & Oosterink, 1988) (Fig. 4A)**
This is the rarest (less than 10 footprints) and most enigmatic ichnotaxon at the Winterswijk site. It is characterised by semiplantigrade footprints of relatively large size (manus length 11-13 cm, manus width 17-18 cm). The manus is pentadactyl and wider than long. The digit length increases between digits I and IV, the digits III and IV are of similar length. The digits I and V are small and proximal. Digits terminate in well-impressed triangular claw impressions, sometimes curved. The angles between digits are relatively high. The pes is placed behind the manus and has only been found incomplete. Only three partial digits are evident, and they are likely digits III-V. Digit IV is the longest, and digit V is oriented more proximal. These digits are relatively long, have marked claw impressions and are sometimes bent outwards. This material from the Oosterink collection was initially described by Demathieu and Oosterink (1988). Because of the apparent tridactyl pes and the digits of the pes of similar length, the new ichnospecies was assigned to the dinosauromorph ichnogenus *Coelurosaurichnus*, known from Italy and France. However, the large pentadactyl manus did not fit this diagnosis. The morphology of the manus does not correspond with the expected morphology of a dinosauromorph track. Instead, there are many analogies (except for the larger size) with the ichnospecies *Procolophonichnium haarmuehlensis* and *Capitosauroides bernburgensis*. Additionally, the pes impression is unlikely to have been tridactyl, because the angle between the lateral digits is very high, which is more typical for a pentadactyl imprint (which is therefore likely incomplete). Also, the digit-claw impressions are bent outwards, a peculiar characteristic only seen in *Procolophonichnium haarmuehlensis* so far. A comprehensive revision of *Coelurosaurichnus, Procolophonichnium* and similar morphotypes is required, the assignment of this ichnospecies to the former ichnogenus is questioned. The analogies between this material and the ichnospecies *P. haarmuehlensis* and *C. bernburgensis* are far greater.

Tetrapod ichnoassociation and trackmakers

The tetrapod ichnoassociaton from Winterswijk is characterized by four ichnospecies (Fig. 4): *Brachychirotherium paraparvum, Rhynchosauroides peabodyi, Procolophonichnium haarmuehlensis,* and *Coelurosaurichnus ratumensis*. The material previously assigned to *Sustenodactylus hollandicus* and *Capitosauroides* isp. by Demathieu & Oosterink (1988) is considered to be too poorly preserved and incomplete to be classified. The above-mentioned ichnotaxa are generally consistent with a Middle Triassic age, especially because of the occurrence of *P. haarmuehlensis* (Klein & Lucas, 2010). The rarity of archosauriform tracks (such as *Brachychirotherium paraparvum*) is rather unusual for Triassic ichnoassociations, but the more common *Rhynchosauroides* and *Procolophonichnium* are similar to several German Muschelkalk ichnoassociations (Diedrich & Oosterink, 2000).

B. paraparvum is a typical chirotheriid track. This kind of track is generally attributed to quadrupedal non-dinosauromorph archosauriforms (e.g., Klein & Lucas, 2010) (Fig. 4A). *B. paraparvum* was initially attributed to sphenosuchid archosaur producers (Demathieu & Oosterink, 1988). However, the relatively long digit IV compared to digit III of the pes suggests a producer with longer phalanges in their fourth toe. This is known from proterosuchids, erythrosuchids, euparkeriids, and some rauisuchian archosauriforms (Klein *et al*., 2011). Probable trackmakers of the ichnogenus *Rhynchosauroides* are lepidosauromorphs or archosauromorphs (Klein *et al*., 2011) (Fig. 4B), because of the long digits with marked increase of length between digits I and IV and the smaller and more proximal digit V. Demathieu & Oosterink (1988) proposed a proterosuchid archosauromorph producer for *R. peabodyi* because of the type of scale/skin impression, consistent with modern archosauromorphs rather than with modern lepidosauromorphs. The ichnogenus *Procolophonichnium* is generally considered a track of procolophonid parareptiles or therocephalian therapsids (Klein *et al*., 2015), because of size- and digit proportions. *P. haarmuehlensis* was initially attributed to procolophonid parareptiles Holst *et al*., 1970; Demathieu & Oosterink, 1983). However, the pedal digit proportions seem more consistent with therapsid producers (Klein *et al*., 2015). We will use this interpretation and notice that the mesaxonic manus (in which the middle digit is the longest) of therocephalian therapsids (Fig. 4C) is more consistent with *P. haarmuehlensis*, because digit III in the manus, albeit slightly bent, is the longest (e.g., the material previously assigned to *Phenacopus*, Demathieu & Oosterink, 1983). Also, the concave proximal margin of the palm/sole is generally more consistent with the arrangement of the distal tarsals of therapsids than with those of procolophonids. *Coelurosaurichnus ratumensis* was initially attributed to unknown quadrupedal dinosauromorphs (Demathieu & Oosterink, 1988). However, the morphology and proportions of the manus point to an affinity with the ichnotaxon *P. haarmuehlensis*, yet perhaps a similar but larger producer. Therefore, the producer may have been a larger therocephalian therapsid (Fig. 4C).

Concluding, the Winterswijk Quarry contains rare archosauriform footprints, abundant footprints of lepidosauromorphs/archosauromorphs, abundant small therocephalian footprints and rare large therocephalian footprints. Nota bene, these groups are presently unknown from the skeletal fossil record, therefore, the Winterswijk palaeoenvironment offers a lot more information when we not only look at the bones. The non-occurrence of these forms in the skeleton record of the site may seem surprising but is a common trait of sites with both tetrapod footprints and skeletons. The main reason is that footprints and skeletons require different conditions to be preserved, so they are found in different lithofacies. It is possible that the skeletons of the producers could not be preserved where the animal lived (seashore) because of the sediment exposure, meaning these skeletons were not transported to the sea floor where they could be preserved.

Palaeoecology

The Winterswijk Quarry yields many other kinds of trace fossils, which can be useful to infer the palaeoecology and palaeoenvironment of this locality (Fig. 5). Tetrapod swimming traces have been recently described (Oosterink, 2009; Schulp *et al*., 2017). These traces are characterised by groups of parallel scratches arranged in sequence. Also, fish swimming traces have been reported (cf. *Paraundichna* isp., according to Oosterink, 2009). These traces are generally continuous or discontinuous sets of lines with highly-detailed patterns. Invertebrate trace fossils are studied less thoroughly, but a remarkable ichnoassociation is present at Winterswijk. Small U-shaped burrows (dwelling structures) are assigned to the ichnotaxon *Bifungites* isp. and possible limulid trackways (i.e., locomotion traces) assigned to the ichnotaxon cf. *Kouphichnium* sp. have been reported by Demathieu & Oosterink (1983). Two thin, parallel and horizontal burrows figured in Demathieu & Oosterink, 1983 (Fig. 5, no 1) can be tentatively assigned to the ichnotaxon *Diplopodichnus biformis*, and consist of traces of invertebrate locomotion or feeding. Small horizontal burrows with striations parallel to the burrow margins were assigned to *Radulichnus* by Oosterink (2009) and possibly register feeding behaviour. Large horizontal and flat spreiten-burrows (web-like construction) assigned to *Rhizocorallium jagense*, have been reported by Oosterink (2009). The spreiten burrows are generated by invertebrates moving back and forth perpendicularly to the margins of the whole structure for feeding. Oosterink (2009) also reported some 'worm crawling traces' that are bilobed structures with additional structures perpendicular to the trace margins, possibly produced during feeding, here assigned to cf. *Cruziana*. Some other structures described as 'cubichnia of insects or lobsters' are bilobed resting traces in sequence, here assigned to the ichnotaxon *Rusophycus* isp. This ichnotaxon is usually associated with *Cruziana*, suggesting that these invertebrates could produce two different kinds of traces through different behaviour. The traces typical of underwater environments such as *Cruziana, Rusophycus, Rhizocorallium, Radulichnus,* cf. *Paraundichna* and tetrapod swimming traces co-occur with traces typical of emerged areas such as *Diplopodichnus*, cf. *Kouphichnium* and the tetrapod tracks. This combination of alternating flooded and dry conditions is evidence of a palaeoenvironment subjected to frequent flooding and drying, such as a tidal flat, in agreement with the sedimentary structures found on the slabs (wave ripples and mud cracks).

Conclusions and perspectives

The Winterswijk Quarry is one of the most interesting Middle Triassic sites for the study of tetrapod footprints. The unusual composition of the ichnoassociation, the preservation quality, and the abundance of footprints encourages further studies in order to integrate the data from the skeletal fossil record and to make precise comparisons with other Muschelkalk sites such as those from Germany. The invertebrate trace fossil association is also important to infer the palaeoecology of Winterswijk. Therefore, more detailed studies on the invertebrate trace fossils and more precise stratigraphic and lithofacies interpretations are highly recommended.

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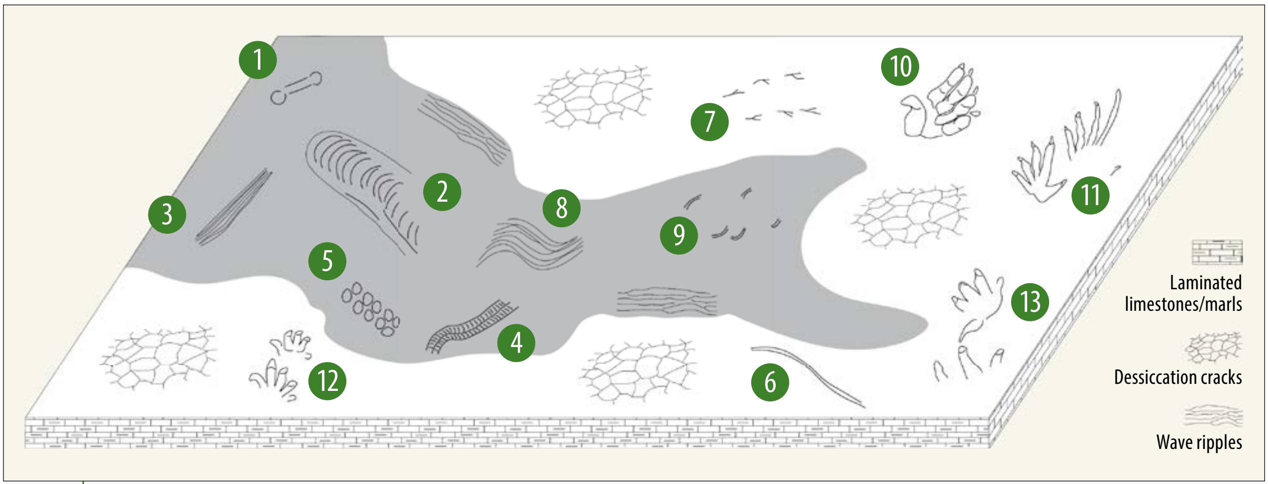

FIGURE 5. | *Trace fossils and palaeoecology at the Winterswijk site. 1-7) Invertebrate trace fossils. 1)* Bifungites *isp. 2)* Rhizocorallium jagense. *3)* Radulichnus *isp. 4) cf.* Cruziana *isp. 5)* Rusophycus *isp. 6)* Diplopodichnus biformis. *7) cf.* Kouphichnium *isp. 8-13) Vertebrate trace fossils. 8) cf.* Paraundichna *isp. 9) Tetrapod swimming traces. 10)* Brachychirotherium paraparvum, *left pes imprint. 11)* Rhynchosauroides peabodyi, *right pes-manus couple. 12)* Procolophonichnium haarmuehlensis, *left pes-manus couple. 13)* Coelurosaurichnus ratumensis, *right pes-manus couple. The grey area indicates submerged conditions. Trace fossils and sedimentary structures are not in scale.*

Samenvatting

De voetsporen van viervoeters (tetrapoden) uit Winterswijk ontvangen wereldwijd aandacht. De steengroeve kent een grote hoeveelheid voetsporen en de lange loopsporen en voetafdrukken worden gekenmerkt door hun unieke preservatie inclusief huid- en nagelindrukken. De voetsporenassociatie van Winterswijk komt overeen met een Midden-Trias ouderdom en bevat vier ichnotaxa: *Brachychirotherium paraparvum, Rhynchosauroides peabodyi, Procolophonichnium haarmuehlensis* en *Coelurosaurichnus ratumensis.* De producenten van deze voetsporen behoren waarschijnlijk tot de reptielen (zowel archosauromorfen als de hagedisachtige lepidosauromorfen) en zowel grote als kleine therocephaliërs ("zij met zoogdierkoppen"). Deze groepen zijn echter zeer zelden als skeletfossielen aangetroffen in de Vossenveld Formatie, welke vooral rijk is aan mariene soorten. Het voorkomen van zwemsporen en invertebratensporen en graafgangen in combinatie met de voetsporen, suggereert dat Winterswijk een kustnabij milieu was dat regelmatig overstroomde en snel uitdroogde.

REFERENCES

- **Demathieu, G.R. & Oosterink, H.W., 1983.** *Die wirbeltier-ichnofauna aus dem unteren muschelkalk von winterswijk. Staringia 7, pp. 1-51.*

- **Demathieu, G.R. & Oosterink, H.W., 1988.** *New discoveries of ichnofossils from the Middle Triassic of Winterswijk (the Netherlands). Geologie en Mijnbouw 67, pp. 3-17.*

- **Diedrich, C. & Oosterink, H.W., 2000.** *Bergings-en documentatietechniek van* Rhynchosauroides peabodyi *(Faber): sauriërsporen op de grens Boven-Bontzandsteen/Muschelkalk van Winterswijk. Grondboor & Hamer 54, pp. 125-130.*

- **Faber, F.J., 1958.** *Fossiele voetstappen in de Muschelkalk van Winterswijk. Geologie en Mijnbouw 20, pp. 317-321.*

- **Holst, H.K.H., Smit, J. & Veenstra, E., 1970.** *Lacertoid footprints from the Early Middle Triassic at Haarmuehle, near Altstaette, W. Germany. Koninklijke Nederlandse Akademie van Wetenschappen Proceedings B 73, pp. 157–165.*

- **Klein, H. & Lucas, S.G., 2010.** *Tetrapod footprints-their use in biostratigraphy and biochronology of the Triassic. Geological Society, London, Special Publications 334, pp. 419-446.*

- **Klein, H., Voigt, S., Saber, H., Schneider, J.W., Hminna, A., Fischer, J., Lagnaoui, A. & Brosig, A., 2011.** *First occurrence of a Middle Triassic tetrapod ichnofauna from the Argana Basin (western High Atlas, Morocco). Palaeogeography, Palaeoclimatology, Palaeoecology 307 (1-4), pp. 218-231.*

- **Klein, H., Lucas, S.G. & Voigt, S., 2015.** *Revision of the ?Permian-Triassic Tetrapod Ichnogenus* Procolophonichnium *Nopcsa 1923 with Description of the New Ichnospecies P. lockleyi. Ichnos 22, pp. 155-176.*

- **Oosterink, H.W., 2009.** *The diversity of trace fossils from the Anisian (Middle Triassic) of Winterswijk, the Netherlands. Deposits 20, pp. 8-11.*

- **Schulp, A.S., Bleeker, R.W., Haarhuis, A., van Spronsen, E., During, M.A.D., Goris, G., Kaskes, P., Matteman, Y., Winkelhorst, W. & Winkelhorst, H., 2017.** *A tetrapod swimming traceway from the Triassic of Winterswijk, the Netherlands. Netherlands Journal of Geosciences 96 (3), pp. 273-277.*

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