

NAMAICHTHYS SCHROEDERI GÜRICH AND OTHER PALAEOZOIC FISHES FROM SOUTH AFRICA

by B. G. GARDINER

ABSTRACT. *Namaichthys schroederi* Gürich is redescribed from new material from Ganikobis and several other species of fish previously described from the Lower Karroo are re-examined.

THE earliest comparative description of a fish fauna of Dwyka age was given by Gürich in 1923 when he described a number of Palaeoniscoid genera from Ganikobis in South-west Africa. He erected one new Palaeoniscoid genus, viz. *Namaichthys*, which was only described from two somewhat incomplete specimens. Recently much new Palaeoniscoid material has been collected from Ganikobis and the majority of the new specimens belong to this genus, and together afford a far more complete picture than that given by Gürich (1923, p. 55).

MATERIAL

The new fish remains were collected by the Geological Survey of South Africa from Ganikobis, 10 miles to the west of Tses Station in the Berseba Native Reserve. The Dwyka succession in this area begins with a hard, calcareous tillite of 'ground moraine' type. Between Tses and Mariental the tillite is overlain by a soft, dark grey or black, bituminous shale and it is in the lower portion of this that the fish fauna of Ganikobis is found (Martin 1953). Above the shale band is another bed of tillite in the form of a boulder shale. Between Tses and Asab this second glacial bed is succeeded by a grey shale containing slabs of limestone which have yielded gastropods and crinoids. Following this second marine bed is a third glacial deposit which is again composed of boulder-shales. Thus the boulder beds in this area contain at least two sets of marine sediments, the first of which contains the Ganikobis fish. These sediments are interspersed between the boulder beds of glacial origin which have been deposited by ice that came from the west and northwest (Martin 1953). These shale beds represent the bottom of the Upper Dwyka Shales and since the White Band of the top of the Upper Dwyka Shales is not developed in this area it seems that the fish beds belong to the Uppermost Carboniferous and may probably be correlated with the Rio Bonito Beds of Brazil and Uruguay (du Toit 1954, p. 351). The fish occur in hard, black, fine-grained calcareous nodules, and no other fossils were found in association with them.

SYSTEMATIC DESCRIPTIONS

Order PALAEOISCOIDEA

Family ACROLEPIDAE

Diagnosis. See Aldinger 1937, pp. 250-2.

[Palaeontology, Vol. 5, Part 1, 1962, pp. 9-21, pl. 6.]

Genus NAMAICHTHYS Gürich 1923

Diagnosis (emended). Body fusiform, caudal fin deeply cleft and inequilateral. Principal rays of the pectoral fin unarticulated for at least a third of their length. Dorsal and anal fin triangular, the former situated in front of the latter, both approximately the same size. Pelvic fin short based and situated much nearer to the anal fin than to the pectorals; all fins with numerous small fulcra and the lepidotrichia distally bifurcating. Scales with a denticulated hinder margin and with the ornamentation finishing in a series of digitations at the anterior overlapped border. Suspensorium oblique, opercular at least twice as deep as the subopercular—teeth consisting of well-formed conical lanianies and numerous smaller teeth; skull roofing bones ornamented with tubercles and ridges of enamel.

Type species. *Namaichthys schroederi* Gürich.

Remarks. The type material described by Gürich 1923 was housed in the Preussischen Geologischen Landesanstalt zu Berlin, now known as Sammlung des Zentralen Geologischen Dienstes der Staatlichen Geologischen Kommission der D.D.R., Berlin. As a result of the war many of the specimens once housed in this museum have been lost, and the director informs me that it is highly unlikely any of Gürich's types still remain.

Namaichthys schroederi Gürich

Plate 6; text-figs. 1-3

1908 H. Schroeder, p. 696.

1913 E. Hennig, p. 310.

1923 *Namaichthys schroederi* Gürich, p. 55, text-figs. 14-16; pl. 2.

1954 *Namaichthys schroederi* Gürich: du Toit, p. 280 (name only).

Diagnosis. A species of *Namaichthys* with a skull length of up to 10 cm. The length of the head is contained rather more than four times in the total body length. Opercular over twice as long as it is broad and twice the size of the subopercular. Skull with a prominent rostrum and a series of four suborbital bones. Fins rather small, scales thick and rhomboidal with seven or eight large tooth-like projections posteriorly.

Material. Proposed Neotype Geological Survey of South Africa no. 7099 and counterpart, head and anterior part of body; six other specimens in the B.M.N.H., all from the Dwyka, Ganikobis.

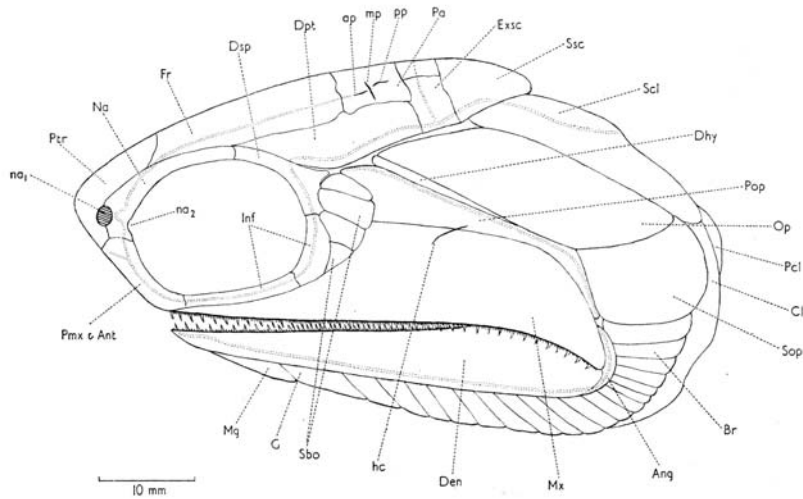
Description. The skull. The general shape of the head can be seen from text-fig. 1. The orbit is large and situated well forward and there is a prominent rostrum as in *Elonichthys* (Moy-Thomas and Dyne 1938, p. 459). The ornamentation of the skull roofing bones is coarse with ridges and tubercles running more or less along the length of the bone on the frontals, parietals, dermopterotics, and nasals. On the preopercular the ridges run forwards and upwards, whilst on the suborbitals they run more or less concentrically. Both the opercular and subopercular show growth-lines and the ridges and tubercles follow the course of these (i.e. they run concentrically round the bone). On

EXPLANATION OF PLATE 6

Namaichthys schroederi Gürich. Part and counterpart of neotype, Geological Survey of South Africa.
× 1½

the supra- and extra-scapular the ridges of ornament follow a much more sinuous course while on the cleithrum and supracleithrum these wavy ridges run more along the length of the bones. Similar wavy striae and ridges are seen on the gulars, branchio-stegal rays and lower jaw.

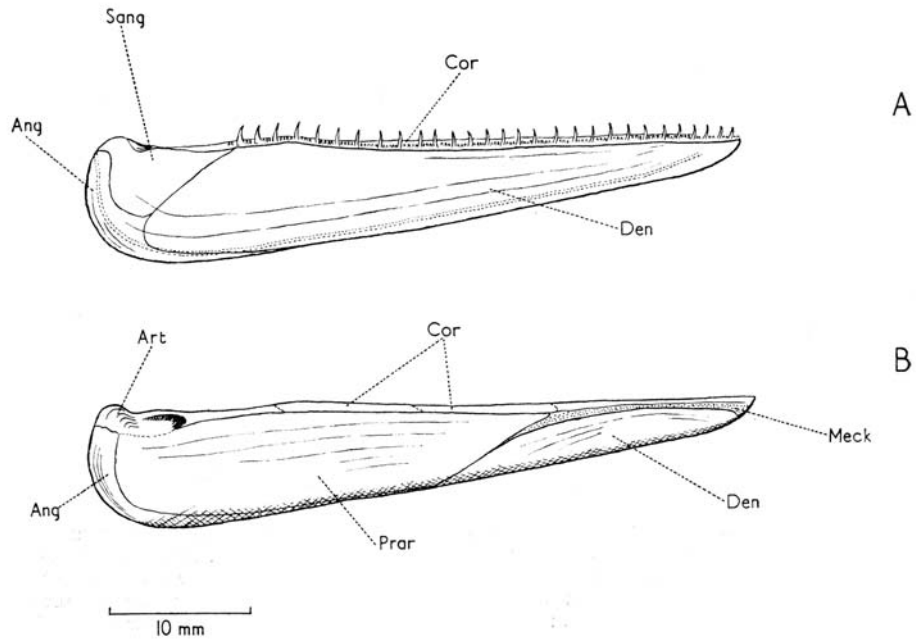
The suprascapular is large and bluntly rounded posteriorly. Anteriorly it meets the



TEXT-FIG. 1. *Namaichthys schroederi* Gürich. Restoration of skull in lateral view. KEY: ap. anterior pit line; Ang. angular; Art. articular; art. pr. process articulating with neurocranium; Br. branchio-stegal ray; Cl. Cleithrum; Cor. coronoid; Den. dentary; Dhy. dermohyal; Dpt. dermatoteric; Dsp. dermosphenotic; Enpt. entopterygoid; Exsc. extrascapular; Fr. frontal; G. gular plate; hc. supra-maxillary sensory line; Inf. infraorbital; Meck. ossified meckelian cartilage; Metpt. metapterygoid; Mg. median gular; mp. median pit line; Mx. maxilla; na₁ anterior nasal aperture; na₂ posterior nasal aperture; Na. nasal; Op. opercular; Pa. parietal; Pal. palatine; Pcl. postcleithrum; Pmx+Ant. premaxillo-antorbital; Pop. preopercular; pp. posterior pit line; Prar. preangular; Ptr. postrostral; Qu. quadrate; Sang. surangular; Sbo. suborbital; Scl. supracleithrum; Sop. subopercular; Spt. supra-ptyergoid; Ssc. suprascapular.

extrascapulars. Of the extrascapular series, there are two pairs of bones as in *Watsonichthys* (Aldinger 1937, p. 254). The parietals and frontals are both large and constitute the major portion of the skull roof. The dermatototics considerably extend the lateral borders of the roof, and are larger than in the genus *Elonichthys*. Anteriorly the frontals meet the postrostral and the nasals. The nasal is a long bone and borders the frontal along almost one half of its lateral edge. The remaining portion of the lateral edge of the frontal is delimited by the dermatototic. The postrostral where it joins the frontals is much more U-shaped than in any of the allied genera (i.e. *Watsonichthys*, *Acrolepis*, *Acropholis*). However, the premaxillary-antorbital which anteriorly joins both postrostral and nasal is very similar to that seen in *Elonichthys*. The orbit is apparently bordered by a series of five bones, the dermosphenotic and nasal above, the premaxillary-antorbital and two infraorbitals below. The dermosphenotic is elongated posteriorly and fits neatly

over the dorsalmost suborbital, almost meeting the preopercular. There is a series of four suborbitals of which the dorsal one and the ventral one are the smallest and are both distinctly triangular in shape. The preopercular does not cover as large an area of the cheek as it does in *Elonichthys* and *Watsonichthys*, but there is a narrow dermohyal present between the preopercular and the opercular.

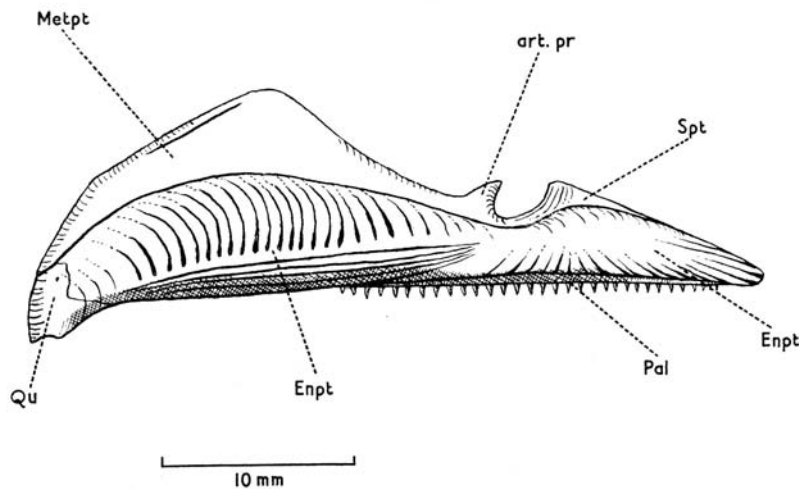


TEXT-FIG. 2. *Namaichthys schroederi* Gürich. Restoration of lower jaw. A, Outer surface. B, Inner surface. For key, see text-fig. 1.

From the angle of the opercular bones the suspensorium can be seen to be very oblique, with the opercular lying at a very acute angle above the preopercular and dermohyal. The opercular is over twice as long as it is broad and twice the size of the subopercular. The subopercular is more vertical in position and broader than it is deep. The maxilla is of much the same shape as in *Elonichthys*, but the posterior members of the larger tooth series are curved so that their tips are directed forwards. The number of branchiostegal rays that could be counted with any accuracy totalled eighteen, with a pair of gulars and a median gular anteriorly.

Lower jaw. The greater portion of the outer surface of the jaw is made up of the dentary. The angular makes up the posterior border of the jaw and reaches upwards behind the surangular (text-fig. 2) to the articulation; it extends anteriorly for about half of the total jaw length. The surangular is more exposed than in many palaeoniscids (cf. *Nematoptychius greenocki*, Watson 1925, fig. 11) with the exposed portion exhibiting

a triangular shape. The dentary anteriorly has a marked symphysis with its opposite member, and on the outer surface of the jaw passes backwards to overlap extensively both the angular and surangular. The upper border of the dentary supports a series of large curved teeth which posteriorly are directed forwards, and an outer row of numerous, closely arranged, small teeth. These are set on a shelf which is overlapped labially to a certain degree by the coronoid. The coronoid also overlaps the dorsal edge of the prearticular. The prearticular is a large bone covering well over half of the inner surface of the jaw, with its lower margin free along most of its length. The posterior end of



TEXT-FIG. 3. *Namaichthys schroederi* Gürich. The palatoquadrate apparatus of the left side, viewed from its admesial surface. For key see text-fig. 1.

Meckel's cartilage is completely ossified, forming a stout articular, and the remainder similarly appears to be ossified, though rather more lightly.

Palate. The palatoquadrate cartilage is completely ossified, and by far the most extensive bone is the entopterygoid (pterygoid of Watson 1925). The entopterygoid is distinctly concave and of pronounced semitubular shape and, together with the maxilla, must have enclosed the maxillary muscles, nerves, and blood-vessels very completely. Posteriorly and not often visible is the ectopterygoid which joins the entopterygoid to the maxilla; when observable it appears as a small sliver of bone. In front of the ectopterygoid the ventral border of the entopterygoid is attached to the palatine. This bone bears a series of pointed teeth, but whether it is of composite structure as in *Watsonichthys pectinatus* (Watson 1925, p. 853) could not be ascertained. Posteriorly the entopterygoid joins the quadrate. The masticatory muscles passed backwards and turned down between the hinder end of the ectopterygoid and the quadrate, to pass into the cavity of the lower jaw. Above the entopterygoid is an expanded, more lightly ossified metapterygoid, but this is more vertical and did not enclose the masticatory muscles,

merely being applied to the inner surface of the maxilla and preopercular. The metapterygoid also articulates with the quadrate posteriorly and has a distinct groove near its dorsal border, similar to that described by Nielsen in *Pteronisculus* (1942, p. 145) and by Rayner in *Kentuckia* (1951, p. 58). In front of this groove is a stout upward projection which articulated with the basiptyergoid process on the neurocranium. Anterior to this the palatoquadrate bar is deeply notched to allow the passage of the maxillary and mandibular branch of the V nerve. The suprapterygoid series continues a little way beyond the notch and finishes before the anterior extremity of the entopterygoid.

Appendicular skeleton. The supracleithrum is very long and extends down from the suprascapular to well beyond the junction of the opercular and subopercular. It is widest dorsally and narrows as it passes backwards and downwards. There is a small postcleithrum present. The cleithrum is both deep and robust, and adjoins the triangular clavicles ventrally. The clavicles, however, have nothing like the immense proportions seen in *Watsonichthys pectinatus*.

The pectoral fin has at least sixteen lepidotrichia, and probably nearer twenty. The principal rays are unarticulated for over a third of their length, but bifurcate distally. Numerous small fulcra are present.

The pelvic fin is not very long based and is formed of about fifteen lepidotrichia. Again the fulcra are small and numerous and the rays distally bifurcated, but they are articulated along the whole of their length.

Unpaired fins. The dorsal and anal fins are of approximately the same size. The dorsal is formed of about twenty-five and the anal twenty-three rays, the fourth and fifth ray being the longest in each fin.

The caudal fin is heterocercal, deeply cleft and unequilobate. All the unpaired fins have numerous small fulcral scales anteriorly.

Squamation. The scales are thick, rhomboidal and deeply imbricating. Posteriorly they are denticulate, the first two or three scale rows behind the opercular apparatus bearing seven or eight tooth-like projections posteriorly. The ornamentation consists of fine transverse ridges, which at times follow the lower margin of the scale. In the posterior third of the body the ridges are better marked. Anteriorly the ornamentation ends in a series of well marked digitations on the overlapped portion of the scale. The layer of enamel is relatively thin.

Other Palaeozoic fishes from South Africa. The following descriptions include all the other fish remains so far described from the Dwyka Series of South Africa together with species of fish of latter age which clearly belong to Dwyka genera (i.e. *Namaichthys sculptus* (Egerton) and *N. molyneuxi* (Woodward)). Finally one other species, *Elonichthys whaitsi* Broom, from the Lower Beaufort, is discussed since it is definitely a member of the genus *Elonichthys* and as such represents the only undoubted *Elonichthys* so far described from the Karroo.

Namaichthys sculptus (Egerton)

1856 *Palaeoniscus sculptus* Egerton, p. 227, pl. 28, figs. 28, 29, 30, 32, 35, 36, 39, 40 (41, 42).

1856 *Palaeoniscus bani* Egerton, p. 227, pl. 28, figs. 26, 27, 31, 33, 34, 37, 38.

1891 *Palaeoniscus bani* Egerton: Woodward, p. 485.

- 1891 *Palaeoniscus sculptus* Egerton: Woodward, p. 485.
 1891 *Acrolepis* (?) *digitata* Woodward, p. 508, pl. 15, fig. 4.
 1909 *Acrolepis digitata* Woodward: Rogers and du Toit, p. 209 (name only).
 1923 ? *Palaeoniscus bani* Egerton: Gürich, p. 32 (name only).
 1923 ? *Palaeoniscus sculptus* Egerton: Gürich, p. 32 (name only).
 1923 *Acrolepis* (?) *digitata* Woodward: Gürich, pp. 32, 51.
 1926 *Acrolepis* (?) *digitata* Woodward: Deeke, p. 105 (name only).
 1926 *Palaeoniscus sculptus* Egerton: Deeke, p. 122 (name only).
 1926 *Palaeoniscus bani* Egerton: Deeke, p. 122 (name only).
 1937 *Palaeoniscus sculptus* Egerton: Aldinger, p. 96.
 1937 *Palaeoniscus bani* Egerton: Aldinger, p. 96.
 1937 *Acrolepis* (?) *digitata* Woodward: Aldinger, p. 258.
 1946 *Palaeoniscus sculptus* Egerton: Bond, p. 128, pl. 10, fig. 4.

Diagnosis (emended). A *Namaichthys* in which the enamel upon each scale terminates in a series of digitations at the anterior overlapped border and the hinder border is denticulated. The ornamentation of the scale is confined to a few pits in the posterior region.

Syntypes. B.M.N.H. P. 12192, P. 12193, and P. 12194 from the Lower Beaufort, Styl Krantz, Cape Colony (scales).

Remarks. Unfortunately this species is only known from scales. The type of this species comes from Styl Krantz, which is considered to be *Cistecephalus* Zone in age. Woodward's type of *Acrolepis* (?) *digitata* (1891, p. 508), however, came from Graaf Reinet, Cape Colony, which according to Watson (1914, p. 205) is definitely *Cistecephalus* Zone. Further, Bond (1946, p. 128) records this species from the Sesame Valley, near the Madziwadzido Native Department Camp. It would appear that Styl Krantz, Graaf Reinet, and the locality in the Sesame Valley are all of roughly comparable age, viz. Lower Beaufort, and probably *Cistecephalus* Zone.

Namaichthys molyneuxi (Woodward)

- 1903 *Acrolepis molyneuxi* Woodward, p. 285, pl. 20.
 1910 *Acrolepis* sp. Woodward, p. 229, pl. 9, figs. 2-4.
 1923 *Acrolepis molyneuxi* Woodward: Gürich, pp. 32, 51.
 1954 *Acrolepis molyneuxi* Woodward: du Toit, p. 323 (name only).

Diagnosis (emended). A *Namaichthys* in which the denticulate hind margin of the scales consists of very prominent long teeth. At the anterior overlapped portion of the scale the enamel ends in a series of digitations and the ornamentation consists of a number of fine ridges.

Holotype. South African Museum, from the Sengwe Coalfield, Rhodesia, Upper Ecca Shales (scales).

Remarks. This species is known only from scales.

Genus WATSONICHTHYS Aldinger 1935

Diagnosis. See Aldinger 1935, p. 254.

Type species. *Watsonichthys pectinatus* (Traquair).

Watsonichthys lotzi (Gürich)

1923 *Acrolepis lotzi* Gürich, p. 34, text-figs. 2, 4–9, pl. 1.

1937 *Acrolepis lotzi* Gürich: Aldinger, p. 260.

1954 *Acrolepis lotzi* Gürich: du Toit, p. 280 (name only).

Diagnosis. See Gürich 1923, p. 34. In addition: a *Watsonichthys* with not such a strong scale ornamentation as that seen in the type species. The ridges of enamel on the scales are not as stout, fewer in number, and a greater percentage of them do not run the whole length of the scale.

Holotype. Incomplete fish, showing underside of head and one third of the body, in the Sammlung des Zentralen Geologischen Dienstes der Staatlichen Geologischen Kommission der D.D.R., Berlin, from the Upper Dwyka Shales, Ganikobis.

Remarks. Aldinger (1935, p. 260) suggests that from the form of the opercular and supracleithrum this species probably belongs to a new genus, although he does not commit himself to giving it a name. Despite the type material not being accessible to the author (it has presumably suffered the same fate as that of *Namaichthys schroederi*), from Gürich's description this species would appear to fit most closely into the genus *Watsonichthys*. It has unarticulated lepidotrichia in its pectoral fins which rules out its inclusion in the genus *Elonichthys*. On the other hand, from the shape and size of both opercular and subopercular it could not possibly be placed in the genus *Acrolepis*. The unarticulated lepidotrichia of the pectoral fin, ornamentation of the scales, shape of the opercular apparatus and the large clavicles all agree with that condition seen in the genus *Watsonichthys*.

Family PALAeoniscidae

Diagnosis. See Aldinger 1937, pp. 229–30.

Genus PALAeoniscus Blainville 1818

Diagnosis. See Westoll in Aldinger 1937, p. 97.

Type species. *Palaeoniscus freieslebeni* Blainville.

Remarks. This genus has been adequately described by Westoll with additional description by Aldinger, in Aldinger 1937, pp. 97–99.

Palaeoniscus capensis Broom

1913a *Palaeoniscus capensis* Broom, p. 1, pl. 2, fig. 1.

1923 *Palaeoniscus capensis* Broom: Gürich, pp. 28, 32.

1926 *Palaeoniscus capensis* Broom: Deecke, p. 122 (name only).

1937 *Palaeoniscus capensis* Broom: Aldinger, p. 96.

1954 *Palaeoniscus capensis* Broom: du Toit, p. 279 (name only).

Diagnosis. See Broom 1913a, p. 1.

Syntypes. Three specimens, one showing all but the head, the other two only the tail halves, in the South African Museum, from the Hantam Mountains, 12 miles west of Calvinia, Upper Dwyka.

Remarks. I have examined the type material of this species and contrary to Aldinger

(1937, p. 96) I agree with Broom (1913a, p. 1) that these specimens undoubtedly belong to the genus *Palaeoniscus*. The scale ornamentation with its series of obtuse ridges is very reminiscent of that condition seen in the type species. Broom (1913a, p. 1) dealing with the age of the specimens states that they 'are probably Upper Dwyka', with which view du Toit (1954, p. 279) agrees, although du Toit is more specific and believes that they come from the White Beds at the very top of the Dwyka. However, both Talbot and Crompton (private communication) believe it to be somewhat later in age.

Family ELONICHTHYIDAE

Diagnosis. See Aldinger 1937, pp. 204–5.

Genus ELONICHTHYS Giebel 1848

Diagnosis. See Aldinger 1937, pp. 16–18.

Type species. *Elonichthys germari* Giebel.

Elonichthys whaitsi Broom

- 1913a *Elonichthys whaitsi* Broom, p. 2, pl. 2, fig. 2.
 1923 *Elonichthys whaitsi* Broom: Gürich, p. 32 (name only).
 1926 *Elonichthys whaitsi* Broom: Deeke, p. 111 (name only).

Diagnosis. See Broom 1913a, p. 2.

Holotype. Nearly complete fish, in the South African Museum, from Droogvoets farm, Fraserburg District, Lower Beaufort.

Remarks. From an examination of this specimen there can be little doubt that Broom (1913a, p. 2) has correctly assigned it to the genus *Elonichthys*. The ornamentation of the scales consists of ridges of enamel running transversally, somewhat more pronounced than the description given by Broom (1913a, p. 3) would lead one to believe. The scales are denticulated posteriorly and the ornamentation finishes as a series of digitations on the anterior overlapped portion. The suspensorium is oblique as in *Elonichthys serratus* Traquair. Gürich (1923, p. 32) assesses the age as possibly *Lystrosaurus* Zone, but du Toit (1954) puts it in the Lower Beaufort (*Cistecephalus* Zone or earlier).

INCERTAE SEDIS

Acrolepis addamsi Broom

- 1907 *Acrolepis* sp. du. Toit, p. 139.
 1913b *Acrolepis addamsi* Broom, p. 400, pl. 20.
 1937 *Acrolepis addamsi* Broom: Aldinger, p. 258.
 1954 *Acrolepis* sp. du Toit, p. 417 (name only).

Diagnosis. See Broom 1913b, p. 400.

Holotype. South African Museum, from the Wesselton Mine, Kimberley, 135-foot level, approximately of Dwyka age.

Remarks. Broom (1913b, p. 400) pointed out that this specimen was not the same as that figured by Woodward (1891, fig. 4) under the name of *Acrolepis* (?) *digitata*: Aldinger

(1937, p. 258) is certain that it is not an *Acrolepid*, and suggests that it is a member of the *Elonichthyidae*. The scales possess six or seven denticles on their posterior borders and the ornamentation consists of a series of flat ridges which pass back and anastomose. I agree with Aldinger (1937, p. 258) as to the relationship of this species and would suggest tentatively its inclusion in the genus *Elonichthys*.

Other recorded remains from the Dwyka Series. The following are included in this paper in order to complete the list of recorded fish remains from the Dwyka series. They are all based on indeterminable, fragmentary remains and are thus all of doubtful affinities.

Elonichthys sp., from the White Beds of the Upper Dwyka Shales, Clavina.

1909 Rogers, A. W., and du Toit, A. L., p. 193.

1909 Broom, R., p. 286.

Elonichthys?, from the Upper Dwyka Shales, Ganikobis.

1923 Gürich, G., p. 64, figs. 18, 19.

1954 du Toit, A. L., p. 280 (name only).

Rhadinichthys?, from the Upper Dwyka Shales, Ganikobis.

1923 Gürich, G., p. 63, fig. 17.

1954 du Toit, A. L., p. 280 (name only).

Genus V, from the Upper Dwyka Shales, Ganikobis.

1923 Gürich, G., p. 66.

DISCUSSION

The relationship of the genus Namaichthys to other palaeoniscoids. The genus *Namaichthys* is related to *Elonichthys* Giebel and more distantly related to both *Acrolepis* Agassiz and *Watsonichthys* Aldinger.

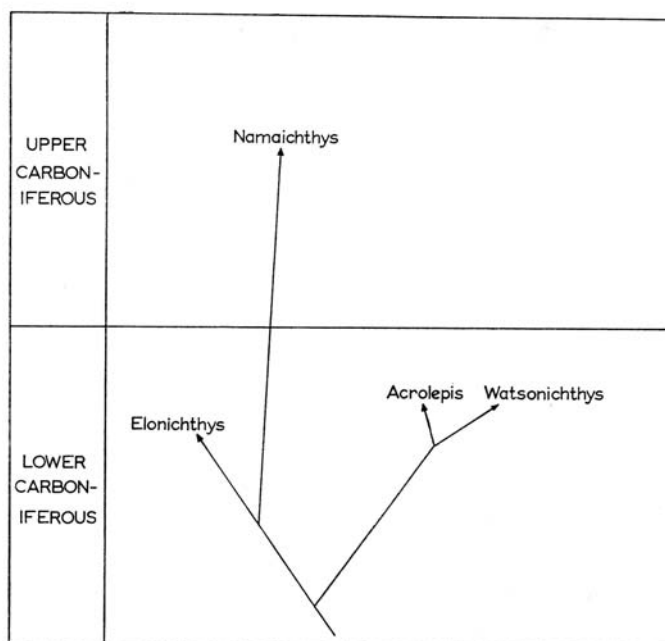
Namaichthys differs from *Watsonichthys* particularly in the structure and ornamentation of the scales, in the make-up of the opercular apparatus and in the shape of the rostrum. In the genus *Watsonichthys* the opercular apparatus is characterized by the presence of an accessory opercular (bone Y of Traquair 1901, p. 84) which is absent in the genus *Namaichthys*, while the prominent rostrum present in *Namaichthys* is not found in the genus *Watsonichthys*. Again the skull of *Watsonichthys pectinatus* (Traquair) possesses only two suborbital bones, but has a sclerotic ring. This sclerotic ring is absent in *Namaichthys schroederi* Gürich and there are four members of the suborbital series. Further, there is a premaxilla present in the skull of *Watsonichthys* which is absent in *Namaichthys* and the preopercular in the latter is much narrower than in *Watsonichthys*. However, in the shape of the body, in the make-up and position of the fins, and in the dentition these two genera are very much alike. In both, the anterior rays of the pectoral fins are unarticulated for at least a third of their length.

The differences between *Namaichthys* and *Acrolepis* are less obvious. If we take Moy-Thomas's (1938, p. 464) definition of the genus *Acrolepis* in which he states that the scales are not denticulated posteriorly, then we have a very neat separation in that in *Namaichthys* the scales are always denticulated posteriorly with four or more large serrations. However, Woodward (1891, p. 509) in his remarks on *Acrolepis (?) digitata*

(*Namaichthys sculptus*) states that 'the scales only differ essentially from those of the typical *Acrolepis* in the presence of posterior denticles, a character usually only of specific value'. I am in complete agreement with Woodward's (1891, p. 509) view after having examined the scales of all the species of *Elonichthys*, *Acrolepis*, and *Watsonichthys* represented in the British Museum (Nat. Hist.) collections. Within the genus *Elonichthys* alone, all the types of scale ornamentation which occur in the genera *Namaichthys*, *Acrolepis* and *Watsonichthys* can be found. In *Elonichthys robisoni* (Hibbert) from the Carboniferous Limestone, the scales are rhomboidal and denticulated posteriorly. The ornamentation of the scales consists of numerous fine ridges on the more anterior members, but towards the caudal region these striae or ridges tail off into pits, leaving anterior digitations on the overlapped position and posterior denticulations. It would appear that primarily there was a very strong ornamentation as in *Elonichthys egertoni* (Egerton) with stout ridges running diagonally across the scale. Later with a reduction in the ornamentation, the points where these ridges ended on the hinder margin, because of their increased thickness remained as projecting teeth or serrations, the areas between the ends of the ridges being resorbed. Similarly the same process has occurred on the anterior overlapped area, leaving a series of digitations, the posterior teeth and the anterior digitations represent the opposite ends of what were in earlier forms pronounced ridges of ornamentation. In the genus *Namaichthys* the scales show exactly this state, with very little ornamentation, but with stout teeth posteriorly and with digitations on the anterior overlapped portion. Both the anterior digitation and the posterior denticulation on the scales represent the remnants of what was in earlier forms strong ridges of ornamentation. The scales of *Elonichthys egertoni* (Egerton) have no denticulations posteriorly or digitations anteriorly, and apart from the ridges of enamel being more delicate, approach that type of ornamentation seen in *Acrolepis*. On the other hand, *Elonichthys germari* Giebel has numerous fine ridges of ornament which end anteriorly just short of the scale margin to give a series of digitations, but posteriorly the scale margin is entire and not denticulated. In *Elonichthys serratus* Traquair the posterior scale margin bears five or six teeth, the ornamentation consists of a few pits and grooves but anteriorly there are no digitations. Again in *Elonichthys semistriatus* Traquair the hinder margin is entire, but there are five or six pointed ridges ending on it, these ridges tail out anteriorly into a few pits with no anterior digitations. Thus it would appear that superficial scale characters have little value in distinguishing between the genera *Elonichthys*, *Namaichthys*, *Watsonichthys*, and *Acrolepis*, and what is more because of the variation in the scale ornamentation which can occur over the length of the body in these genera, assignment of isolated scales to individual species can be very dubious. However, from the structure of the skull alone the distinction between *Namaichthys* and *Acrolepis* is quite apparent. The opercular apparatus is far less oblique in *Acrolepis* (Westoll in Aldinger 1937, fig. 74) than in *Namaichthys* and the maxilla is quite differently shaped in the last two genera. The prominent rostrum seen in *Namaichthys* is missing in *Acrolepis* and in this respect *Acrolepis* more closely approaches the genus *Watsonichthys*. Other features include the opercular apparatus, the opercular being almost equal to the subopercular in size in *Acrolepis*, whereas in *Namaichthys* the opercular is at least twice as large as the subopercular. The extrascapular series is represented by two pairs of bones in *Namaichthys* as against at least four pairs in *Acrolepis*. However, these two genera resemble one another fairly closely in body shape, disposition and make-up of

the fins and in their dentitions. In both the anterior rays of the pectoral fin are unarticulated for the first third of their length.

The relationship of *Namaichthys* to the genus *Elonichthys* is closer than to either *Watsonichthys* or *Acrolepis*. The body shape, structure, and ornamentation of the scales, dentition and the disposition of the fins are similar in both *Elonichthys* and *Namaichthys*, but the pectoral fin in *Elonichthys* unlike that in *Namaichthys* has all its fin rays articulated to their bases. The general pattern of the skull roofing bones is similar except for



TEXT-FIG. 4. Evolutionary tree of *Namaichthys* and its relatives.

the increased number of infraorbitals in the genus *Elonichthys*, eight in *Elonichthys serratus* Traquair as against two in *Namaichthys schroederi*. Other differences include the number of suborbitals, four in *Namaichthys schroederi*, two in *Elonichthys serratus*, the preopercular which is much narrower in the genus *Namaichthys*, and the presence of two pair of extrascapulars in *Namaichthys* instead of the more usual single pair as in *Elonichthys*. In *Namaichthys* the opercular apparatus is slightly more oblique and there is a greater number of branchiostegal rays.

From this survey it appears to me that the genera *Namaichthys* and *Elonichthys* are fairly closely related and have arisen from the same ancestral stock (text-fig. 4). The genera *Watsonichthys* and *Acrolepis* are also both closely related and have come from that same ancestral stock which gave rise to *Elonichthys* and *Namaichthys*, separating off a little earlier in time than did *Namaichthys*.

I would like to thank Dr. E. I. White of the British Museum (Nat. Hist.) for putting this material at my disposal and for access to specimens in his department. In addition I am pleased to acknowledge the generous assistance received from Mr. H. A. Toombs of the same department.

REFERENCES

- ALDINGER, H. 1937. Permischeganoid Fische aus Ostgrönland. *Medd. Grönland*, **102**, no. 3, xlv+392 pp., 44 pl.
- BOND, G. 1946. A Lower Beaufort (Karoo) Invertebrate Fauna from Southern Rhodesia. *Trans. roy. Soc. S. Afr.* **31**, 125-31, pl. 10.
- BROOM, R. 1909. An attempt to determine the horizons of the fossil vertebrates of the Karro. *Ann. S. Afr. Mus.* **7**, 3, 285-9.
- 1913a. On some fishes from the Lower and Middle Karro Beds. *Ibid.* **12**, 1-5.
- 1913b. On some fossil fishes from the diamond bearing pipes of Kimberley. *Trans. roy. Soc. S. Afr.* **3**, 399-402.
- DEECKE, W. 1926. *Fossilium Catalogus 33: Pisces triadici*, 201 pp. W. Junk edit. Berlin.
- DU TOIT, A. L. 1907. Geological Survey of the eastern portion of Griqualand West. *Rep. geol. Comm. C.G.H.* 1906, 89-176.
- 1954. *The Geology of South Africa*, xiv+611, 41 pl. Third edition, London.
- EGERTON, P. 1856. Note on the fish remains from Styl Krantz, South Africa. *Trans. geol. Soc. Lond.* (2), **7**, 226-7, pl. 28.
- GÜRICH, G. 1923. *Acrolepis lotzi* und andere Ganoiden aus den Dwyka-Schichten von Ganikobis, Südwestafrika. *Beitr. geol. Erforsch. dtsh. SchGeb.* **19**, 26-73.
- HENNIG, E. 1913. Über neuere Funde fossiler Fische aus Aequatorial und Südafrika und ihre palaeogeographische Bedeutung. *S.B. Ges. naturf. Fr. Berl.* **7**, 305-18.
- MARTIN, H. 1953. Notes on the Dwyka Succession and some Pre-Dwyka valleys in South West Africa. *Trans. geol. Soc. S. Afr.* **56**, 37-41.
- MOY THOMAS, J. A. and DYNE, M.B. 1938. Actinopterygian fishes from the Lower Carboniferous of Glencarholm, Eskdale, Dumfriesshire. *Trans. roy. Soc. Edinb.* **59**, 2, 437-80, 2 pl.
- NIELSEN, E. 1942. Studies on Triassic fishes from East Greenland. 1. *Glaucolepis* and *Boreosomus*. *Medd. Grönland*, **138**, 403+31 pp., 30 pl.
- RAYNER, D. H. 1951. On the cranial structure of an Early Palaeoniscid, *Kentuckia*, gen. nov. *Trans. roy. Soc. Edinb.* **62**, 1, 53-83.
- ROGERS, A. W. and DU TOIT, A. L. 1909. *An Introduction to the Geology of Cape Colony . . . with a chapter on the Fossil Reptiles of the Karro formation by R. Broom*, xii (i), 491. Second edition, London.
- SCHROEDER, H. 1908. Marine Fossilien in Verbindung mit Permischen Glazialkonglomerat in Deutsch-Südwestafrika. *Jb. preuss. geol. Landesants.* **1**, 694-7.
- WATSON, D. M. S. 1914. The zones of the Beaufort Beds of the Karro System in South Africa. *Geol. Mag. Lond.* (6), **1**, 203-8.
- 1925. The structure of certain Palaeoniscids and the relationship of that group with other bony fish. *Proc. zool. Soc. Lond.* **3**, 815-70.
- WOODWARD, A. S. 1891. *Catalogue of the Fossil Fishes*, **2**, xlv+567 pp., 16 pl. London.
- 1903. On a New Species of *Acrolepis* obtained by Mr. Molyneux from the Sengwe Coalfield. *Quart. J. geol. Soc. Lond.* **59**, 285-6, pl. 20.
- 1907. Fossil Fish remains of Natal, Part I, II. Note on some Fossil fish scales from the Coal Measures of Somkele, Zululand. *Rep. geol. Surv. Natal Zululd.*, p. 101, pl. 10.
- 1910. Note on Palaeoniscid Fish-scales from the Ecca Shales, near Ladysmith. *Ann. Natal Mus.* **2**, 2, 229-31.

B. G. GARDINER,
Department of Biology,
Queen Elizabeth College,
Campden Hill Road,
London, W. 8.



GARDINER, *Namaichthys schroederi*