FISH TRAILS FROM THE EARLY PERMIAN OF SOUTH AFRICA

by ANN M. ANDERSON

ABSTRACT. In the lower Karroo Dwyka and Ecca Series there are widespread trace fossils which can be attributed with reasonable confidence to fish. Each trail is composed of a bilaterally symmetrical set of up to nine distinct waves. The waves in a set share a common wavelength and direction of travel, but they vary in form and amplitude. The marginal pair of waves has the lowest amplitude; this pair was apparently left by the pectoral fins. Pelvic appendages appear to have been responsible for the remaining paired wave(s). The unpaired wave has the greatest amplitude and was probably produced by the caudal fin. A new ichnogenus is erected to contain these trails. It is divided into three ichnospecies on the basis of increasing complexity: *Undichna bina*, *U. simplicitas*, and *U. insolentia*.

THE early Permian in South Africa is represented by the lower Karroo Dwyka and Ecca Series (see Anderson, J. M. 1973, Chart 35). The Dwyka Series consists essentially of glacial diamictites; the succeeding Ecca Series is predominantly argillaceous (see Haughton 1969). These two litho-units are diachronous. The fish trails are preserved in isolated glacial lake deposits in the Dwyka Series and in various finely laminated sequences in the more extensive Ecca basin.

Haughton (1925) first reported the 'peculiar parallel sinuous lines' from the Ecca Series. He suggested then that they could be markings made by ventral spines of a fish armed after the fashion of *Acanthodes*. One of these trails was illustrated by Abel (1935, fig. 161). He held amphibians responsible. The Dwyka Series examples were introduced by Plumstead (1970, pl. XI) and discussed by Anderson (1970), who favoured the piscean interpretation.

SEVEN FISH-TRAIL LOCALITIES IN THE GREAT KARROO BASIN

The first two localities described are in Dwyka limnoglacial deposits at opposite ends of the Great Karroo basin. The other five localities are in the Ecca Series: two are from the southern 'turbidite' facies, two are from the quiet-water facies towards the centre of the basin (see Ryan 1967*b*), and the last, also from the centre of the basin, is in the transition zone between the Ecca Series and the overlying Beaufort Series, which is rich in tetrapod remains. Refer to text-fig. 1.

1. *Swart Umfolozi* (lat. 27° 57′ 6″ S., long. 31° 10′ 48″ E.)

Swart Umfolozi is the type locality of the arthropod trackway *Umfolozia sinuosa* Savage, 1971. It is also the only glacial deposit that has yielded well-preserved fish trails (text-fig. 2). Fish trails account for less than 5% of the trails at the locality. However, a good collection of them has been obtained as they could be selected from the vast amount of material made available by commercial quarrying operations.

The quarry, no longer worked, is on the southern bank of the Thongwane (Hloyan) River, in the north-eastern corner of the farm Rooipoort 565, about 45 km south-east of Vryheid.

The varves in which the fish trails are preserved are approximately 200 m from the top of the glacial sequence. They are underlain by a massive diamictite which includes some local fluvioglacial elements. The diamictite directly overlying the varves is shaly and bedded for about 6 m before becoming massive.

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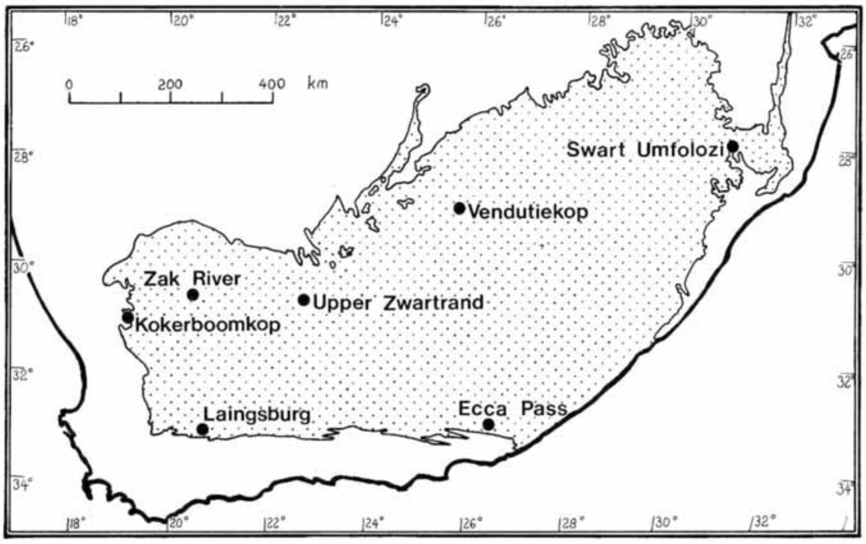


TEXT-FIG. 1. Sketch map of South Africa showing the present extent of the lower Karroo strata in the Great Karroo basin (stippled) and the general positions of the *Undichna* fish-trail localities described in this article.

Individual varves range between a few to 20 mm in thickness. The contact between the pale silty 'summer' portion of a varve and the dark carbonaceous fine-grained 'winter' portion is usually sharp. The fish trails and arthropod trackways are preserved in the carbonaceous partings, less than 1 mm thick. Dropped pebbles and grit are frequent in some units.

2. *Kokerboomkop* (lat. 31° 07′ S., long. 19° 16′ 30″ E.)

This locality is west of Kokerboomkop hill on the farm Potkley Clv. Q. 24-31, about 33 km north-north-east of Nieuwoudtville.

The single fish trail from Kokerboomkop is from a flagstone horizon which has also yielded arthropod trackways and turbidity-current scour structures (Anderson, in press). Individual flagstones are a few millimetres to 15 cm thick. They occupy approximately 1 m within a thick sequence of otherwise massive diamictite. The horizon is approximately 100 m below the advent of widespread lamination preceding the final disappearance of direct glacial deposition in the area.

3. *Laingsburg* (lat. 33° 11′ 30″ S., long. 20° 50′ E.)

Cuttings along the national road both east and west of Laingsburg transect the steeply dipping Karroo deposits almost perpendicular to strike, so bedding plane exposures are infrequent. The largest productive surface is north of the road, 2 km west of the Buffels River bridge on the outskirts of the town.

Theron (1967) logged in detail the lower Ecca Stages exposed in the cuttings. He recognized a vertical transition up the section from distal turbidity current deposits to proximal. Intrasediment horizontal burrows are common, but surfaces with arthropod trackways and associated fish and gastropod trails are rare.

4. *Ecca Pass* (lat. 33° 11′ S., long. 26° 37′ E.)

Ecca Pass, on the main road between Fort Beaufort and Grahamstown, is one of the Ecca Series localities mentioned by Haughton (1925) (Pl. 54, fig. 1). Fish trails and arthropod trackways still can be found *in situ* in the cuttings there but they are extremely scarce. Marginally more success is enjoyed further east along the national road between Grahamstown and King William's Town, 6 km south-west of the bridge over the Great Fish River.

Greywackes, shales, and flagstones are present. As at Laingsburg, this is a turbidite succession (Lock 1973). Intrasediment burrows are common. Fish trails are preserved occasionally on partings between flagstone layers. Arthropod trackways are not necessarily also represented.

5. *Upper Zwartrand* (lat. 30° 45′ S., long. 22° 31′ E.)

The farm Upper Zwartrand V.W. Q. 1-24 is about 45 km north-east of Carnarvon. Outcrops of central Ecca facies flagstones, intruded by dolerite, are fairly good along the Uintjiesleegte River.

The river bed is usually dry. It is littered with loose slabs of flagstone, often lavishly inscribed with pairs of parallel sinusoidal waves (Pl. 54, fig. 2). No trackways are preserved, and intrasediment burrows are rare.

6. *Zak River* (lat. 31° 01′ 24″ S., long. 20° 17′ E.)

The South African Museum, Cape Town, has a fine collection of fish trails, arthropod trackways, and other trace fossils from Zak River. Flagstone has been quarried commercially at the locality since the turn of the century.

The quarries are on the farm Brasse Fontein 371, Clv. Q. 13B-51, about 58 km south of Brandvlei. They exploit a 2-m thickness of yellow, somewhat silty, flagstones over a wide area. Individual units, frequently with subsidiary laminations, are usually less than 4 cm thick. A dolerite sill outcrops approximately 6 m stratigraphically above the flagstones.

7. *Vendutiekop* (lat. 29° 43′ 54″ S., long. 25° 37′ 24″ E.)

At Vendutiekop the fish trails (Pl. 54, figs. 3, 4) are not associated with *Umfolozia*-style arthropod trackways as is the case elsewhere, instead there are limulid trackways (Anderson, 1975). This distinction has both environmental and interpretational implications (see below).

The farm Vendutiekop 120 is about 19 km east of Jagersfontein. The flagstones bearing the trace fossils are being quarried in the bed of a tributary to the Kromellenboogspruit stream.

There are 2 m of light grey fine-grained flagstones. Beaufort Series type sandstone outcrops in the vicinity less than 30 m stratigraphically above the flagstones, but it could not be established whether similar sandstone occurs below as well. The 1:1 000 000 geological map (1970) indicates that the site falls within the Beaufort Series. However, as the map was based on reconnaissance mapping (Ryan 1967*a*) and as the two characteristic lithologies (Ecca shale/Beaufort sandstone) interfinger, the boundary must be regarded as somewhat arbitrarily defined at present (Haughton 1969, p. 358). The lithofacies of the trail-bearing horizon is of the Ecca type.

SYSTEMATIC PALAEONTOLOGY

Fish leave a variety of traces: see Richter 1930, Wachs 1930, Häntzschel 1935, Abel 1935, Linck 1938, Fiege 1951, van Dijk 1959, Fliri *et al.* 1970, 1971, Anderson 1970, Stanley 1971, Cook 1971, and Nicholson 1971.

Anything without a particular name is awkward to discuss and apt to be overlooked. This is a minor problem where there is only a single occurrence; the problem is greater where the occurrence is widespread. It is for this reason that the lower Karroo fish trails need to be systematically defined.

As the Zoological Code (1964) provides little specific guidance, a binomial nomenclature is employed in the sense of the Botanical 'form' nomenclature (1972, Articles 3, 59). It is a classification based on the morphologies of the trace fossils themselves (Sarjeant and Kennedy 1973). As such, the connotation of the 'ichno-genera' and '-species' is necessarily different from that of phylogenetic genera and species. None the less, because the Karroo fish trails do reveal something of the anatomy of the animals responsible, there is a phylogenetic element in their classification.

The following abbreviations for repositories are used herein:

Bernard Price Institute for Palaeontological Research, Johannesburg	B.P.I.P.R.
Geological Survey, Pretoria	G.S.P.
Natal University Geology Departments in Durban and Pietermaritzburg	N.U.
South African Museum, Cape Town	S.A.M.

Unless otherwise stated, museum specimen numbers refer to B.P.I.P.R. material.

In Anderson (1970) photographs 1–8 are of B.P.I.P.R. specimens S.U./K.D. 25, 23, 29, 33, 1, 5, 26, and 2 respectively.

Phylum CHORDATA
Subphylum VERTEBRATA
Class PISCES
Ichnogenus UNDICHNA nov.

Type species. Undichna simplicitas sp. nov.

Definition. The genus includes those trace fossils comprising a set of distinct, horizontal waves with a common wavelength and direction of travel. Most of the waves are paired, and a set is more or less bilaterally symmetrical. There may be as many as nine waves in a set. Frequently there are only two. Occasionally only one wave is preserved. The waves are impressions on epichnial surfaces (and mould ridges on hypichnial surfaces).

Derivation of name. Unda -ae f. (Latin) = wave + ichna.

Comparison. Where there is more than one wave present, certainly where there is more than two, there does not appear to be another ichnogenus with which *Undichna* readily may be confused (see Häntzschel 1962). If none but isolated waves are encountered at a locality, and especially where these are sinusoidal, identification as *Undichna* is unwarranted (cf. ichnogenus *Cochlichnus* Hitchcock, 1858).

Material examined in this study

(*a*) B.P.I.P.R. material selected at various localities: Kb./K.D. 1–3 (1 trail); S.U./K.D. 1–134 (at least 32 trails); B.R./K.E. 1–4 (several trails); Bb./K.E. 1–8 (5 trails, silicone rubber moulds); E.P./K.E. 1–10 (several poor trails); Lb./K.E. 1–45 (several trails); U.Z./K.E. 1–8 (several long trails); Vd./K.E. 1–16 (a few trails); Z.R./K.E. 1–29 (1 trail).

(*b*) N.U. material from Swart Umfolozi (several good trails) uncatalogued except for Savage's (1971) figured specimens.

(*c*) Dr. D. E. van Dijk, Zoology Department, Pietermaritzburg, private collection.

(*d*) S.A.M. specimens 11333–11335 from Ecca Pass (1 good trail); 3535–3551, 3584–3591, 11598–11617, 11680–11688, and nine other specimens from Zak River (about 10 good trails).

(*e*) G.S.P. specimens I 1–64 from a locality in the southern Ecca facies (1 poor trail).

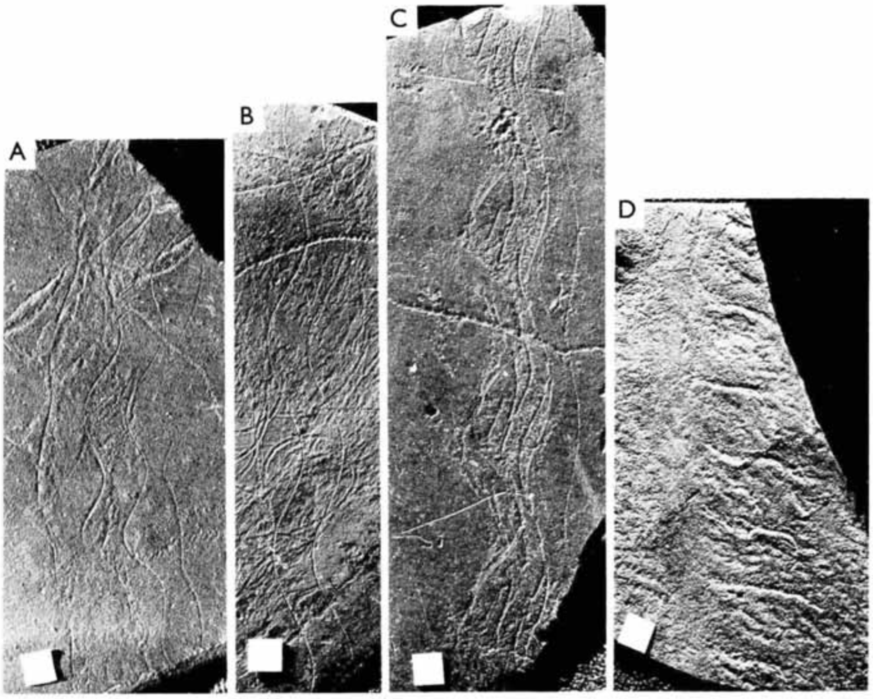
Undichna simplicitas nov.

Plate 54, figs. 3–4; text-fig. 2A, D

1970 undesignated fish trails, Anderson, pl. 1, figs. 2, 4.
1972 undesignated trails of eel-shaped animals, Warren, figs. 2–3.

Definition. In this species there are two sets of paired waves and one unpaired wave in a complete set.

The paired waves with members furthest apart have a lower amplitude than the



TEXT-FIG. 2. *Undichna* fish trails from the Swart Umfolozi fresh-water glacial locality ($\times 0{\cdot}5$—the white scale is 1 cm²). A, S.U./K.D. 4, holotype of *U. simplicitas* nov. showing the two marginal scolloped waves made by the pectoral fins, the two sinusoidal waves made by the pelvic fins, and the vague disturbance caused by the caudal fin. This disturbance partly obscured both the pectoral and pelvic wave on the left side. It is not possible to determine the direction of movement because the caudal wave is not cleanly incised (cf. Anderson 1970, pl. I) and there are no extensions on the scolloped waves. B, S.U./K.D. 8, *U. bina* nov. which consists of two sinusoidal waves in phase. C, S.U./K.D. 6, *U. insolentia* nov. paratype with three pairs of sinusoidal waves almost in phase: the wave-pair with members closest together has the highest amplitude and its phase position is slightly further towards the top of the photograph than the others, while the wave-pair with members the intermediate distance apart has the lowest amplitude and its phase position is slightly further towards the bottom of the photograph than the others. This indicates that the animal moved from the bottom to the top of the photograph as orientated. The scolloped wave on the right is complete, but that on the left is preserved only on the 'bottom' end of each scollop. The unpaired wave is represented by the asymmetrical sinusoidal area of disturbance obscuring parts of the paired sinusoidal waves on the left. D, S.U./K.D. 117, *U. simplicitas* nov. in which only the unpaired wave is recorded. Its form is unusual, consisting of a series of unconnected transverse sigmoids similar to those in the more complete trail illustrated in Anderson (1970, pl. II-7). In this case the fish probably was swimming at an angle with its head higher than its tail.

other waves in a set. These waves generally define the outer margins of the set, although the unpaired wave often does extend beyond. Each wave of this widest pair is usually scolloped with the convex side of the scollops directed outwards. The scollops often overlap, the major extensions off the general scolloped wave are consistently on the same ends of the scollops in both members. Sometimes these outer scolloped waves are composite, being composed of a number of concentric lines.

The other paired waves have a smaller distance between them than the scolloped pair, and usually are contained by them, but do tend to lie nearer to one of the limiting waves than to the other. Their form, ideally, is sinusoidal, but asymmetry increases with displacement from the central position. These waves rarely are broken. Their amplitude is always greater than that of the continuous scolloped waves (Anderson 1970, pl. I-4).

The unpaired wave has a median position when the sinusoidal waves are centrally placed and both scolloped waves are present; otherwise, it can extend well beyond the outer edge of one of the scolloped waves. It is seldom cleanly incised and its expression is very variable: it can take the form of a continuous sinusoidal wave (Pl. 54, fig. 3), a chain of linked (Anderson 1970, pl. I-3) or unconnected sigmoids (Pl. 54, fig. 4; text-fig. 2D), a series of aligned ladle-shaped scoops (1970, pl. I-2), or of opposing herring-bone-like flicks (1970, pl. I-1).

Any of the waves can be missing in one trail, but if the paired sinusoidal waves are represented at all, both members of the pair are usually present. At least one of the scolloped waves or the unpaired wave must be preserved to permit identification of this species.

Derivation of name. Simplicitas -atis f. (Latin) = straightforwardness.

Types. Type locality: Swart Umfolozi. Holotype: B.P.I.P.R. specimen S.U./K.D. 4 (text-fig. 2A). Paratypes: B.P.I.P.R. S.U./K.D. 10-12, 23, 25, 27, 29-34, 106, 118.

Museum specimens studied

B.P.I.P.R. material from Swart Umfolozi; Vd./K.E. 8, 11, 15.

Comparison

U. insolentia nov. has more than one pair of sinusoidal waves. *U. bina* nov. has only the pair of sinusoidal waves, no paired scolloped or unpaired waves.

Notes on the occurrence of the ichnospecies

In the South African early Permian glacial deposits, *U. simplicitas* has been observed only at Swart Umfolozi where a variety of forms are represented (text-fig. 2A; Anderson 1970, pl. I). It has been nominated type locality for the ichnospecies, but the possibility that the trails there may merely be incomplete *U. insolentia* cannot be refuted.

The presence of diatectic varves at Swart Umfolozi indicates that the water was fresh, because saline conditions would have inhibited their formation due to flocculation of the clay particles (cf. Flint 1971, p. 402; Pettijohn 1957, p. 163; Duff *et al.* 1967, p. 50). Conversely, the presence of limulid trackways at the only other *U. simplicitas* locality, Vendutiekop, suggests that conditions there were at least marginally marine (cf. Goldring and Seilacher 1971).

Two characteristic trails were collected from the upper Ecca Series at Vendutiekop. One of these (Pl. 54, fig. 3) is almost identical with a trail illustrated from the late Permian in Queensland, Australia (Warren 1972, fig. 2): each has a prominent high-amplitude sinusoidal wave flanked (on the left in both pictures) by a fainter sinusoidal wave with a lower amplitude. The two waves are attributed respectively to the caudal and one of the pectoral fins. The other fish trail from Vendutiekop (Pl. 54, fig. 4) is closely comparable with a rare form at Swart Umfolozi (text-fig. 2D).

Undichna bina nov.

Plate 54, fig. 2; text-fig. 2B

Definition. This trail consists of one pair of clear-cut lines a constant distance apart. These usually follow a sinusoidal or slightly asymmetrical sinusoidal course, but at times they may undulate in an irregular way; they are never altogether straight.

Derivation of name. Binus -a -um f. (Latin) = two.

Types. Type locality: Upper Zwartrand. Holotype: B.P.I.P.R. specimen U.Z./K.E. 8 (Pl. 54, fig. 2). Paratypes: B.P.I.P.R. U.Z./K.E. 1, 2, 4, 6, 7.

Museum specimens studied

B.P.I.P.R. material from Upper Zwartrand; S.U./K.D. 8, 13; B.R./K.E. 1–4; Bb./K.E. 8 (silicone rubber mould); E.P./K.E. 3–6, 8; Lb./K.E. 1, 5, 7, 8, 10–14, 18, 30, 32, 39, 43, 44B.

Comparison

U. simplicitas nov. has the pair of sinusoidal waves accompanied by at least one other wave.

Notes on the occurrence of the ichnospecies

U. bina is present in the early Permian of South Africa at one glacial locality (Swart Umfolozi) and it is common in the southern and central Ecca facies. At the type locality, Upper Zwartrand, the trails of various widths occur *en masse* (Pl. 54, fig. 2), accompanied occasionally by a *U. insolentia* wave set. Where there are also trackways, the *U. bina* trails are less frequent. At Laingsburg they may be unusually irregular in form.

Undichna insolentia nov.

Plate 54, fig. 1; text-fig. 2C

1935 ? amphibian swimming trail, Abel, fig. 161.
1970 undesignated fish trail, Plumstead, pl. XI.
1970 undesignated fish trails, Anderson, pl. II, fig. 5.

Definition. Like *U. simplicitas*, this species is more or less bilaterally symmetrical with a pair of low-amplitude scolloped waves at the outer limits and a very variable, high-amplitude, unpaired wave that may project beyond the scolloped margin. Instead of having only one pair of unbroken, generally sinusoidal waves as in *U. simplicitas* and *U. bina*, this species has two or three such pairs.

The distance between the members of each pair of sinusoidal waves is distinctive, as is the amplitude. The wave-pair with the lowest amplitude is the pair the intermediate distance apart; the wave-pair with the intermediate amplitude is the pair the greatest distance apart; the wave-pair with the greatest amplitude is the pair the closest together. The phase-positions of the waves are staggered according to amplitude: the phase of the pair an intermediate distance apart approaches that of the scolloped waves more nearly than does that of the other two pairs, while the phase of the closest pair is more like that of the unpaired wave, with the pair of greatest width in the intermediate position. The direction of declining amplitude of the three pairs of sinusoidal waves, which are only slightly out of phase, is the same as the major overlap extensions off the scolloped waves and also the longer arm of the asymmetrical markings in the unpaired wave.

The two or three pairs of sinusoidal waves are not necessarily accompanied by any of the other waves.

Derivation of name. Insolentia -ae f. (Latin) = unusual character, excess, extravagance.

Types. Type locality: Swart Umfolozi. Holotype: B.P.I.P.R. specimen S.U./K.D. 5 (Anderson 1970, pl. II-6; Plumstead 1970, pl. XI). Paratypes: B.P.I.P.R. S.U./K.D. 1-4, 24, 26, 130.

Museum specimens studied

(*a*) B.P.I.P.R. material from Swart Umfolozi; E.P./K.E. 9-10; Kb./K.D. 3; Bb./K.E. 1-3 (silicone rubber moulds); Lb./K.E. 41; Z.R./K.E. 29.

(*b*) S.A.M. 11334 from Ecca Pass; 3541, 11598, 11606, 11610-11612, 11616 from Zak River.

Comparison

U. simplicitas nov. has only one pair of sinusoidal waves with its pair of scolloped waves and variable unpaired wave; *U. insolentia* has three pairs of sinusoidal waves. *U. bina* nov. consists of only the one pair of sinusoidal waves.

Notes on the occurrence of the ichnospecies

Complete *U. insolentia* wave sets have been found only at Swart Umfolozi, the type locality (text-fig. 2C). Elsewhere in South African early Permian the ichnospecies is represented by only the three pairs of sinusoidal waves (Pl. 54, fig. 1) although there

EXPLANATION OF PLATE 54

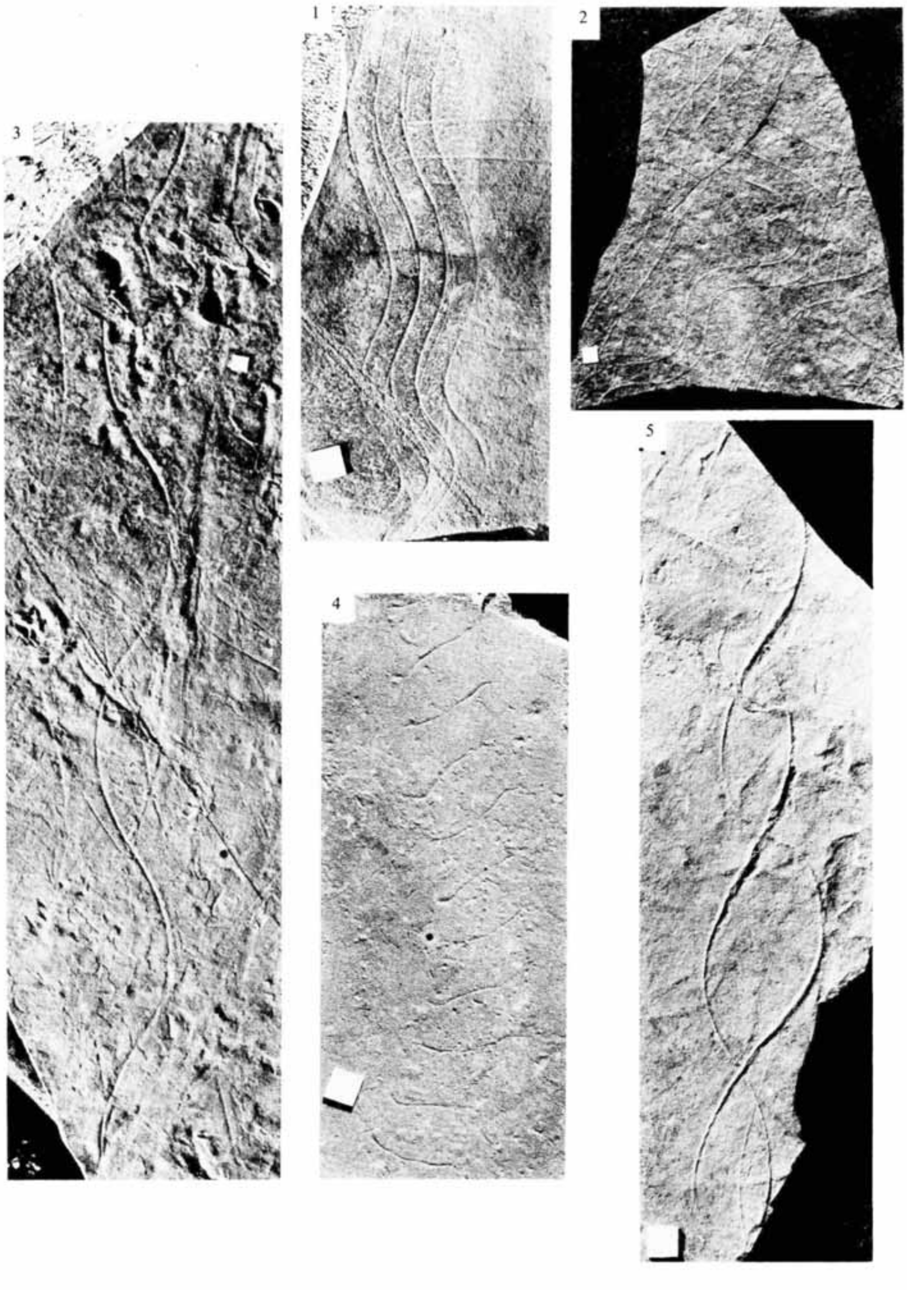
Undichna fish trails from non-glacial localities (the white scale is 1 cm²).

Fig. 1. *Undichna insolentia* nov. S.A.M. 11334 Ecca Pass, ×0·5, in which only the three pairs of sinusoidal waves are preserved. As in text-fig. 2C the wave-pair with members closest together has the highest amplitude and its phase position is slightly further towards the top of the photograph than the others, while the wave-pair with members the intermediate distance apart has the lowest amplitude and its phase position is slightly further towards the bottom of the photograph than the others.

Fig. 2. *Undichna bina* nov. Holotype U.Z./K.E. 8 Upper Zwartrand, ×0·25, with numerous paired sinusoidal waves travelling in various directions. Each pair has a constant distance between its members and a generally constant wavelength and amplitude.

Figs. 3-5. Examples from the marginally marine Vendutiekop locality. 3, *Undichna simplicitas* nov. Vd./K.E. 15, ×0·25, in which the dominant wave (on the right) was made by the caudal fin, while the other fainter sinusoidal wave (on the left) was made by one of the pectoral fins. Compare Warren 1972, fig. 2. 4, *Undichna simplicitas* nov. Vd./K.E. 8, ×0·5, in which only the unpaired wave is recorded. Its form is similar to that of the glacial, non-marine example shown in text-fig. 2D. 5, ? *Undichna* sp. Vd./K.E. 9, ×0·5, in which two parallel sinusoidal waves with the same wavelength and different amplitudes are superimposed, crossing one another. This trail might have been left by a pair of mating limulid arthropods (see King 1975).

PLATE 54



ANDERSON, Permian fish trails

is no such example from the type locality. There is a second glacial locality (Kokerboomkop), and these incomplete trails are common in the post-glacial Ecca deposits in the southern and central facies, where they usually occur with *U. bina* (Pl. 54, fig. 2).

The more widespread occurrence of the three pairs of sinusoidal waves unattended by the scolloped and unpaired members is a preservational feature. Goldring and Seilacher (1971) showed that for arthropod trackways the best-preserved tracks are likely to be those made slightly below the free sediment surface by the walking appendages penetrating the substrate and intersecting buried laminar interfaces. The same principle applies to the *Undichna* fish trails. In this case the propulsive thrust is not made against the sediment itself but against the water. It follows that the traces made by the active swimming organs are least likely to be preserved as undertracks. It has been demonstrated that the three pairs of spines responsible for the sinusoidal waves were rigid extensions not actively employed in propulsion (Anderson 1970, p. 641). However, in the complete trails it is the sinusoidal waves that are the most sharply incised, penetrating further into the sediment. Hence, these waves had the best preservation potential.

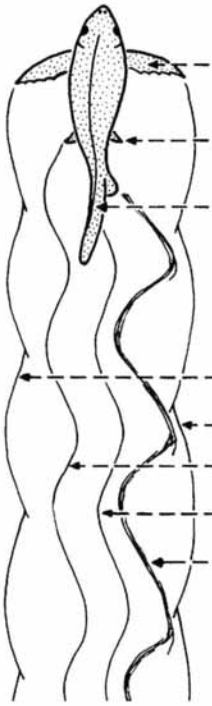
Although *U. bina* has been separated from *U. simplicitas* there is hardly justification for the creation of another ichnospecies similarly related to *U. insolentia*: the three pairs of sinusoidal waves certainly have a more exclusive explanation than the single pair.

COMMENTS ON THE IDENTITY OF THE CREATURES RESPONSIBLE FOR THE *UNDICHNA* TRAILS

The trace fossils have been attributed both to fish (Haughton 1925; Anderson 1970) and amphibians (Abel 1935; Warren 1972). Swimming animals of both classes could leave similar trails because the locomotion of a typical amphibian, even on land, and a typical fish are essentially similar: propulsion is chiefly by lateral undulation of the body. However, the piscean interpretation is favoured because of the absence of footprints or distinct points of pivot indicating that the creature was not attempting to walk in spite of maintaining contact with the substrate.

According to this reconstruction, the outermost paired scolloped waves with the lowest amplitude were left by the pectoral fins, the paired sinusoidal waves between them by the pelvic appendages, and the median unpaired markings with the largest amplitude by the caudal fin (text-fig. 3 and Anderson 1970, fig. 2). *U. simplicitas*, then, would have been made by classical Actinopterygiian fish, but the fish responsible for *U. insolentia* apparently has *three* pairs of pelvic appendages (1970, fig. 3), the nature of which is obscure. The direction of movement can be determined from the phase positioning of these three pairs of sinusoidal pelvic waves, which have slightly unequal characteristic amplitudes: the outer tips of the asymmetrical caudal flicks and the extensions on the scolloped pectoral waves point in the direction from which the animal moved (1970, p. 639).

The producers of the wave sets with fewer waves are less certain. *U. insolentia* examples may consist of only the three pairs of pelvic sinusoidal waves due to the 'undertrack fallout' effect described by Goldring and Seilacher (1971) (see above). By extension, *U. bina*, at least where the wave form is regular, can be regarded as the



TEXT-FIG. 3. Idealized sketch of a slightly asymmetrical *Undichna simplicitas* trail showing the proposed correlation between the component waves of the trail and fish fins (dorsal view).

trace of the pelvic fins of classical fish. Other interpretations doubtless can be applied (cf. Stanley 1971, fig. 7), but too little information generally is available to allow much extrapolation.

More problematic are those unnamed trails in which the two sinusoidal waves are not parallel, but out of phase and superimposed. Some such wave sets have been attributed to fish (Fliri *et al.* 1970, fig. 9; 1971, fig. 8), but King (1965) provided an ingenious explanation for other such which occur with limulid trackways. He reconstructed a Xiphosurid nuptial scene (1965, fig. 1): the sinusoidal wave with the lower amplitude apparently was left by the tail of the female, and the other wave by that of her mate. The same explanation could well apply to certain of the trails occurring with limulid trackways at Vendutiekop (Pl. 54, fig. 5), although they lack the lower amplitude discontinuous waves on either side of the crossed sinusoidal waves described by King (1965).

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