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# New discoveries of ichnofossils from the Middle Triassic of Winterswijk (the Netherlands)

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## Abstract

The Middle Triassic of Winterswijk has yielded an interesting ichnofauna (reptilian and amphibian footprints) during the past few years. Recently discovered new species add greatly to our knowledge of the Winterswijk fauna. Three vertebrate tracks are described and illustrated: *Brachychirotherium paraparvum, Coelurosaurichnus ratumensis* and *Sustenodactylus hollandicus*. Some remarks on species described earlier are added.

## Geological setting

A comparatively small area east of Winterswijk is the only spot in the Netherlands where Buntsandstein and Lower Muschelkalk (Wellenkalk) are exposed or are covered by thin Quaternary deposits (Fig. 1). After their deposition these strata were subsequently tectonized (oro- or epirogenetically) during several phases, and that resulted in the folding and faulting of the deposits. In the outcrop area, tectonic uplift exposed younger deposits to erosion, an uplift possibly along faults that were initiated by halokinesis that began as early as the Late Triassic (Ziegler, 1978). The Triassic sediments form an overturned anticline and the Muschelkalk strata exposed in the south are older than those in the north. To the south Buntsandstein is present underneath the Lower Muschelkalk and to the north younger deposits top the Muschelkalk (Fig. 2).

The Muschelkalk is well exposed in three large quarries (B.V. Winterswijksche Steen- en Kalkgroeve), about three km east of Winterswijk. Several dolomite beds and some clay layers are intercalated in the 25 to 30 m thick limestone section that is exposed.

Besides the minerals pyrite, marcasite, galena, sphalerite, calcite and celestite numerous body fossils have been found, amongst them some twenty species of bivalves (species of *Myophoria* are by far

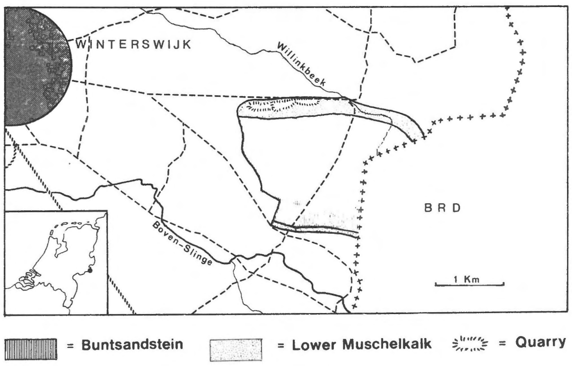


*Fig. 1.* Outcrop of Triassic deposits east of Winterswijk (without Quarternary) (Demathieu & Oosterink, 1983).

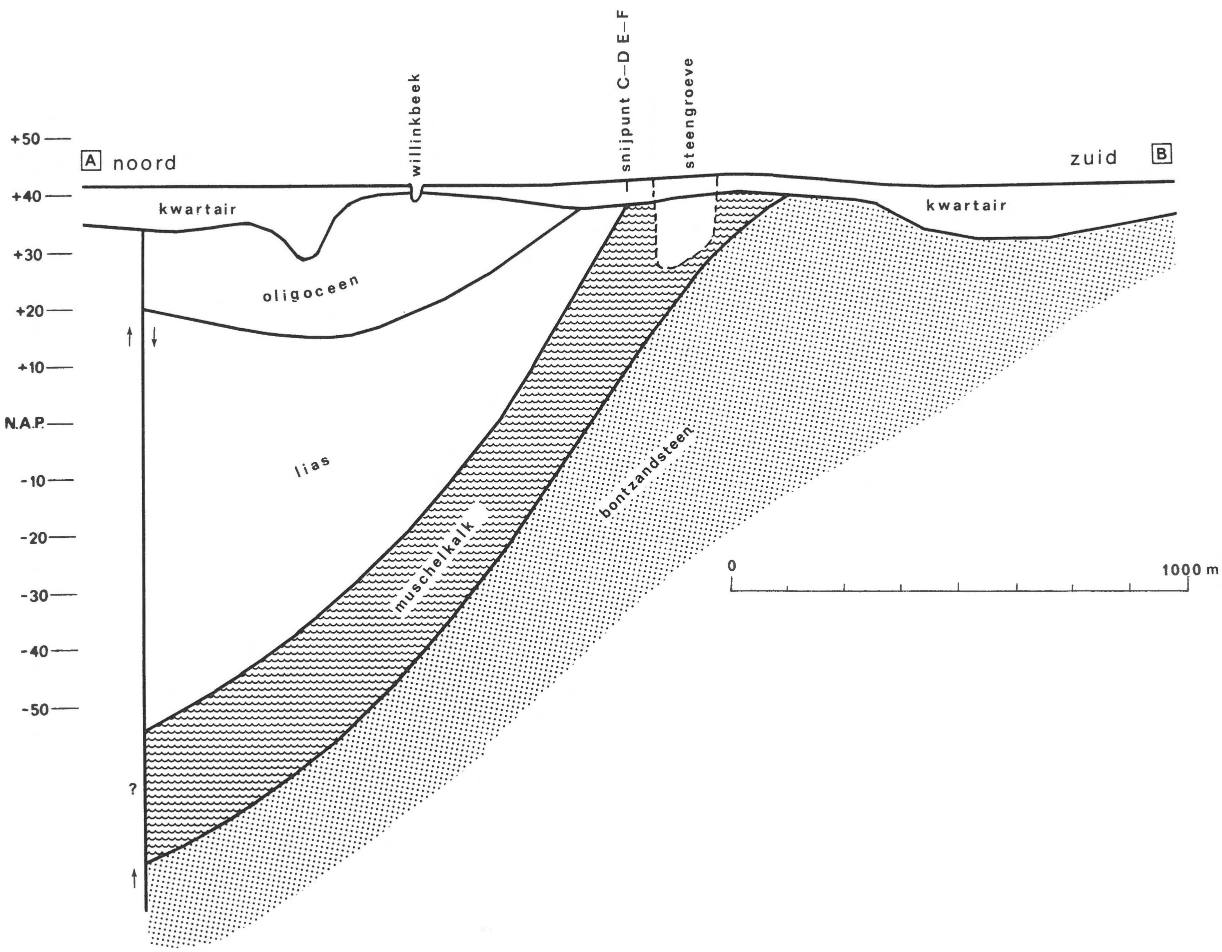


*Fig. 2.* North-south section through the Triassic saddle near Winterswijk (Oosterink, 1986).

the most common), gastropods (*Loxonema* sp.), ammonites (*Beneckia buchi*), brachiopods (*Lingula tenuissima*), crustaceans and *Rhizocorallium* trace fossils. Vertebrates are represented by nine species of bony and cartilaginous fish (*Coelacanthus* sp., *Gyrolepis* sp., *Colobodus* sp., *Dollopterus* sp., *Saurichthys tenuirostrus, Pholidophorus* sp. and *Eosemionotus* cf. *vogeli; Acrodus* sp. and *Palaeobates angustissimus*) as well as by reptiles (*Nothosaurus venustus, Cymatosaurus* sp., *Placodus* sp. and *Tanystropheus antiquus*). An extensive outline of the geology, minerals and fossils of the Winterswijk Triassic is given by Oosterink (1986).

In the deepest parts of the quarries sediments are exposed whose bedding planes exhibit platelike depressions which are surrounded by fossil mud cracks that are arranged in polygons. The filled cracks often form an extensive network. These beds with numerous cracks have regularly yielded saurian tracks and trails* during the past few years. Especially rich in fossil tracks are strata on top of and immediately below a wine-red coloured (iron oxide) marly limestone near the base of the Lower Muschelkalk.

* A track (mark or print) as specifically used in this paper means the impression of a single autopod (hand or foot), while trail as used means a succession of marks or prints made by the passage of an individual animal.

## Remarks on the statistical methods*

Tracks are the impressions or prints of the soles of animal autopodia (hands or feet). The impression is strongly dependent on the grain size and the physical condition of the sediment as well as on the manner of the animal locomotion. The most striking characteristic of these fossils is their variability. Therefore, a measured value on its own is of limited importance, and one has to turn to statistical methods. Moreover, a single animal produces a large quantity of tracks during its life. The statistics applied here are elementary. They concern the usual parameters of frequency distribution, mean, standard deviation and confidence interval for the mean. For instance, a slight variability (<10%) and a high probability in the Cramer's test indicate a reliable distribution of the measurements of a certain character, if the random sample is small (<10). This means that the character measured is constant and that it can be used for comparisons without limitations. If a sample is smaller than 5 the Cramer's test cannot be applied. For a comparison of means the ratios of two measured values, not the measured characters should be used.

However, a statistical comparison does not furnish conclusive evidence, but together with morphological data it can yield clues to help determine the similarities or diversities of random samples.

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* The so-called *variability* (= variation coefficient) is the quotient of a hundred times the standard deviation divided by the mean of the sample. This parameter is defined as:

$$V = \frac{100 * s}{m}$$

s = standard deviation
m = arithmetic mean

It is a number without unit, i.e., independent of the utilized units. It indicates whether or not the distribution has a wide spread. It depends on a) the physical condition and nature of the sediment, b) the patterns of placement and retraction of the feet during locomotion and c) the size differences for the trackmakers. This coefficient is less than 10%, when in tracks the causes of variability are points a and b above. In the case of animals of different sizes forming the same ichnospecies, variability can be over 20%, but in this case the norm is between 10 and 20%.

The highest values of variability are generally found with the divarications of the digits, although these characters are not influenced by size differences. The cross axis angle formed by the axis of digit III and the digit metapodial line is a very important character for comparisons with skeletons (Demathieu & Haubold, 1978).

The *Cramer's test* is based on the asymmetry coefficient which results from the estimate of the third moment of the distribution ($m_3$) and from the estimate of the second moment of the distribution ($m_2$). Asymmetry is given by the formula:

$$g = \frac{m_3}{m_2^{3/2}}$$

When one deals with small sample (n) size, g must be replaced by

$$G = \frac{\sqrt{n\ (n-1)}}{n-2}\ g$$

The variance of G is

$$\sigma^2 = \frac{6n\ (n-1)}{(n-2)(n+1)(n+3)}$$

with $\frac{G}{\sigma}$ then being a variable test for normality. It is asymptotically normally distributed, with a zero mean and a standard deviation equal to 1.

The table of normal curve

$$\frac{1}{\sqrt{2\pi}} \int_{-t}^{+t} e^{-t^2/2}\, dt$$

gives the probability of excess of the value of the test variable. A high probability suggests (good) homogeneity of the sample. Between 10 percent and 5 percent the homogeneity is doubtful and for values less than 5 percent there is no homogeneity. For an ichnospecies one must take into consideration the whole set of tests. Just one or two tests may not be significant and cannot permit one to conclude that an ichnospecies is invalid, because one or two distributions may be biased by unknown external factors.

### *Vertebrate trace fossils*

Ichnogenus *Rhynchosauroides* Maidwell 1911
*Rhynchosauroides peabodyi* (Faber 1958) (Fig. 3)**

** All figs: Bar scale = 5 cm.

*Fig. 3. Rhynchosauroides peabodyi* manus/pes set. Scale bar in Figs 3–9 = 5 cm.

This species has already been discribed in a previous paper (Demathieu & Oosterink, 1983). We do not repeat ourselves here, but remark that it is not as abundant in this newly discovered bed as in the beds described in the earlier paper. All that has been stated in that paper still holds.

Ichnogenus *Brachychirotherium* Beurlen 1950
*Brachychirotherium paraparvum* n. sp. (Fig. 4)
About twenty pes and manus impressions which probably constitute one track were discovered by F. Bonnes and H.W. Oosterink.
*Type:* a manus-pes set on slab no. D 277, Geological Collection Freriks Museum, Winterswijk, The Netherlands.
*Hypodigm:* a collection of six pes and manus impressions.
*Occurrence:* Muschelkalk quarry near Winterswijk, The Netherlands.
*Diagnosis:* Foot: straight, not much divergent digits (angle I–IV: ca.20°). Claw of digit 1 straight, lengthening the first digit. Claws of digit II and III curved outwards, that of IV being very small. Fifth toe short and directed outwards. Metatarsal pad of digit V relatively small.

Hand: length somewhat exceeding width. Second, third and fourth fingers directed outwards to some degree. Relatively small claws, except for the one of digit I. Ratio hand/foot areas ca. 4/10.
*Derivatio nominis:* From Latin parvus, small, a name applied by Hitchcock (1889) to Triassic footprints from Connecticut and Greek para, connected with, related to.
*Description:* In our previous paper (Demathieu & Oosterink, 1983) an incomplete manus/pes set was described sub nomen *B.* cf. *circaparvum,* which is here considered to be conspecific with the newly discovered footprints.

The reliefs (convex hyporeliefs) of these tracks are weak and indicate that they were impressed when the sediment was relatively dry. Sometimes the skin is impressed under the hands and feet and under the pads. The scales are granular, small on the interior faces of the digits, a little larger under the sole where they reach ca. 1 mm. Often toe pads are visible on the foot, enabling one to determine the phalanx formula of the first four digits: 2, 3, 4, 4. The same formulae have been found in *B. paeneparvum* from the Upper Buntsandstein of Kronach (FRG) (Demathieu & Leitz, 1982). As in other, related ichnospecies the pads on the tip of toes II and III are thick and broad. The claw of digit I is strong and long, makin up half the entire length of this digit. The one of IV is very small in comparison; those of III and IV are pointed, rather long and curved outwards. The first four toes are separated from V and its metatarsal pad.

The statistical analysis reveals a large uniformity for these footprints (Table 1), with slight variabilities for the measurements of the feet, from 3,2 to 7,6%; 4,8% on average. These values are characteristic for the present trail and show that these impressions were produced by one individual only. With regard to the angles the variabilities are large

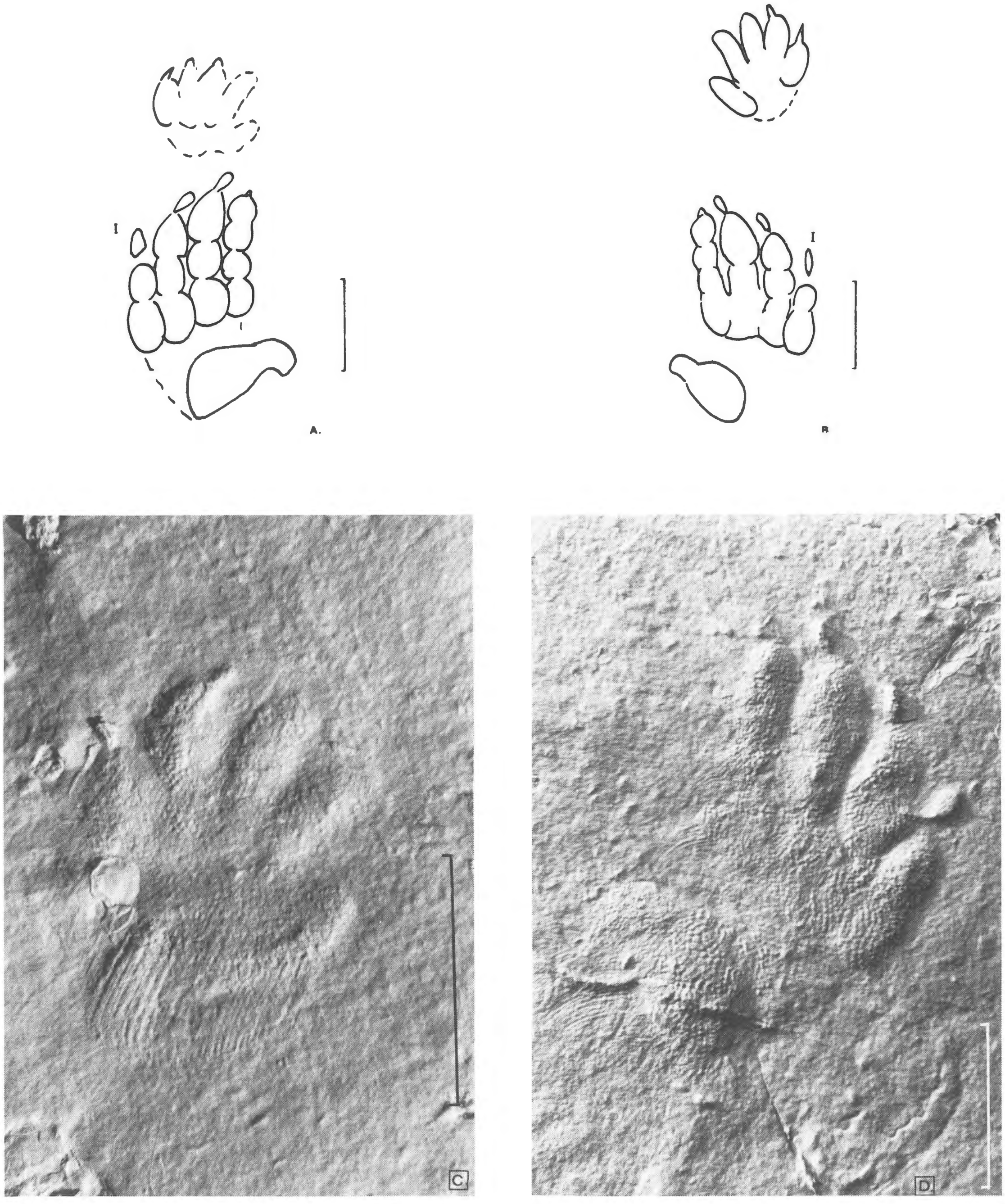



*Fig. 4. Brachychirotherium paraparvum.*
A. Left manus/pes set; B. right manus/pes set; C. photo manus; D. photo pes.

except for the cross axis which, as usual, forms a constant character.

Table 2 presents the ratios of several lengths. The variabilities are slight (from 3 to 7,1%), implying that there is no growth allometry, which already became apparent from the low percentages of the measurements.

The hand area measures ca. 4/10 of that of the foot. The impressed area comprises part of the sole in between the proximal ends of the first and fifth toes. Scales are sometimes visible; these are smaller than those of the foot. On some imprints claws can be discerned. Their lengh decreases from digit I to IV. It is possible that digit V possesses a claw, but this cannot be confirmed. Apparently there is only one pad for each toe. The distance manus/pes measures ca. 160 mm.

Table 1 shows that the dimensions of the hands have greater variabilities than those of the feet, on average 8% for the lengths. With 7%, the cross axis seems to be constant. The ratios of the hand dimensions (Table 2), like those for the feet, often show large variabilities and rather poor correlations. The reasons for this are probably the condition of the sediment and the irregular pressure of the limbs.

*Discussion:* the present ichnospecies is reminiscent

*Table 1. Brachychirotherium paraparvum.* Statistical parameters of the measurement of characters.

| Characters | N | Mean length | Standard deviation (mm) | Coefficient of variability (%) | Confidence interval for the mean at the level 5% (mm) | Cramer's test | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | Asymmetry | Test variable (a) | Probability (%) x>(a) |
| *Feet:* | | (mm) | | | | | | |
| Digites I | 7 | 60.7 | 2.752 | 4.5 | 58.1– 63.3 | 0.012 | 0.016 | 99 |
| II | 7 | 74.4 | 3.994 | 5.4 | 70.7– 78.2 | − 1.343 | 1.69 | 9 |
| III | 7 | 79.3 | 3.147 | 4.0 | 76.3– 82.2 | − 0.637 | 0.80 | 42 |
| IV | 7 | 69.6 | 3.952 | 5.7 | 65.9– 73.3 | 0.197 | 0.25 | 80 |
| V | 5 | 57.8 | 1.613 | 2.8 | 55.7– 59.9 | − 1.736 | 1.90 | 6 |
| Footprint Length (L) | 5 | 129.4 | 4.099 | 3.2 | 124.3–134.5 | − 0.441 | 0.48 | 73 |
| Width (W) | 6 | 78.8 | 4.956 | 6.3 | 73.6– 84.1 | − 0.797 | 0.94 | 35 |
| Set of the 4 first digits | | | | | | | | |
| Length (M) | 7 | 86.6 | 6.579 | 7.6 | 80.4– 92.7 | 0.399 | 0.50 | 62 |
| Width (m) | 7 | 71.9 | 2.853 | 4.0 | 69.2– 74.5 | − 0.221 | 0.28 | 78 |
| Angles II–IV | 7 | 9.9 (°) | 2.854 | 28.9 | 7.2– 12.5 | − 0.402 | 0.51 | 61 |
| I–IV | 7 | 17.4 | 2.149 | 12.3 | 15.4– 19.5 | 0.066 | 0.08 | 94 |
| I–V | 5 | 59.2 | 3.962 | 6.7 | 54.2– 64.2 | 0.598 | 0.66 | 51 |
| Cross axis | 7 | 70.4 | 3.047 | 4.3 | 67.6– 73.3 | 0.716 | 0.90 | 37 |
| *Hands:* | | (mm) | | | | | | |
| Digits I | 6 | 32.2 | 3.869 | 12.0 | 28.1– 36.3 | 0.060 | 0.07 | 94 |
| II | 6 | 42.0 | 2.098 | 5.0 | 39.7– 44.3 | 0.585 | 0.69 | 49 |
| III | 6 | 37.7 | 1.966 | 5.2 | 35.6– 39.0 | − 1.674 | 1.98 | 5 |
| IV | 6 | 31.0 | 3.847 | 12.4 | 26.9– 35.1 | 0.316 | 0.37 | 71 |
| V | 6 | 27.8 | 3.312 | 11.9 | 24.3– 31.4 | − 0.128 | 0.15 | 88 |
| Imprint Length (L) | 6 | 67.3 | 1.862 | 2.8 | 65.3– 69.3 | − 0.165 | 0.20 | 84 |
| Width (W) | 6 | 61.8 | 4.490 | 7.3 | 57.1– 66.6 | 0.263 | 0.31 | 76 |
| Set of the 4 first digits | | | | | | | | |
| Length (M) | 6 | 46.5 | 3.391 | 7.3 | 42.9– 50.1 | − 0.277 | 0.33 | 74 |
| Width (m) | 6 | 57.0 | 4.690 | 8.2 | 52.0– 62.0 | 0.855 | 1.01 | 31 |
| Angles II–IV | 6 | 31.7 (°) | 10.783 | 34.1 | 20.3–43.0 | 0.973 | 1.15 | 25 |
| I–IV | 6 | 46.2 | 13.703 | 29.7 | 31.7– 60.1 | 0.845 | 1.31 | 19 |
| I–V | 6 | 62.0 | 11.296 | 18.2 | 50.1– 73.9 | 0.326 | 0.39 | 70 |
| Cross axis | 6 | 67.7 | 4.761 | 7.0 | 62.6– 72.7 | − 0.657 | 0.78 | 44 |

of *B. circaparvum,* with which it might be confused. However, the characters presented in the diagnosis and a comparison of the corresponding ratios point to two different species. Indeed the ratios III/I, III/IV, IV/I, II/I of the foot and III/I, M/III, L/III of the hand are unlike those of *B. circaparvum.*
*A palaeontological analysis:* The footprints are of a quadruped pentadactyl reptile of comparatively large size. Because there are no measurements for the width and pace length of the trail it is not feasible to accurately estimate the length of the trackmaker's limbs. However, on the basis of the foot length (ca. 13 cm) one might assume that the hind leg measured ca. 50–60 cm. This implies a body length of 50–55 cm and a total length of ca. 200 cm.

The hands are relatively large which means that the head must have been comparatively massive, implying a great weight of the front part of the animal. The presence of a curved fifth toe similar to that of *Chirotherium barthii* and a small claw on the fourth show that the maker of these tracks had not reached the evolutionary level of *B. circaparvum.* The main characters suggest that this *Brachychirotherium*-maker was a pre-crocodilian, probably belonging to the Sphenosuchia.

Ichnogenus *Coelurosaurichnus* Huene 1941
*Coelurosaurichnus ratumensis* n. sp. (Fig. 5)
*Type:* Slab no. D 416, Geological Collection Freriks Museum, Winterswijk, The Netherlands.
*Hypodigm:* five manus and four partial pes impressions.

*Table 2. Brachychirotherium paraparvum.* Statistical parameters of ratios in lengths of footprint characters.

| Characters | N | Mean (mm) | Standard deviation (mm) | Coefficient of variability (%) | Confidence interval for the mean at the level 5% (mm) | Correlations | |
|---|---|---|---|---|---|---|---|
| | | | | | | Coefficient | Minimum coefficient (5%) |
| *Feet:* | | | | | | | |
| III/I | 7 | 1.31 | 0.045 | 3.5 | 1.26–1.35 | 0.685 | 0.755 |
| III/II | 7 | 1.07 | 0.032 | 3.0 | 1.03–1.10 | 0.837 | 0.755 |
| III/IV | 7 | 1.14 | 0.047 | 4.1 | 1.09–1.19 | 0.681 | 0.755 |
| III/V | 4 | 1.41 | 0.069 | 4.9 | 1.29–1.52 | − 0.391 | 0.950 |
| IV/I | 7 | 1.15 | 0.081 | 7.1 | 1.07–1.23 | 0.079 | 0.755 |
| IV/II | 7 | 0.94 | 0.061 | 6.5 | 0.87–1.00 | 0.309 | 0.755 |
| II/I | 7 | 1.23 | 0.050 | 4.0 | 1.18–1.28 | 0.680 | 0.755 |
| L/I | 4 | 1.67 | 0.075 | 4.5 | 1.54–1.79 | 0.864 | 0.755 |
| M/m | 7 | 1.21 | 0.083 | 6.9 | 1.12–1.29 | 0.422 | 0.755 |
| M/III | 7 | 1.09 | 0.070 | 6.4 | 1.02–1.16 | 0.514 | 0.755 |
| L/III | 5 | 1.63 | 0.062 | 5.0 | 1.53–1.74 | 0.157 | 0.950 |
| *Hands:* | | | | | | | |
| III/I | 6 | 1.18 | 0.145 | 12.3 | 1.03–1.34 | 0.219 | 0.811 |
| III/II | 6 | 0.90 | 0.072 | 8.1 | 0.82–0.98 | − 0.291 | 0.811 |
| III/IV | 6 | 1.23 | 0.150 | 12.2 | 1.07–1.39 | 0.185 | 0.811 |
| III/V | 6 | 1.36 | 0.105 | 7.7 | 1.25–1.48 | 0.850 | 0.811 |
| IV/I | 6 | 0.99 | 0.229 | 23.2 | 0.74–1.23 | − 0.779 | 0.811 |
| IV/II | 6 | 0.74 | 0.119 | 16.0 | 0.61–0.87 | − 0.620 | 0.811 |
| II/I | 6 | 1.32 | 0.126 | 9.5 | 1.18–1.45 | 0.665 | 0.811 |
| M/m | 6 | 0.82 | 0.076 | 9.3 | 0.73–0.90 | 0.339 | 0.811 |
| L/I | 6 | 1.09 | 0.053 | 4.9 | 1.03–1.15 | 0.893 | 0.811 |
| M/III | 6 | 1.24 | 0.078 | 6.3 | 1.15–1.32 | 0.510 | 0.811 |
| L/III | 6 | 1.79 | 0.072 | 4.0 | 1.71–1.87 | 0.620 | 0.811 |

Abbreviations as in Table 1.

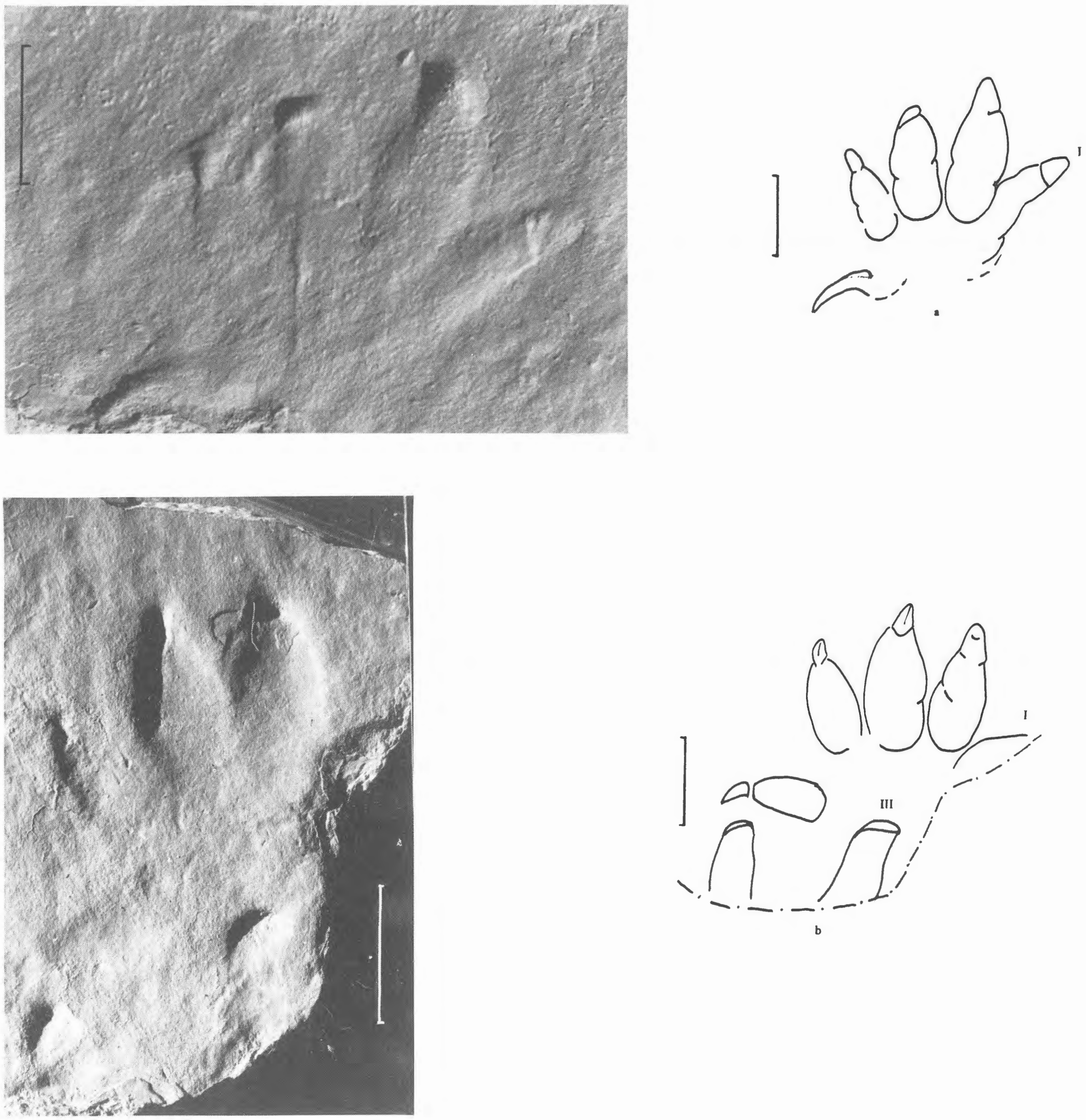



*Fig. 5. Coelurosaurichnus ratumensis.*
A. Right manus; B. Right manus and partial right pes.

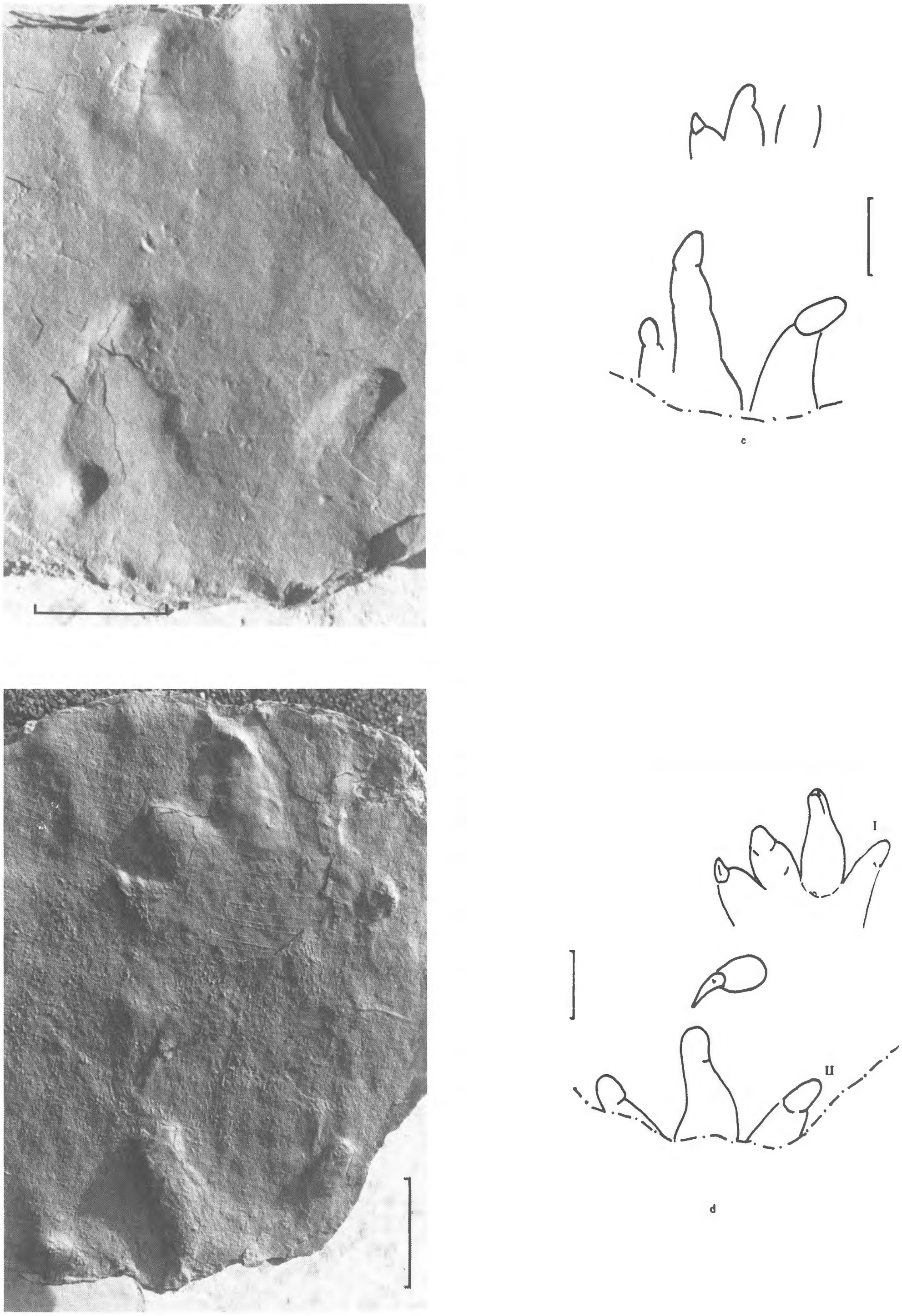



*Fig. 5. Coelurosaurichnus ratumensis.*
C. Partial manus/pes set; D. Right manus and partial right pes.

*Occurrence:* Muschelkalk quarry near Winterswijk, The Netherlands.
*Diagnosis:* quadruped, digitigrad imprints.
Hand: pentadactyl, broad. Digit II longest, hardly longer than digit III. First digit long and slender, bent towards midline. Fingers II, III and IV thick. Digit V rather short and provided with a sharp, curved claw. Fingers not really divergent except for the angle I–V. Cross axis ca. 70°. Hand situated in front of the foot and closer to the midline than that autopodium.

Foot: tridactyl. Long and rather slender toes. Digit III longest and somewhat curved, IV hardly longer than II. Angle II–IV up to 60°. The greater length of III in comparison to the other digits is not of importance.
*Derivatio nominis:* After Ratum, a hamlet of Winterswijk where the Muschelkalk limestone quarries are situated.
*Description:* Compared to the foot, the hand is large; it is directed a little inwards. The main support must have rested on the three middle toes which are impressed clearest. Because of the fact that the limb is digitigrad, the fingers are not always clearly marked. The slight curve of digit I, its slenderness and the sharp claw of V are the specific characters of this form. The class of the other fingers are relatively strong and they increase in size from IV to I, as is usually the case with archosaurians. Unfortunately, the foot is never completely impressed. We know only the distal parts of the toes. The position of the second to fourth digits in relation to III, and the angles (ca. 60°) show this impression to have been very probably tridactyl. The distance between the tip of the claw of digit III and the line connecting the tips of II and IV is not very large (ca. 40 mm). Digit III shows an unusual curvature which has been noted before for this ichnogenus (Demathieu & Weidmann, 1982). On the whole the reliefs are not high but they are higher towards the distal ends of the digits because of the digitigrad character of this form. Measurements are given in Table 3. The number of specimens is too small for statistical analysis. However, we have computed the numerical ratios of the fingers in order to compare this form with congeneric species. Thus it can be shown that the variabilities are relatively slight (4,4 to 8%) with comparable low correlations for the three toes. This is dependent on the irregularity in length of the first four digits. The length of toe V, however, is constant.
*Discussion:* Because of the presence of a hand and the small difference in the length of III compared to II and IV, we have assigned this trace to the genus *Coelurosaurichnus*. However, we must remark that all the other species of this genus have smaller hands. Indeed the hand of the present species is comparatively large, its area is probably as large as that of the foot.
*A palaeontological analysis:* The position and size of the fingers as well as the toes allows one to number them. The form of the autopodia and their characteristics suggest that the tracemaker is to be found amongst the archosaurians. The impossibility of measuring the trail characteristics makes a more definite assignment difficult. What we do know is that the maker was a quadruped reptile with strong forelegs, tridactyl feet and pentadactyl hands. From the early Middle Triassic only skeletons of thecodonts are known among the archo-

*Table 3. Coelurosaurichnus ratumensis.* Measurement of characters.

| | Length of toes in mm | | | | | Length (L) | Width (W) | Angles in degrees | | | Cross axis (q) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | I | II | III | IV | V | in mm | in mm | II–IV | I–IV | I–V | in degrees |
| *Feet* | | | | | | | 170 | 60 | | | |
| *Hands* | | 90 | 83 | 61 | 58 | 132 | 175 | 30 | 50 | 130 | 75 |
| | 64 | 86 | 73 | 58 | 56 | 119 | 169 | 35 | 70 | 150 | 65 |
| | 65 | 76 | 60 | 44 | 62 | 131 | 171 | 35 | 60 | 140 | 65 |

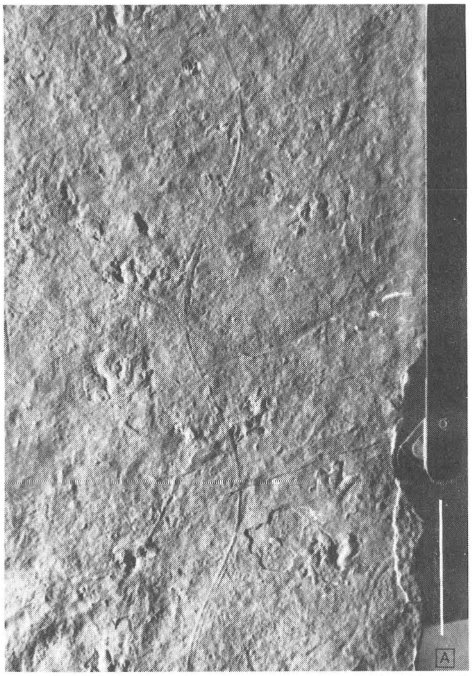


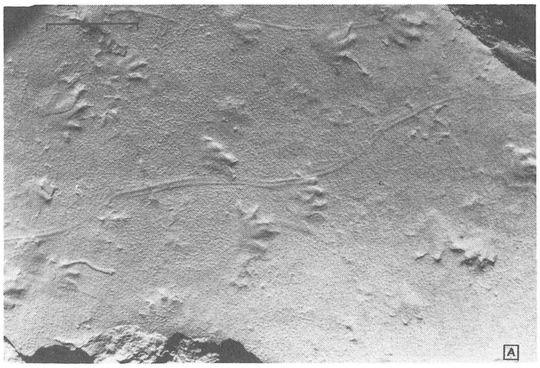
*Fig. 6. Procolophonichnium winterswijkense.*
A. Footprints with tail trace; B. Skin impressions.

saurians. As far as we know, judged from the characteristics of the impressions, the maker was not a thecodont, neither a prosauropod on account of the form of the hand, nor a crocodile because of the size of the hand and its position. It was probably one of the yet unknown Triassic primitive dinosaurs.

Ichnogenus *Procolophonichnium* Nopcsa 1923
*Procolophonichnium winterswijkense* Demathieu & Oosterink 1983 (Fig. 6)
These footprints are still being found rather commonly and numerous tracks have been collected since the publication of our previous paper. These new specimens do not provide any new details. New are, however, two winding, regular tail traces (Fig. 6a). The ratio between 'wave length'/amplitude in both cases is ca. 6,2. Sometimes two parallel ridges can be observed. The second of these, hardly visible, lies close to the main track, then left, then right. This proves that there were three rows of scales on the underside of the tail. In addition, scales are visible underneath the toes of another impression (Fig. 6b). These are small round warts, comparable to those of *Brachychirotherium*. The trackmaker can be assumed to have been a small procolophonid cotylosaur.

Ichnogenus *Phenacopus* Demathieu & Oosterink 1983
*Phenacopus faberi* Demathieu & Oosterink 1983 (Fig. 7a)
*Phenacopus agilis* Demathieu & Oosterink 1983 (Fig. 7b)
Both species have been described before. As far as we know impressions of this kind have not been found again.

Ichnogenus *Sustenodactylus* Lull 1904
*Sustenodactylus hollandicus* n. sp. (Fig. 8a)
*Type:* the first imprint of a trail on slab no. D. 340, Geological Collection Freriks Museum, Winterswijk, The Netherlands.
*Hypodigm:* the other foor prints of the same trail.



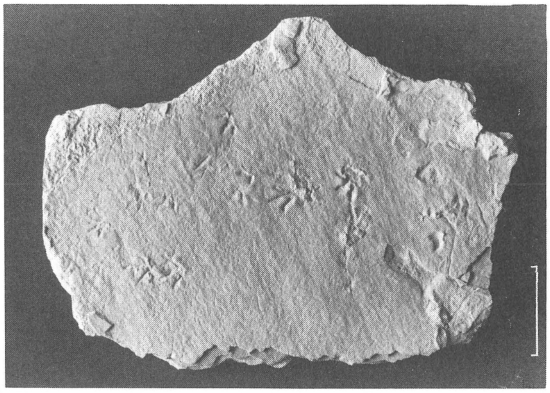



*Fig. 7.* A. *Phenacopus faberi* trail; B. *Phenacopus agilis* trail.

*Diagnosis:* pentadactyl hand and foot, digits II, III, IV impressed clearest. When present, I and V seem to be the smallest digits. The size of the digits increase from I to IV but the differences are slight and not always apparent. The width of the foot is slightly less than the length. Behind the toes a backward directed convex sole is visible whose length is nearly equal to the length of the toes. The angle of the foot axis with the midline is ca. 15–20° outwards. The hand is circa two and a half times as long as broad. Hand positioned in front of the foot. Track width, pes angulation about 60° so that the pace displays the same measurements as the stride.
*Description:* These tracks are very small (1 cm long) and not really well preserved. The manus is longer than broad and similar to a lacertoid foot, but reversed. The cross axis forms an angle of ca. 30° with the midline. The outline of the foot is quite different. Hardly longer than broad, the toes are straight. The foot has a lacertoid form but the differences in toe length are slight. The toe angles are small. The length of the convex sole is almost equal to the length of digit IV. Because of the smallness of the autopodia, it is not feasible to measure the length of the digits. The statistical parameters of footprint characters and trail are listed in Table 4. Despite the small size of the imprints and their poor preservation the variability is on the whole rather slight.
*Discussion:* This trail is assigned to the ichnogenus *Sustenodactylus* on account of the characteristics of the impressions, the position of the autopodia and the similarity between these.
*A palaeontological analysis:* The specific characters point to a small primitive tetrapod with curved limbs and consequently a rather primitive type of locomotion. Hind and forelegs may have had the same length, possibly about 30–35 mm. Again the body must have been long, about 50–55 mm. The difference between front and hind autopodia suggests that the maker belonged to the more primitive vertebrates; perhaps it was a small cotylosaurian or an amphibian.

Ichnogenus *Capitosauroides* Haubold 1971
*Capitosauroides* sp. (Fig. 8b)
Trail: slab no. D 367
*Description:* this trail consists of three sets of manus/pes and an additional manus impression, which are rather poorly preserved. Possibly they are 'undertracks'. The foot appears to be digitigrad and pentadactyl, mesaxonic. Digit III is longest and thickest. The others are symmetrically positioned so that the length of II and V on the one hand and I and V on the other are practically identical. I, II, IV and V show small claws, but a pad is not visible. The posterior margin of the toes forms a concave curve which is hard to interpret: it should be the edge between toes and metatarsal pads, but it could equally well be a sediment structure. The overall length corresponds roughly to the width (27 mm). The hand is less well preserved than the foot. It is

*Fig. 8.* A. *Sustenodactylus hollandicus* trail; B. *Capitosauroides* sp. trail; C. Vertebrate trace. Incertae sedis (no. D 377).

*Table 4. Sustenodactylus hollandicus* (Slab no. D 340). Statistical parameters of the measurement of characters.

| Characters | N | Mean length | Standard deviation | Coefficient of variability (%) | Confidence interval for the mean at the 5% level | Cramer's test | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | Asymmetry | Test variable (a) | Probability (%) ×>(a) |
| *Feet:* | | | | | | | | |
| | | (mm) | | | | | | |
| Length | 7 | 9.9 | 1.069 | 10.8 | 8.8–10.9 | −0.772 | 0.97 | 33 |
| Width | 7 | 8.3 | 0.951 | 11.5 | 7.4– 9.2 | −0.764 | 0.96 | 34 |
| Pace | 6 | 48.7 | 2.160 | 4.4 | 46.4–51.0 | −0.965 | 1.14 | 25 |
| Stride | 5 | 49 | 2.740 | 5.6 | 45.5–52.5 | −0.609 | 0.67 | 50 |
| | | (°) | | | | | | |
| Pace angulation | 5 | 60.6 | 2.510 | 4.1 | 57.4–63.8 | −0.512 | 0.56 | 58 |
| *Hands:* | | | | | | | | |
| | | (mm) | | | | | | |
| Length | 4 | 11.8 | 0.957 | 8.1 | 10.2–13.3 | 0.854 | 0.84 | 40 |
| Width | 4 | 4.5 | 0.577 | 12.8 | 3.5– 5.5 | 0 | 0 | 100 |
| Pace | 4 | 45.8 | 2.630 | 5.7 | 41.5–50.0 | −0.124 | 0.12 | 90 |
| Stride | 4 | 49.5 | 3.109 | 6.3 | 44.5–54.5 | 1.597 | 1.57 | 12 |
| Manus-pes distance | 6 | 19.2 | 1.602 | 8.4 | 17.4–20.9 | 0.041 | 0.05 | 96 |

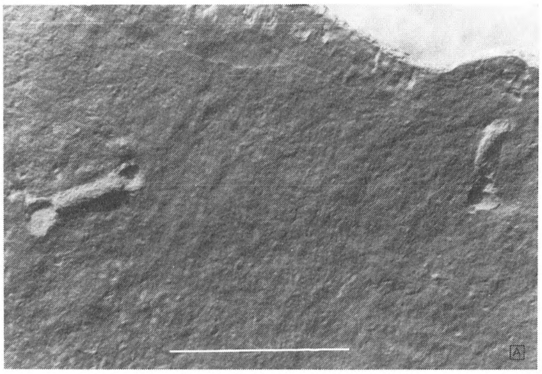


*Fig. 9.* A. *Bifungites* sp.; B. Invertebrate trace (*Kouphichnium*?) on manus of *Brachychirotherium paraparvum*.

smaller than the foot, slightly longer than broad, and has a comparable form with digit III being stronger than the other digits. A tail trace, broad and faint with a regular slight wind, is associated with these impressions. The ratio stride/foot length is ca. 4.8. The pace is about 95 mm on average and the stride 135 mm, the cross axis 90°.

*A palaeontological analysis:* The specific characters of the present form are the broad trail, the mesaxonic limbs and the tail trace. The uncertainties that remain prevent a good interpretation of its maker. What we do know is that it must have been a primitive tetrapod, probably a stereospondyl amphibian.

*Incertae sedis*

Trail: slab no. D 377 (Fig. 8c)

*Description:* This trail is even more enigmatic than the foregoing. Five pentadactyl autopodia connected in a regular order with a slightly impressed tail. We assume the clearly visible autopodia to be the feet. These are strongly varus (directed inwards) and display three long, curved, slender toes (probably II, III and IV). The fifth digit is very short and hardly visible. The first, if our interpretation is correct, is even shorter so that in life the weight must have rested on the middle digits only. Their length is variable because the foot has slipped a little. Probably IV was longest judging from the second, better impressed foot which shows sharp claws. Characteristic is the strong inward bend of the axis, from 60° to 70°, which is considerable. The overall length resembles that of IV, 23 mm on average. The hand is not well visible, when present at all. Indeed, in front of the foot indeterminate impressions can be discerned which may be partial hand impressions. When correctly interpreted, the hand is directed forwards. The trail stride is 130 mm on average, pace 95 mm, the width 95 mm and the pes angulation 85°. The tail trace varies in width from 8 to 17 mm.

*A palaeontological analysis:* Rhynchosauroid feet, manus unknown, inward direction of foot axis, wide trail: these are the specific characters of this form. Its maker was again a primitive tetrapod, a reptile with impaired locomotion because its limbs were not positioned vertically. What kind of reptile can it have been? Possibly a small cotylosaurian or a sauropterygian: an aquatic animal.

*Invertebrate trace fossils*

Ichnogenus *Bifungites* Desio 1940

*Bifungites* sp. (Fig. 9a)

*Description:* Convex dumbbell-shaped hyporeliefs. Variable lengths (15–55 mm). The ends are elliptical and lie flat on the straight part, which sometimes measures less than its length.

The traces consist of two openings of burrows produced by a U-shaped worm or a crustacean. The convex hyporeliefs were formed by the overlying sediment filling in the original burrows.

*Indeterminate ichnogenus* (Fig. 9b)
Slab no. D 277 shows two weak, double branched traces which form two irregular parallel rows. One of them appears to be complete, the other does not and this one comprises few impressions and some marks outside of the row. Each track resembles a small firneedle and is positioned obliquely to the direction of locomotion (?). The opening of the fork is directed inwards. The length varies from 8 to 20 mm. There is an irregularity in the distribution of these impressions (distances from 14 to 30 mm), in the rows as well as between the rows so that an interpretation is difficult. It is possibly an arthropod trace: *Kouphichnium* ? (limulid trail).

## Conclusions

The most recent discoversies have brought to light three new ichnospecies: *Brachychirotherium paraparvum,* a thecodont which was only briefly mentioned in our earlier paper, and *Coelurosaurichnus ratumensis,* a quadruped dinosaur, which was then not even known. Both these ichnospecies have been produced by relatively large animals. The other footprints indicate the one-time presence of several smaller animals whose locomotion must have been primitive: a small amphibian, a microvertebrate, a reptile and an indeterminate creature. The difficulty in interpreting the footprints and their makers is that in comparison to the number of ichnospecies only very few autopodia-skeletons are known.

To date twelve vertebrate and four invertebrate ichnospecies are recognised from the Middle Triassic at Winterswijk. *Rhynchosauroides peabodyi* remains the most common species, followed by *Procolophonichnium winterswijkense.* The others are probably known from only one trail each. Two of these prove the one-time presence of large animals. Small or very small vertebrates are represented by six types of tracks. Consequently we have a fauna consisting of amphibians, cotylosaurians, lepidosaurians, thecodonts and dinosaurs. What we have written earlier (Demathieu & Oosterink, 1983) still holds: 'The Winterswijk tracks probably formed in the littoral zone of small bays after the sea had receded: mud cracks give evidence of this. Were these waters fresh or salt? Body fossils like *Myophoria, Pecten, Lingula* and *Beneckia* indicate a marine littoral environment.'

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