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A NEW LATE PERMIAN RAY-FINNED (ACTINOPTERYGIAN) FISH FROM THE BEAUFORT GROUP, SOUTH AFRICA

by

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ABSTRACT

A new genus and species of actinopterygian (ray-finned) fish, *Kompasia delaharpe*i, is described from Late Permian (Tatarian) fluvio-lacustrine, siltstone dominated deposits within the lower Beaufort Group of South Africa. It is currently known from two localities on adjoining farms, Wilgerbosch and Ganora, both in the New Bethesda district of the Eastern Cape Karoo region. The fossils were recovered from an uncertain formation, possibly closely equivalent to the Balfour Formation, within the *Dicynodon* Assemblage Zone. *Kompasia delaharpei* differs from previously described early actinopterygians, including the recently described new lower Beaufort Group taxon *Bethesdaichthys kitchingi*, on the basis of a combination of skull and post cranial characters. The genus is characterised by: a uniquely shaped subrectangular posterior blade of the maxilla, a shortened dorsal limb of the preopercular, and a dermopterotic and dermosphenotic contacting the nasal; furthermore, the subopercular is equal to or longer than the opercular, the dorsal fin is situated in the posterior third of the body, slightly behind the position of the anal fin, and the anterior midflank scales exhibit a smooth dermal pattern or surface, with a number of faint ganoine ridges present parallel to the posterior and ventral scale margins. *Kompasia* appears to exhibit a relatively conservative morphology similar to that in the lower Beaufort Group taxon *Bethesdaichthys kitchingi*. As such, *Kompasia* is derived relative to stem-actinopterans such as *Howqualepis, Mimia* and *Moythomasia,* and also derived relative to earlier southern African Palaeozoic actinopterygians such as *Mentzichthys jubbi* and *Namaichthys schroederi,* but basal to stem-neopterygians such as *Australosomus* and *Saurichthys.*

KEYWORDS: *Kompasia,* palaeoniscid, Late Permian, Tatarian, Beaufort Group, Actinopterygii.

INTRODUCTION

A new genus and species of Late Permian actinopterygian fish was initially identified by the author, within collections of fossil fishes made by Croonie and James Kitching from the Wilgerbosch farm, New Bethesda district, South Africa. This is a second paper based on the author's investigations of lower Beaufort Group fossil fishes, in which a new species of early actinopterygian fish from the rocks of the Adelaide Subgroup, Beaufort Group is described (see Bender, 2001, for the description of *Bethesdaichthys kitchingi*).

Actinopterygian fishes are bony fishes particularly characterized by the morphology of the fins, which are supported by stiff bony spines (Caroll 1987; Romer 1966), they constitute the largest group of living fishes with a least 23 700 living species (Nelson 1994). The major actinopterygian groups diverged before the end of the Palaeozoic, with the early or 'lower' actinopterygians representing the 'primitive' or basal members of the Teleostei (Gardiner 1973).

The new taxon, *Kompasia delaharpei gen.et sp.nov.*, belongs to a group of early actinopterygian taxa which, owing to a lack of phylogenetic resolution, are usually grade-classified as 'palaeoniscids' (see Coates 1998), or consigned to the paraphyletic 'palaeonisciforms' (Coates 1999). Traquair (1877-1914) was the first to use the term 'palaeoniscid' to refer to Palaeozoic ray-finned fishes which he assigned to the genus *Palaeoniscus.* These palaeoniscids, palaeonisciforms, or 'Palaeoniscimorpha' (Lund, Poplin, & McCarthy, 1995), consist of mostly Palaeozoic, globally distributed actinopterygians (Coates 1993). The work of Patterson (1982), Gardiner (1984), and Gardiner & Schaeffer (1989) shows that these 'palaeoniscids' include stem-taxa related to the Actinopterygii, Actinopteri, Chondrostei, and Neopterygii (Coates 1998). The 'palaeoniscid' early actinoptgerygians are generally characterised by thick ganoine-covered scales articulated by interlocking peg and socket joints, a heterocercal tail, and a maxilla with extended postorbital blade attached to the cheek (Gardiner & Schaeffer 1989).

The Permo-Triassic Beaufort Group of the Karoo Basin of South Africa is world-renowned for its diverse and abundant therapsid ('mammal-like reptile') fauna (Rubidge 1995). Fossil fish are relatively rare, but where present are useful indicators of palaeoenvironment and also have biostratigraphic potential (Bender *et al.* 1991; Hancox & Rubidge 1997). Despite being rare, a fair number of fossil actinopterygian fish specimens have over the years been collected from the Late Permian lower Beaufort Group in South Africa (Jubb & Gardiner 1975; Bender 1998, 2000, 2001). Egerton (1856) was the first to publish on lower Beaufort fish remains collected from the Graaff-Reinet district. More than a hundred years later, Jubb & Gardiner (1975) provided a comprehensive revision and update of the Beaufort Group fossil fish

remains described by various researchers in the intervening years. A total of nine lower Beaufort Group actinopterygian species are now known, including the new species *Kompasia delaharpei gen.et sp.nov.*, and the recently described *Bethesdaichthys kitchingi* (Bender 2001).

MATERIALS AND METHODS

Five laterally compressed *Kompasia* gen.nov. specimens were recovered from a *Dicynodon* Assemblage Zone roadside locality on the farm Wilgerbosch, New Bethesda district (Adelaide Subgroup, Beaufort Group). These specimens were derived from a blue-green to green, ripple cross-laminated, silty mudstone with a mudstone veneer on the upper surface, and also from an interbedded mudstone/siltstone/fine-grained sandstone sequence, up to 13 cm thick with fossil fish found throughout the sequence. A single specimen was recovered from a site located in a stream bed on the farm Ganora apparently located within, or very close to, the same stratigraphic horizon as at the above-mentioned Wilgerbosch site, being situated approximately three to five kilometres to the north, and preserved in a blue-green siltstone horizon, very similar in form and appearance to that at the Wilgerbosch roadside site. The formational designation of the Ganora and Wilgerbosch sites is uncertain (Cole and others, in press) but appears to be situated in roughly the stratigraphic equivalent of the Balfour Formation.

A number of the referred specimens required mechanical and chemical preparation (see Bender 2000, 2001 for preparation details). Latex rubber casts or peels, enhanced by whitening with ammonium chloride were used to illustrate underlying morphological detail. Thin sections of scales were prepared and studied for histological analysis using a Zeiss standard petrographic microscope with polarised light. Interpretive drawings were made using a Leica MZ6 microscope with drawing tube. Photographs were taken using a Nikon FM camera mounted on a copy stand; for the thin sections a Zeiss polaroid camera was used. The phylogenetics and interrelationships of *Kompasia delaharpei gen.et sp.nov.*, are investigated using the Gardiner & Schaeffer (1989) cladogram III as a basis, since this is the most recent comprehensive phylogenetic analysis of early actinopterygians, and no alternative hypothesis of equivalent depth and taxonomic breadth is available (Coates 1999).

SYSTEMATIC PALAEONTOLOGY

Class: Actinopterygii Woodward 1891
Infraclass: Actinopteri Cope 1871
Genus: *Kompasia* gen. nov.

Derivation of name: The name *Kompasia* is derived from the neighbouring mountain peak Kompasberg, close to where specimens of this taxon were first discovered. Kompasberg at 2 502 m.a.s.l. is the highest peak in the region.

Diagnosis: Small to medium sized fusiform actinopterygian fish. Dermopterotic and dermosphenotic contact the nasal. Rostral bulbous with well developed broad dermal ridges. Maxilla has a rhombohedral-shaped postorbital blade. Preopercular has a reduced anterodorsal horizontal limb. Three suborbitals. Dermohyal triangular, relatively broad and long. Opercular square to rectangular and slightly shorter and narrower than the subopercular. Moderately oblique jaw suspension angle of *ca.* 55 degrees to the horizontal. Branchiostegal series has 10 rays. Supracleithrum relatively long and broad, cleithrum vertical blade crescentic and relatively short and broad. Flank scales relatively large, with an almost smooth, free field dermal ornamentation consisting of two or three faint parallel grooves along the entire posterior margin, and three or four faint parallel ribs close to the ventral margin. Lateral-line scales have a posterior digitation dorsal to the lateral-line aperture.

Remarks and comparisons: Kompasia gen.nov. is readily distinguished from the other Lower Beaufort Group fusiform taxa *Atherstonia scutata* and cf. *Atherstonia minor* on the basis of less than 12-13 branchiostegal rays (see Bender 2000), and *Bethesdaichthys kitchingi* on the basis of the opercular being smaller than the subopercular, and reduced horizontal limb of the preopercular (see Bender 2001). *Kompasia* appears to be similar to the Late Carboniferous genus *Mesopoma* with regard to a number of morphological characters, including: reduction of the branchiostegal rays below 12-13, reduced preopercular, and subopercular equal to or larger than the opercular (see Coates 1993). However *Kompasia* differs from *Mesopoma* in that the dermopterotic reaches the nasal, the jaw articulation is situated posterior to the parieto-extrascapular suture, and the postorbital blade of the maxilla is broad.

Type species: Kompasia delaharpei nov.

Derivation of name: In honour of Mr Lionel de la Harpe, farm owner of Wilgerbosch, whose hospitality and enthusiasm has greatly assisted in the development of the rare and unique fossil fish sites situated at Wilgerbosch.

Syntypes: BP/1/4373/1, in the Bernard Price Institute for Palaeontological Research (BPI Palaeontology), University of the Witwatersrand, Johannesburg, from the Wilgerbosch roadside locality, *Dicynodon* Assemblage Zone, Beaufort Group; GAN 1, housed within the Ganora private collection, from the Ganora upper riverside locality, Ganora, New Bethesda district.

Referred specimens: BP/1/2042; BP/1/4373/1, 1a, 47, 130, 136, K1, housed at the BPI Palaeontology, Johannesburg. GAN 1, housed at Ganora, New Bethesda district.

Horizon and locality: GAN 1 from the Ganora upper riverside site, *Dicynodon* Assemblage Zone, Beaufort Group. All of the other referred specimens are from the Wilgerbosch roadside quarry, *Dicynodon* Assemblage Zone, Beaufort Group.

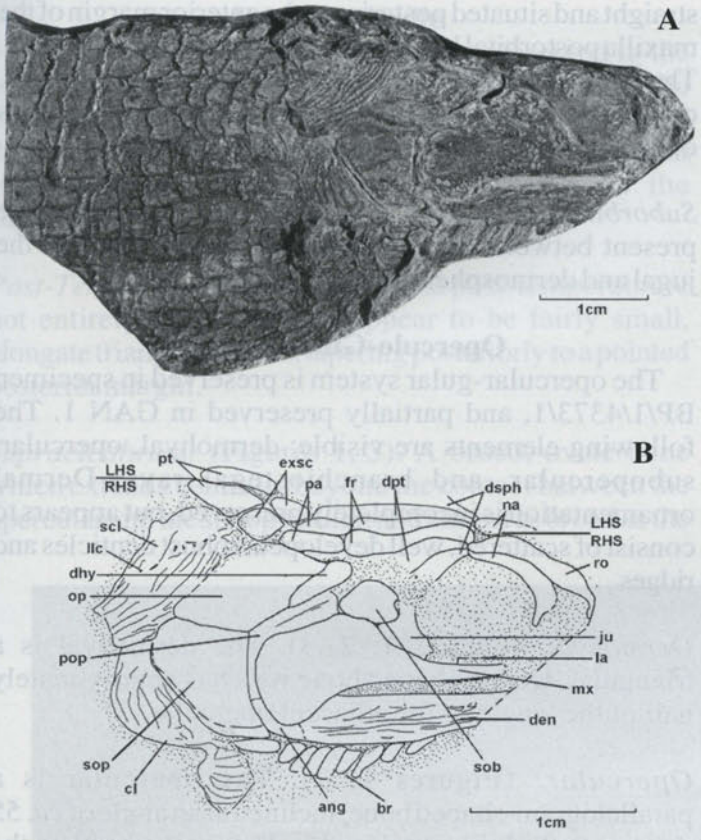


Figure 1. *Kompasia delaharpei* syntype BP/1/4373/1. A – photograph in lateral view showing skull region; B – camera lucida interpretation. (See p12 for abbreviations.)

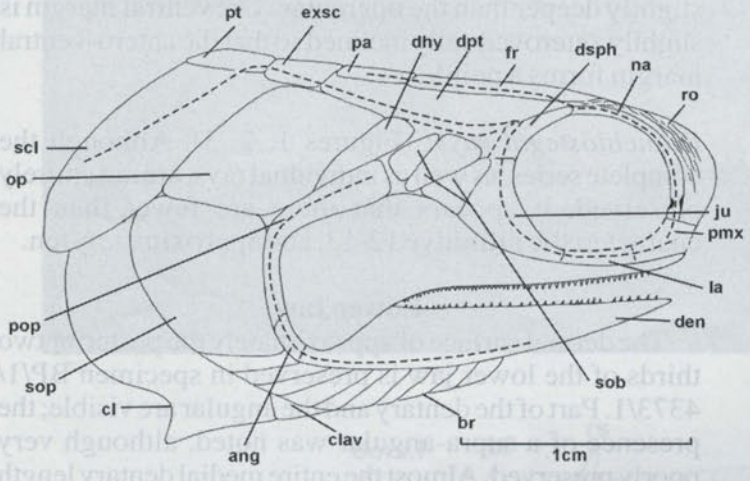


Figure 3. *Kompasia delaharpei*, restoration of the head in lateral view. (See p12 for abbreviations.)

Diagnosis: As for the genus.

Remarks: This taxon is currently known from two apparently stratigraphically linked localities (Ganora and Wilgerbosch) within sight of one another.

DESCRIPTION

Skull Roof

The skull roof region was analysed on the basis of the single almost complete, although relatively poorly preserved specimen GAN 1, and the fairly well preserved

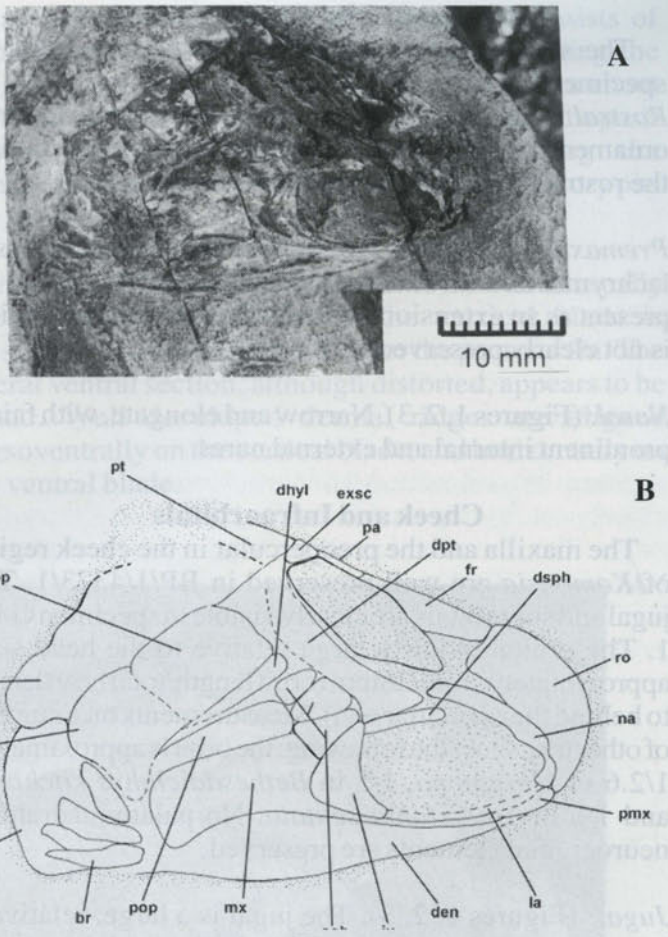


Figure 2. *Kompasia delaharpei* syntype GAN 1. A – photograph in lateral view showing skull region; B – camera lucida interpretation. (See p12 for abbreviations).

specimen BP/1/4373/1. The skull roof region is slightly distorted in the study specimens, consisting of frontals, parietals, dermosphenotics, dermopterotics and extrascapulars.

Parietals: (Figures 1, 2, 3). The parietals although not too well preserved in the study specimens, are subrectangular. They are less than half of the length of the frontals. Dermal ornament consists of well developed broad, robust denticles.

Frontals: (Figures 1, 2, 3). The frontals are narrow and rectangular posteriorly, appearing to taper slightly anteriorly where they suture with the nasal and the rostral. The median suture between the frontals appears to be relatively straight. The dermal ornament is not preserved.

Dermopterotic: (Figures 1, 2, 3). Posteriorly sutures with the extrascapular, tapering anteriorly where it curves dorsally to contact the nasal. Dermal ornament consisting of a broad robust denticular ornamentation.

Dermosphenotic: (Figures 1, 2, 3). An elongate, subrectangular bone, which tapers anteriorly where the intact antero-dorsal margin contacts the nasal.

Extrascapulars: (Figures 1, 2, 3). These are not well preserved, but appear to be narrow and paired, situated between the post-temporals and the parietals.

Snout

The snout region, although distorted, is visible in specimen GAN 1.

Rostral: (Figures 1, 2, 3). A large bulbous bone. Dermal ornament consists of well developed broad ridges, giving the rostral its prominent appearance.

Premaxillae: (Figures 1, 2, 3). Visible beneath the naso-lachrymal/antororbital suture. An *antorbital* could be present as an extension of the lachrymal, but this region is not clearly preserved.

Nasal: (Figures 1, 2, 3). Narrow and elongate, with fairly prominent internal and external nares.

Cheek and Infraorbitals

The maxilla and the preopercular in the cheek region of *Kompasia* are well preserved in BP/1/4373/1. The jugal and suborbitals are clearly visible in specimen GAN 1. The orbital is fairly large relative to the head size, approximately 7mm/28mm (orbit length/total head length to behind the opercular = ¼). Measurements on a number of other taxa show the following: the orbit is approximately 1/2.6 in *Mesopoma*, 1/5 in *Bethesdaichthys kitchingi,* and 1/6 in *Atherstonia scutata.* No palatoquadrate or neurocranial elements are preserved.

Jugal: (Figures 1, 2, 3). The jugal is a large, relatively broad, crescentic bone. The *lachrymal* is poorly preserved in GAN 1 with the anterior margin not clearly visible.

Maxilla: (Figures 1, 2, 3). The postorbital blade is approximately half of the total bone length, and is thus slightly reduced compared to that in primitive taxa such as *Cheirolepis,* but more elongated than in *Mesopoma.* The infraorbital blade appears to be slightly curved and narrow, not reaching the snout tip. The postorbital blade is postero-ventrally/antero-dorsally inclined at an angle of *ca.* 30%, it is moderately high and roughly rectangular with rounded corners, and a slightly indented dorsal margin. The dermal ornament consists of series of robust denticles. The jaw articulation is sited posteriorly relative to the parieto-extrascapular suture. This is generally the case in taxa with an oblique suspensorium, whereas in taxa with a more upright suspensorium, such as *Mesopoma,* the jaw articulation is sited anterior to the parieto-extrascapular suture.

Dentition: (Figures 1, 3). Teeth are preserved only on the occlusal margin of the maxilla. They are relatively small, straight conical teeth, which are preserved along the entire upper jaw margin. There appears to be a single marginal row, possibly slightly forward pointing. In terms of size, the following ratio applies: dh/th: 15mm/0.5mm = 30.

Preopercular: (Figures 1, 2, 3). The preopercular consists of a vertically orientated, narrow posterior limb and a narrow, reduced dorsal limb close to horizontal, inclined at an angle of *ca.* 15-20%. The anterior head is straight and situated posterior to the anterior margin of the maxilla postorbital blade, where it contacts the suborbital. The preopercular canal is faintly visible in the dorsal blade, close to the dorsal margin. The dermal ornament consists of characteristically broad robust denticles.

Suborbitals: (Figures 1, 2, 3). Three ovate suborbitals are present between the preopercular posteriorly, and the jugal and dermosphenotic anteriorly.

Operculo-Gular System

The opercular-gular system is preserved in specimen BP/1/4373/1, and partially preserved in GAN 1. The following elements are visible: dermohyal, opercular, subopercular, and branchiostegal rays. Dermal ornamentation is incompletely preserved, but appears to consist of scattered, well developed, robust denticles and ridges.

Dermohyal: (Figures 1, 2, 3). The dermohyal is a triangular, wedge-shaped bone which is approximately half of the length of the adjacent opercular.

Opercular: (Figures 1, 3). The opercular is a parallelogram-shaped bone, inclined at an angle of *ca.* 55 degrees to the horizontal, and is slightly shorter than the subopercular.

Subopercular: (Figures 1, 3). The subopercular has the posterior margin incompletely preserved. It is broader and slightly deeper than the opercular. The ventral margin is slightly anteroventrally inclined so that the antero-ventral margin forms a point.

Branchiostegal rays: (Figures 1, 2, 3). Although the complete series, as well as individual rays, are not entirely preserved, it appears that there are fewer than the characteristic primitive 12-13, and approximately ten.

Lower Jaw

The dermal surface of approximately the posterior two thirds of the lower jaw is preserved in specimen BP/1/4373/1. Part of the dentary and the angular are visible; the presence of a supra-angular was noted, although very poorly preserved. Almost the entire medial dentary length is preserved in GAN 1, although incompletely preserved.

Dentary: (Figures 1, 2, 3). The dentary has a depth/length ratio of approximately 4mm: 18mm = 1:4. It is very similar in shape to that in *Mesopoma* which also has a d/l ratio of approximately 1:4. The dermal ornament consists of broad ridges running the length of the bone with smaller denticles close to the occlusal surface.

Angular: (Figures 1, 2, 3). The ventral limb of the angular is relatively narrow at the posterior end of the dentary, with the outline of the dorsal limb faintly visible beneath the preopercular.

Pectoral Girdle

The pectoral girdle is incompletely preserved in the study specimens BP/1/4373/1 and GAN 1. Most of the post-temporals and the supracleithrum, and a somewhat distorted cleithrum are preserved. The clavicles are not visible. Broad dermal ridges are visible on the supracleithrum and cleithrum.

Post-Temporals: (Figures 1, 3). The post-temporals are not entirely preserved, but appear to be fairly small, elongate triangular bones, tapering posteriorly to a pointed posterior margin.

Supracleithrum: (Figures 1, 3). A broad, ovate bone which extends ventrally beyond the contact between the opercular and the subopercular, and almost as broad as the adjacent opercular. The dermal ornament consists of approximately nine heavy enamel ridges running the length of the bone. The lateral-line canal enters about halfway down its posterior length and exits under the post-temporal approximately half way along the supracleithrum dorsal margin. A number of sensory pits are visible along the line of the canal.

Cleithrum: (Figures 1, 3). It appears to have an unusually short, broad vertical blade. The vertical blade is crescentic, with a deep insertion for the pectoral fin. The lateral ventral section, although distorted, appears to be broad. Well developed dermal ridges are aligned dorsoventrally on the vertical blade, and horizontally on the ventral blade.

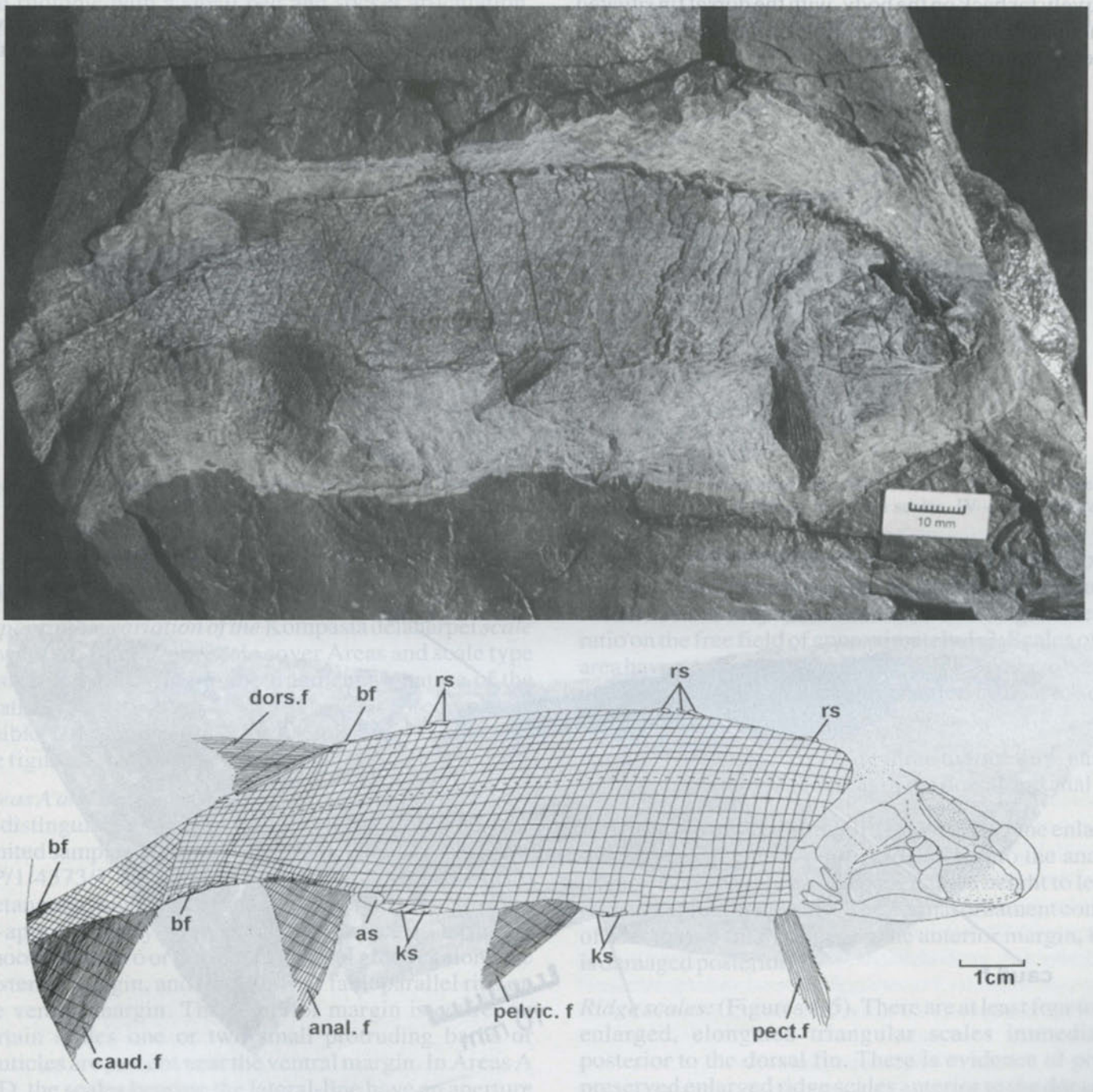


Figure 4. *Kompasia delaharpei* syntype GAN 1. A – photograph in lateral view showing head, body and fins; B – camera lucida interpretation. (See p12 for abbreviations.)

Body and Fins

GAN 1 exhibits an almost complete body and most of the fins, with only the posterior margin of the caudal fin absent (Figure 4). *Kompasia* is a small to medium sized fusiform fish: the total fish length is up to approximately 180mm in specimen GAN 1, with a body length of approximately 130mm (body length is from snout tip to start of the caudal fin). The head length in BP/1/4373/1 is approximately 30mm, and 38mm in GAN 1, indicating that the head is contained just over four times within the total body length (Figure 4).

The fins are incompletely preserved, but visible in GAN 1 (Figure 4). The posterior and distal margins of all fins are not preserved. The dorsal, anal and pelvic fins appear to be triangular. All fins are composed of numerous closely set fin- rays, with fringing fulcra on the leading edges. The dorsal and anal fins in particular are situated relatively far back on the body, with the dorsal fin situated immediately behind the position of the anal fin, in the posterior third of the body (Figure 4).

Pectoral fin: (Figure 4). A proximal portion of the fin is preserved in specimen GAN 1. The fin is at least 20mm long, with at least ten, apparently unjointed fin-rays visible. Since the distal fin margin is not preserved, distal bifurcation could not be observed.

Pelvic fin: (Figure 4). Also a proximal portion of the fin preserved in GAN 1, with at least 17 fin-rays visible. Although not clearly visible, it appears that jointing of the fin-rays is present.

Anal Fin: (Figure 4). More than 35 fin-rays are preserved in specimen GAN 1 (it is also preserved in a fragmentary state in specimen BP/1/4373/47). The fin base length is approximately 20mm, with closely articulated, fairly long fin-rays of *ca.* 30-32mm in length preserved in the anterior part of the fin; distal bifurcation is visible on some of the distal fin-rays.

Dorsal Fin: (Figures 4, 5). Most of the fin is preserved in specimens GAN 1 and BP/1/4373/130, indicating that

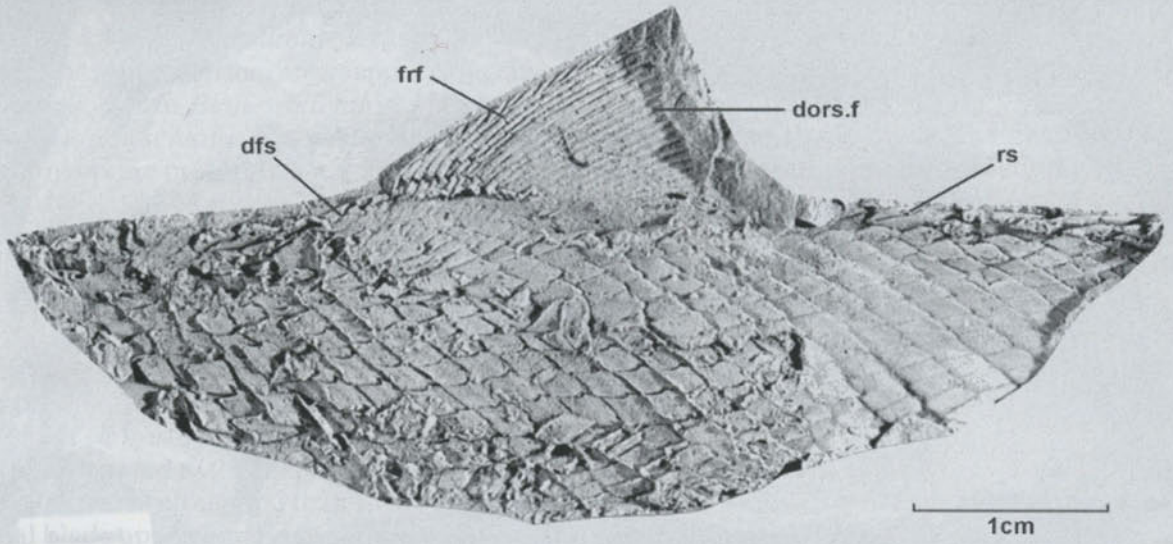


Figure 5. *Kompasia delaharpei* specimen BP/1/4373/130 in medial view, showing dorsal fin. (See p12 for abbreviations.)

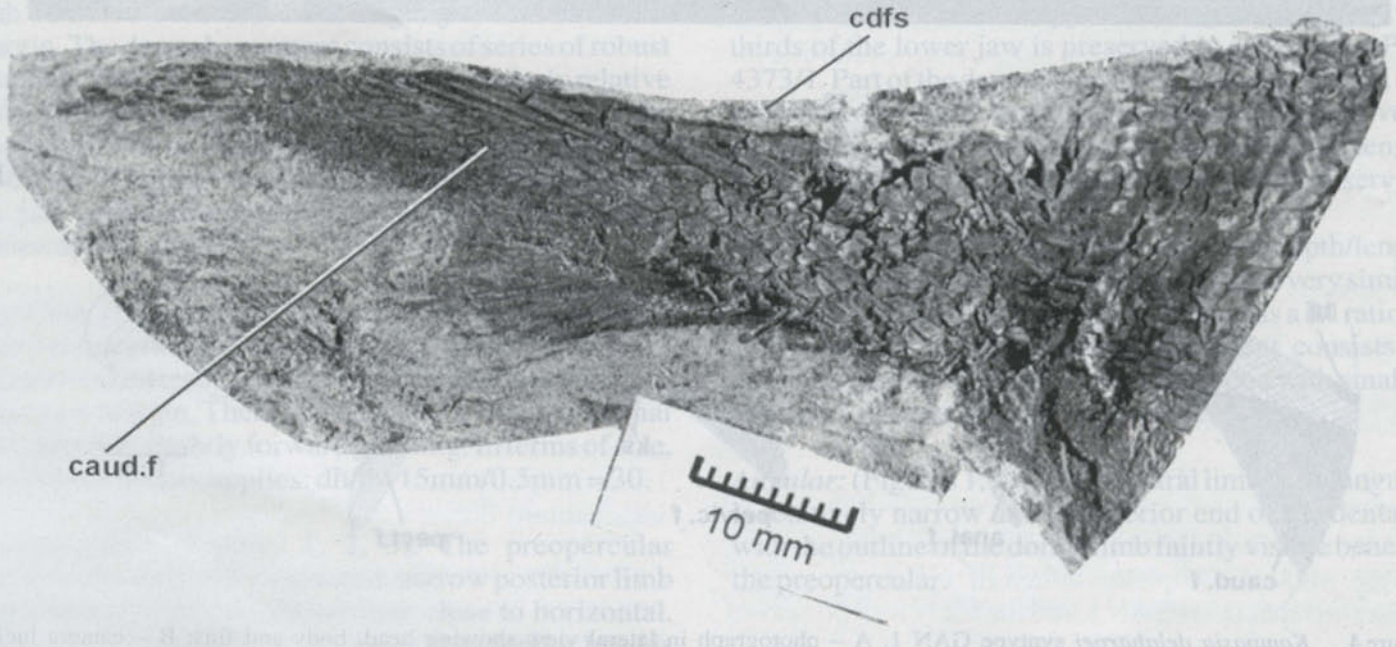


Figure 6. *Kompasia delaharpei* specimen BP/1/4373/136 in lateral view, showing caudal fin. (See p12 for abbreviations.)

it is a triangular fin. Fringing fulcra are present on the leading edge. The fin is made up of more than 21 (*ca.* 25) articulated fin-rays, with a fin base length of *ca.* 20mm. There are four to five short fin-rays situated at the fin insertion, anterior to the main body of the fin; distal bifurcation is visible on the distal fin margin.

Caudal Fin: (Figures 4, 6). The caudal fin is incompletely preserved, but is clearly heterocercal with an elongate hypochordal body lobe. Caudal inversion is present although a definite hinge line is not visible. The caudal fin consists of at least 60 articulated fin-rays; distal bifurcation is visible on the distal fin margin.

Scales and Squamation

Scale cover and squamation was studied in specimens BP/1/4373/1, 47, 130, 136, and GAN 1. Scales are broad and rhombic with a small peg and socket articulation. Dermal ornament on the free field is characteristically minimal, giving the free field an almost smooth appearance.

Topographic variation of the Kompasia delaharpei *scale cover*: (see figure 7 for scale cover Areas and scale type designations): Owing to the fragmentary nature of the relatively few specimens, the scale cover is not completely visible. Only the diagnostic and clearly visible scale areas are figured.

Areas A and B: (Figure 8). Area A and B scales could not be distinguished from one another, possibly owing to the limited sample size. Scales from this region are visible in BP/1/4373/1 up to scale row 17. The scales are rectangular, higher than long, with a height to length ratio of approximately 3:2. The scale surface is basically smooth, with two or three faint parallel grooves along the posterior margin, and three or four faint parallel ribs on the ventral margin. The posterior margin is entire, on certain scales one or two small protruding barbs or denticles are present near the ventral margin. In Areas A to D, the scales bearing the lateral-line have an aperture in the posterior margin, with a posterior denticle above it. There are pit-lines present above the indentation of the canals which are particularly evident in areas A and B.

Area C: (Figures 4, 5). Scales from this area are clearly visible on BP/1/4373/47 and appear to occur from approximately ten rows anterior to the insertion of the anal fin, to the insertion of the caudal fin. The scales are rectangular, longer than high, with a height to length ratio of approximately 2:3, diminishing progressively in size posteriorly. The free field is typically almost smooth, with two to four very faint grooves along the posterior and ventral margins.

Area D: (Figures 4, 6). The scales in the caudal region are small, diamond-shaped, diminishing in size posteriorly, and with a height to length ratio of approximately 2:3. The free field is basically smooth with a number of pits present.

Area F: (Figure 8). Indications from BP/1/4373/1, 47, and GAN 1, are that the scales from this area probably extend to the region of the anal fin insertion. There are up to four rows of very narrow scales, with a height to length ratio on the free field of approximately 1:2. Scales of this area have a particularly markedly pointed postero-ventral margin, and a free field ornamentation typical to scales from the abovementioned Scale Areas.

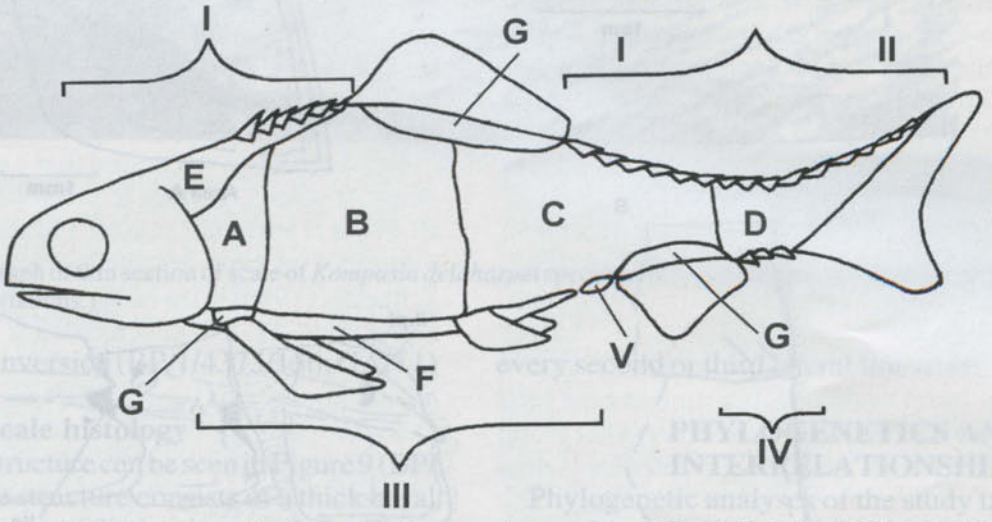


Figure 7. Diagram showing the various areas of scale cover in lower actinopterygian fishes (after Esin 1991). A,B,C,D,E,F and G are areas of the scale cover on the lateral surfaces of the body: I – ridge scales; II – basal fulcra; III – keel scales, IV – basal fulcra; V – anal scale(s).

Area G: (Figure 5). There are three to four tiny, narrow upright scale rows in the areas of the dorsal and anal fins.

Anal scales: (Figure 4 and BP/1/4373/47). One enlarged oval to round scale is preserved anterior to the anal fin insertion, probably one of a pair. It has a height to length ratio of approximately 4:5. The dermal ornament consists of four to five small ridges on the anterior margin, but it is damaged posteriorly.

Ridge scales: (Figures 4, 5). There are at least four to five enlarged, elongated triangular scales immediately posterior to the dorsal fin. There is evidence of poorly preserved enlarged ridge scales anterior to the dorsal fin in specimen GAN 1.

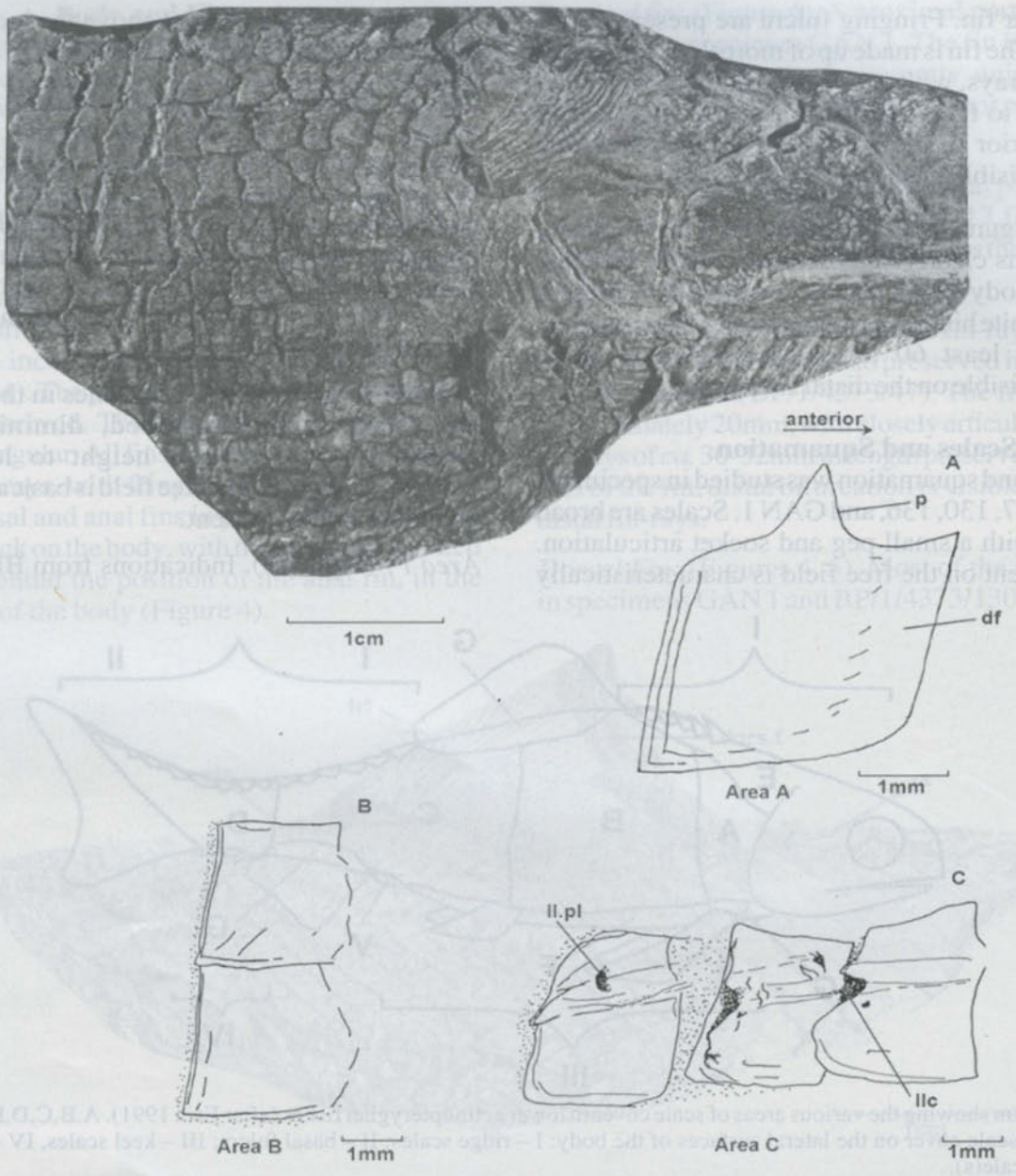


Figure 8. *Kompasia delaharpei* specimen BP/1/4373/1 (syntype) in lateral view, illustrating dermal scale morphology. A and B are camera lucida interpretations of scale areas A and B respectively; C – camera lucida interpretations of lateral-line detail in scale area B. (See p12 for abbreviations.)

Keel scales: (Figure 4). There is evidence of poorly preserved enlarged keel scales anterior to the anal fin, on the ventral body margin.

Basal fulcra:

- Dorsal fin, basal fulcra (Figure 5). There are two or three small triangular scales anterior to the dorsal fin.
- Caudal fin, dorsal basal fulcra (Figure 6). A series of at least nine enlarged, elongated, acutely triangular scales are situated above the caudal fin. The dermal ornamentation is basically smooth.
- Caudal fin, ventral basal fulcra. A poorly preserved row of four to six enlarged basal fulcra situated immediately anterior to the insertion of the caudal fin.

Squamation

The scale row column configuration is not completely preserved, but can be seen in specimens BP/1/4373/1, 47, 137, and GAN 1 (Figures 4, 5, 8). The scale rows, particularly those in areas A and B, are steeply inclined. Caudal inversion is present immediately posterior to the insertion of the caudal fin.

Scale counting data:

- Scale rows to pelvic fin (GAN 1): *ca.* 12.
- Scale rows to dorsal fin (GAN 1): *ca.* 33.
- Scale rows to anal fin (GAN 1): *ca.* 26.
- Scale rows to the caudal fin (GAN 1): *ca.* 42.
- Scale rows to caudal inversion (GAN 1): *ca.* 47

Number of scales in a single scale column:

- In front of pelvic fin (BP/1/4373/1; GAN 1) *ca.* 17-18.
- In front of anal fin (BP/1/4373/47; GAN 1) *ca.* 17.
- In front of caudal fin (BP/1/4373/136; GAN 1) *ca.* 12-15.

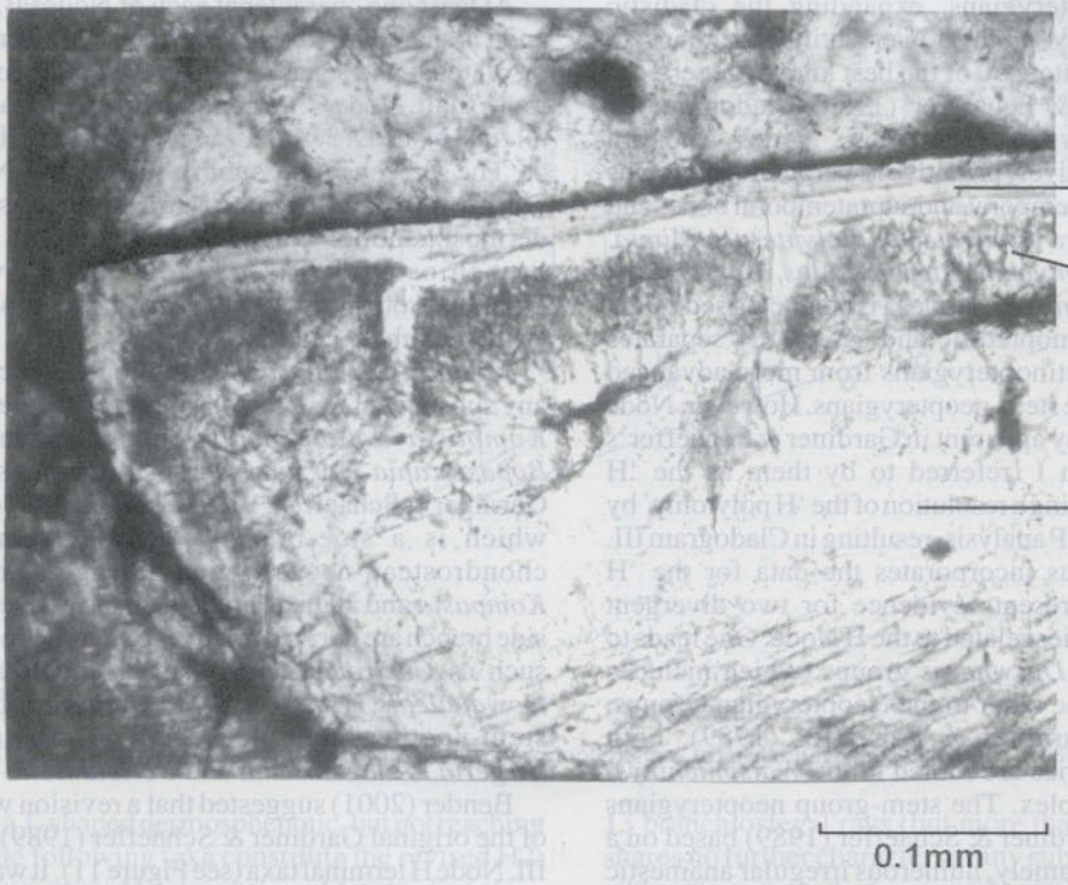


Figure 9. Photomicrograph of thin section of scale of *Kompasia delaharpei* specimen K1, showing the morphology of the scale layers. (See p12 for abbreviations.)

- In front of caudal inversion (BP/1/4373/136; GAN 1) *ca.* 9-10.

Scale histology

The general scale structure can be seen in Figure 9 (BP/1/4373/47). The scale structure consists of a thick basal bony layer with a number of distinctive canals for fibres of Sharpey visible, a middle dentine layer with prominent thick branched plexi or clusters of dentine tubules passing up through the dentine layer. On the surface is a ganoine layer consisting of generally one or two layers, with superimposed generations of buried ganoine probably towards the scale margins, as in taxa such as *Moythomasia durgaringa, Gonatodus* and *Pseudogonatodus.* In terms of the prominent canals of Sharpey, these are apparent in *Pseudogonatodus macrolepis*, but are also present in *Moythomasia durgaringa.* The thick clusters of dentine tubules also seen in *Moythomasia,* are to a lesser extent manifest in *Pseudogonatodus.*

Laterosensory System

A well developed lateral-line canal is present and was observed in BP/1/4373/1 (Figure 8). The canal system is carried by a single row of flank scales, presumably along the entire body length. The lateral line can be seen as a prominent, raised ridge area running the length of the lateral line scales and underlying the dermal lateral line ornamentation. The dermal lateral line ornamentation consists of a rounded aperture on the posterior margin of the scale, above which is a posterior denticle. There is also a series of canal pores just above the rounded ridge on every second or third lateral line scale.

PHYLOGENETICS AND INTERRELATIONSHIPS

Phylogenetic analyses of the study taxa were carried out using cladistic methods, since most recent comprehensive lower actinopterygian phylogenies utilize cladistics to analyse the interrelationships of lower actinopterygian fish (Gardiner 1984; Gardiner & Schaeffer 1989; Coates 1999; Poplin & Lund 2000). In addition the rigorous methodology utilized by cladistics, involving documentation of character states at each node or branching within the cladogram, means the results of the analyses can be verified.

The comprehensive lower actinopterygian phylogenetic analysis of Gardiner & Schaeffer (1989) (Figure 10) was used as a basis for phylogenetic analysis, since their analysis largely utilises the visual comparison of dermal skull characters, an essential analytical tool within the context of the present study, owing to the lack of well-preserved endoskeletal characters used in the more recent, fairly comprehensive phylogenetic analysis conducted by Coates (1999). In addition, the Gardiner & Schaeffer (1989) analysis is generally accepted as the most comprehensive phylogenetic basis for examining lower or early actinopterygian interrelationships (see Coates 1993, 1998, 1999). In particular, Cladogram III generated by Gardiner & Schaeffer (Figure 10) was used as a basis for the current analysis. Gardiner & Schaeffer (1989) produced a large-scale cladistic analysis of

primitive actinopterygians, expanding the cladistic phylogenetic study of the lower actinopterygians to include approximately 60 of the best known genera.

The Gardiner & Schaeffer (1989) Cladogram III (Figure 10) shows the following: Nodes A-G are represented by relatively primitive lower actinopterygians with separate intertemporal and supratemporal bones and include the genera *Cheirolepis, Polypterus, Mimia, Moythomasia, Kentuckia, Pteronisculus, Boreosomus* groups and *Palaeoniscus*. Node H is characterised by the presence of a dermopterotic and essentially separates primitive lower actinopterygians from more advanced forms including the stem-neopterygians. However, Node H is also a polytomy apparent in Gardiner & Schaeffer's (1989) Cladogram I (referred to by them as the 'H polytomy'), providing a resolution of the 'H polytomy' by carrying out a PAUP analysis, resulting in Cladogram III. Cladogram III thus incorporates the data for the 'H polytomy', and presents evidence for two divergent transformation series related to the H Node. One leads to the *Bobasatrania-Dorypterus* groups (which includes *Kompasia*), and the other to the Neopterygian Groups. According to Gardiner & Schaeffer (1989), both transformation series are rooted to the *Watsonichthys-Amblypterus* complex. The stem-group neopterygians are defined by Gardiner & Schaeffer (1989) based on a single character, namely, numerous irregular anamestic supraorbital bones between the nasal and the keystone-shaped dermosphenotic. Taxa such as *Mesopoma, Aeduella* and most other Palaeozoic lower actinopterygian taxa, including the study taxon *Kompasia,* and the deep-bodied early actinopterans such as *Platysomus*, are excluded from the neopterygian group and appear as plesion stem-lineage actinopterans (*sensu* Patterson 1982). However, more recently the comprehensive phylogenetic analysis of Coates (1999) indicates that the stem-neopterygians diverged earlier than indicated by Gardiner & Schaeffer (1989), and on that basis *Kompasia* could probably be termed a stem-neopterygian. Unfortunately Coates' results could not be reconciled or verified by *Kompasia* owing to the lack of the endoskeletal characters used.

Kompasia delaharpei shares the following Gardiner & Schaeffer (1989) Cladogram III characters (see Figure 10 for cladogram; the following nodal characters are derived from Table 1 of the original article), which are typical of basal actinopterygians: Node A characters: 2. Dermohyal covering head of the hyomandibular which notches the dermosphenotic. 3. Dermal bones with buried layers of ganoine. 4. Shield-shaped rostral with ethmoid commissure. 5. Nasal bone with notches for anterior and posterior nares. 6. Dermosphenotic T-shaped, and in contact with nasal bone. 8. One or two pairs of extrascapulars. 9. Two infraorbitals including a lacrymal and jugal, and no postorbital. 14. Dentary with enclosed mandibular canal. 17. Single dorsal fin. 18. Tail with hinge line (caudal inversion). 19. Basal fulcra bordering upper lobe of caudal fin. 20. Rhomboidal scales with anterodorsal angle plus peg and socket articulation.

At least one character at each of Nodes B, C, D, E, H, and I is shared by *Kompasia*: Node B. 1. Acrodin crown on all teeth and separated from the collar enamel of the tooth shaft. Node C. 6. Fringing fulcra on leading rays of all fins. Node D. 3. Supra-angular on mandible. Node E. 4. The presence of suborbital bones. Node H. 1. Dermopterotic present and overlaps or abuts dermosphenotic. Node I. Reduction in number of branchiostegal rays below primitive 12-13. Dermopterotic normally never overlaps more than one-third of dermosphenotic.

Kompasia delaharpei shares no further characters at any subsequent nodes and is therefore rooted at Node I. *Kompasia delaharpei* is thus contained on the *Bobasatrania-Dorypterus* transformation series of the Gardiner & Schaeffer (1989) Cladogram III (Figure 10), which is a side-branch separate from the main chondrostean-neopterygian lineage. Accordingly, *Kompasia* and all taxa situated on the above-mentioned side branch are derived relative to stem-actinopterygians such as *Cheirolepis,* and stem-actinopterans such as *Howqualepis, Mimia* and *Moythomasia,* but basal to stem-neopterygian taxa such as *Australosomus, Birgeria, Palaeoniscum* and *Perleidus.*

Bender (2001) suggested that a revision was required of the original Gardiner & Schaeffer (1989) Cladogram III, Node H terminal taxa (see Figure 11). It was found that a number of taxa originally included by Gardiner & Schaeffer (1989) in the Node H terminal groups in fact had fewer than 12-13 branchiostegal rays, and should be rooted at Node I (Bender 2001). Furthermore, a revision of all the nodes contained on the *Bobasatrania-Dorypteryus* side-branch was carried out (see Bender 2001, figure 15 for the revised cladogram). A description of the revised nodes and their terminal taxa is now included in this paper. In particular revised Nodes H, J, K, L and their revised terminal taxa are discussed.

It was found that only three Node H terminal groups existed. Terminal group H4, the *Amblypterus* Group and its member taxa, is found to be invalid since all its member taxa have fewer than 12-13 branchiostegal rays. *Pseudogonatodus* is now rooted at revised terminal Node K1 and *Amblypterus* at revised Node J1. The other member taxa of H4, *Rhadinichthys ornatissimus, Gyrolepidotus,* and *Oxypteriscus* are excluded because of the lack of verifiable characters.

Revised terminal group H1 (see Figure 11) is defined on the same basis as that by Gardiner & Schaeffer (1989), namely: a dermopterotic with a narrowing anterior end, in contact with the nasal. The following taxa constitute revised H1: *Cosmoptychius, Mesonichthys, Rhabdolepis* and *Watsonichthys* (*Strepheoschema* and *Willomorichthys,* originally included, do not belong in this group since they have fewer than 12-13 branchiostegal rays) (see Gardiner 1963, 1967, 1969, 1985 for description of the abovementioned taxa).

Revised terminal group H2 (Figure 11) is also based on the same defining characters used by Gardiner & Schaeffer (1989), in this case: the dermopterotic

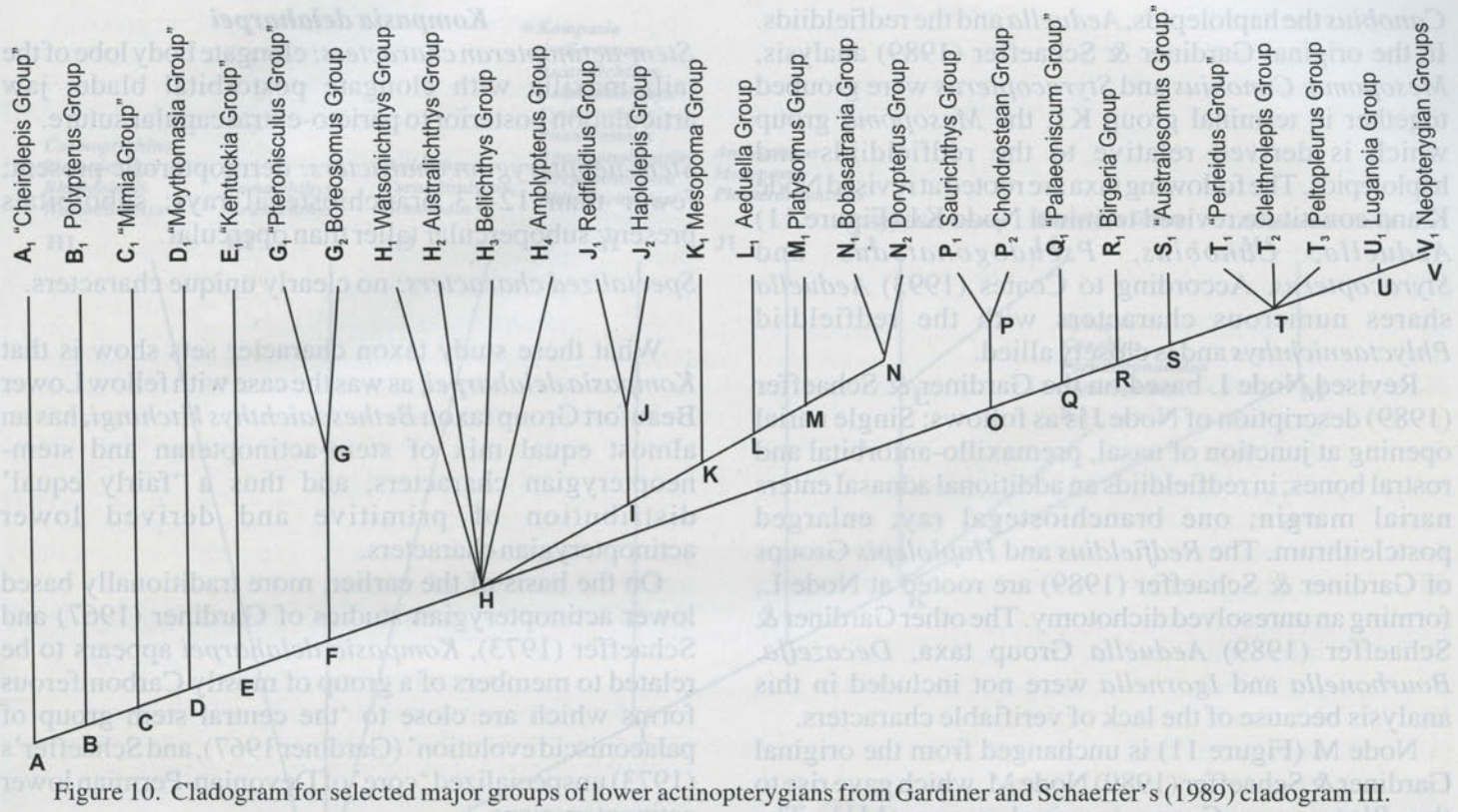


Figure 10. Cladogram for selected major groups of lower actinopterygians from Gardiner and Schaeffer's (1989) cladogram III.

overlapping a T-shaped dermosphenotic, but not reaching the nasal. The following taxa constitute the revised H2: *Namaichthys* and *Mentzichthys* (*Australichthys, Cycloptychius, Rhadinichthys canobiensis* and *Phanerorhynchus,* all originally included do not belong in this group since they have fewer than 12-13 branchiostegal rays) (see Gardiner 1962, 1967, 1969; and Moy-Thomas & Dyne 1938 for morphological descriptions of all of the abovementioned taxa).

Revised terminal Node H3 (Figure 11) can be defined as follows, basically as described by Gardiner & Schaeffer (1989): wide separation of the dermopterotic from the nasal; crescent- or sickle-shaped dermosphenotic. The following taxa constitute the revised H3: *Belichthys, Cornuboniscus,* and *Gonatodus* (*Aetheretmon* and *Phanerosteon* have fewer than 12-13 branchiostegal rays — see Gardiner 1985; *Rhadinichthys carinatus* and *Commentrya* could not included because of a lack of substantiated characters) (see Gardiner 1967; Hutchinson 1975; White 1939, for description of the first mentioned three taxa).

Coates (1993), suggested an alternative arrangement for the terminal taxa at Nodes I, J, K, and L, to that set out in the Gardiner & Schaeffer (1989) cladogram. These suggestions are noted in particular with regard to the interrelationships of *Mesopoma* and *Canobius.* The redfieldiids and the haplolepids are not considered in this study, and thus the original designation of these two groups forming an unresolved dichotomy, as outlined by Gardiner & Schaeffer (1989) is adhered to, although Coates's (1993) alternative proposal that the redfieldiids and the haplolepids might be derived relative to *Mesopoma* and *Canobius* is reinforced.

Revised Node I is defined as originally described by Gardiner & Schaeffer (1989) as follows: fewer than 12-13 branchiostegal rays (but more than two). *Kompasia* shares no further characters at any subsequent nodes and is therefore rooted at revised Node I (Figure 11). The following revised group of taxa, comprising those analysed by Gardiner & Schaeffer (1989) and including *Kompasia*, are rooted at Node I (Bender 2001) (see Figure 11): *Aetheretmon, Australichthys, Bethesdaichthys, Cycloptychius, Kompasia, Phanerosteon, Rhadinichthys canobiensis, Strepheoschema* and *Willomorichthys.* Rooted together with Late Permian Lower Beaufort Group forms *Kompasia* and *Bethesdaichthys* at Node I are the Early Carboniferous South African forms *Australichthys* and *Willomorichthys,* with the other member taxa all essentially Carboniferous taxa. The following taxa now constitute terminal Node I1: *Aetheretmon, Australichthys, Bethesdaichthys, Cycloptychius, Kompasia, Phanerosteon, Rhadinichthys canobiensis, Strepheoschema,* and *Willomorichthys.*

Node J is revised relative to the original defining characters (Gardiner & Schaeffer 1989) and is based on character three in the Coates (1993) alternative scheme, namely: jaw articulation sited anterior to the parieto-extrascapular suture. The following taxa are rooted at revised Node J and constitute revised terminal Node J1 (Figure 11): *Amblypterus, Mesopoma,* and *Phanerorhynchus* (*Phanerorhynchus* is included here and is not rooted at Node K, on the basis that the preopercular is not as upright as found in the node K rooted taxa).

Node K is also revised, and is based on characters four, five and six of the Coates (1993) alternative phylogenetic scheme: vertical jaw suspensorium; reduced terminal gape; upright triangular preopercular. In the Coates alternative scheme *Mesopoma* is sister-group to

Canobius the haplolepids, *Aeduella* and the redfieldiids. In the original Gardiner & Schaeffer (1989) analysis, *Mesopoma, Canobius* and *Styracopterus* were grouped together in terminal group K1, the *Mesopoma* group which is derived relative to the redfieldiids and haplolepids. The following taxa are rooted at revised Node K and constitute revised terminal Node K1 (Figure 11) *Aeduella, Canobius, Pseudogonatodus* and *Styracopterus.* According to Coates (1993) *Aeduella* shares numerous characters with the redfieldiid *Phlyctaenichthys* and is closely allied.

Revised Node L based on the Gardiner & Schaeffer (1989) description of Node J is as follows: Single narial opening at junction of nasal, premaxillo-antorbital and rostral bones; in redfieldiids an additional adnasal enters narial margin; one branchiostegal ray; enlarged postcleithrum. The *Redfieldius* and *Haplolepis* Groups of Gardiner & Schaeffer (1989) are rooted at Node L, forming an unresolved dichotomy. The other Gardiner & Schaeffer (1989) *Aeduella* Group taxa, *Decazella, Bourbonella* and *Igornella* were not included in this analysis because of the lack of verifiable characters.

Node M (Figure 11) is unchanged from the original Gardiner & Schaeffer (1989) Node M, which gave rise to the *Platysomus* Group terminal group (M1). The *Platysomus* Group contains members of two families originally assigned to the Platysomoidei, namely the Platysomidae and the Amphicentridae (Gardiner & Schaeffer 1989). The amphicentrids consist of forms with a crushing dentition of broad toothplates, and the platysomids of forms with more conventional, pointed, marginal teeth. The nodal characters are as follows (as for the original Node M): marginal teeth peg-like or absent; crushing toothplates present; two sets of radials in median fins; long basal radials fewer in number than distal radials; body deep and laterally compressed, flank scales deepened. Terminal Node M1 may be characterized by the same set of characters used to define the *Platysomus* Group: maxilla approaches a right-angle triangle with curved corners; premaxillo-antorbital enlarged and elongated dorsally; mandible deep posteriorly, tapering markedly toward the premaxillo-antorbital. The following taxa are rooted at Node M: *Adroichthys, Amphicentrum, Cheirodopsis, Paramesolepis, Platysomus, Plectrolepis, Proteurynotus.*

Poplin & Veran (1996) and Lund & Poplin (1997), in discussion of the interrelationships of various lower actinopterygian taxa, utilized a system of listing and ranking characters in terms of their basal, derived or more specialized nature, in order to clarify the primitive and/or derived nature of the characters which typify specific taxa. Similarly, the character states of the study taxon are documented below using this type of system to assist in defining the primitive/derived morphological nature of the study species. The study taxon shares primitive actinopterygian characters such as fringing fulcra, rhomboidal scales with peg-and-socket articulation and anterodorsal angle, and shares the stem-neopterygian presence of a dermopterotic, and suborbitals.

Kompasia delaharpei

Stem-actinopteran characters: elongate body lobe of the tail; maxilla with elongate postorbital blade; jaw articulation posterior to parieto-extrascapular suture.

Stem-neopterygian characters: dermopterotic present; fewer than 12-13 branchiostegal rays; suborbitals present; subopercular taller than opercular.

Specialized characters: no clearly unique characters.

What these study taxon character sets show is that *Kompasia delaharpei,* as was the case with fellow Lower Beaufort Group taxon *Bethesdaichthys kitchingi*, has an almost equal mix of stem-actinopteran and stem-neopterygian characters, and thus a 'fairly equal' distribution of primitive and derived lower actinopterygian characters.

On the basis of the earlier, more traditionally based lower actinopterygian studies of Gardiner (1967) and Schaeffer (1973), *Kompasia delaharpei* appears to be related to members of a group of mostly Carboniferous forms which are close to 'the central stem group of palaeoniscid evolution' (Gardiner 1967), and Schaeffer's (1973) unspecialized 'core' of Devonian-Permian lower actinopterygians.

SUMMARY AND CONCLUSIONS

A new genus and species of early actinopterygian is described from the Late Permian lower Beaufort Group of South Africa. The new taxon, *Kompasia delaharpei,* is documented from two lower Beaufort Group localities, both in the *Dicynodon* Assemblage Zone, New Bethesda district of the Eastern Cape Province, South Africa. *Kompasia delaharpei* is part of a Beaufort Group, Late Permian (Tatarian) high latitude freshwater ichthyofauna which consists essentially of lower actinopteryian taxa (Bender 2000). This ichthyofauna is made up of the following taxa: *Atherstonia scutata, Atherstonia minor, Atherstonia seeleyi, Bethesdaichthys kitchingi, Caruichthys ornatus, Elonichthys whaitsi, Kompasia delaharpei, Namaichthys digitata,* and *Pteronisculus meiringi.*

In terms of its biostratigraphic implications, *Kompasia delaharpei* has been documented from apparently stratigraphically closely linked localities within the *Dicynodon* Assemblage Zone. It is at this stage confined to the *Dicynodon* Assemblage biozone, and thus could prove useful as a biozonal indicator within the *Dicynodon* Assemblage Zone.

Phylogenetic analysis is based on a comprehensive phylogenetic study conducted by Gardiner & Schaeffer (1989) (Figure 10); revision of their Cladogram III revealed a re-ordering of the terminal taxa at Nodes H and I (including the study taxon – Figure 11) (Bender 2001), and a re-ordering of terminal taxa at subsequent Nodes J, K, and L. It is shown that *Kompasia delaharpei* is derived relative to Node H of Gardiner & Schaeffer (1989) (which includes the southern African taxa *Mentzichthys jubbi* and *Namaichthys schroederi*), and belongs within the

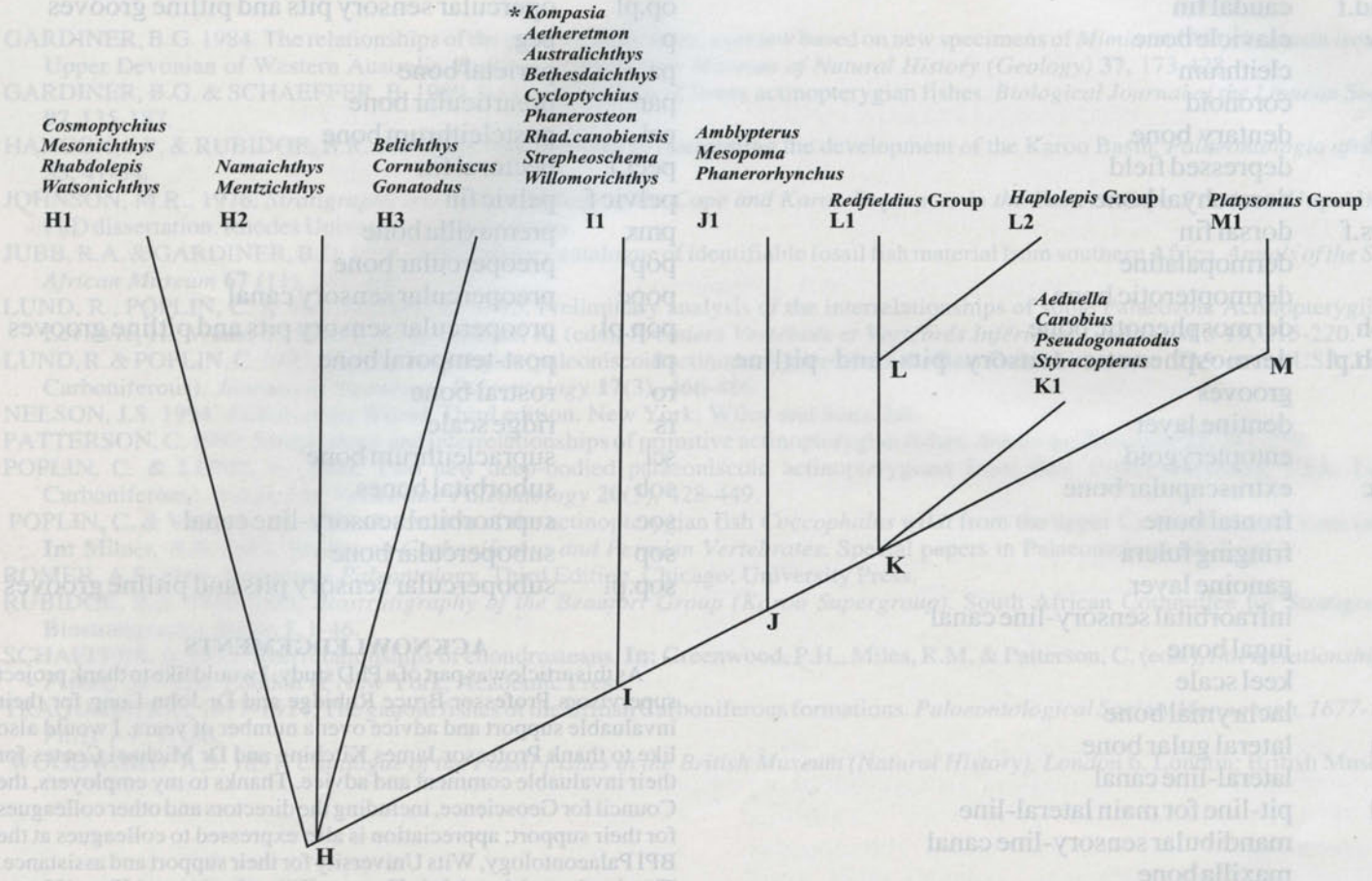


Figure 11. Revision of the Gardiner and Schaeffer (1989) cladogram III, including study taxon*.

NODE I. Less than 12-13 branchiostegal rays present.

I1. Dermosphenotic smaller than dermopterotic and/or T-, keystone-, or cresent-shaped; pelvic fin with short base.

NODE J. Jaw articulation sited anterior to the parieto-extrascapular suture.

J1. Maxilla postorbital blade less than length of infraorbital blade.

NODE K. Jaw suspensorium vertical. Terminal gape reduced. Preopercular upright and triangular.

NODE L. Single narial opening at junction of nasal, premaxillo-antorbital and rostral bones. In redfieldiids an additional adnasal enters narial margin. One branchiostegal ray. Enlarged postcleithrum.

NODE M. Marginal teeth peg-like or absent. Crushing toothplates present. Median fins two sets of radials. Basal radials long and fewer in number than distal radials. Body deep and laterally compressed, flank scales deepened.

M1. Maxilla approaches right-angled triangle with curved corners. Premaxillo-antorbital enlarged and elongated dorsally. Mandible deep posteriorly, tapering markedly towards premaxillo-antorbital.

recently defined Node I terminal taxa group which includes the recently described lower Beaufort taxon *Bethesdaichthys kitchingi* (Bender 2001). Furthermore that *Kompasia* appears to be part of a 'side-group' of taxa which are separate from the Gardiner & Schaeffer (1989) chondrostean-neopterygian lineage leading to the teleost taxa. *Kompasia delaharpei* exhibits a relatively conservative unspecialised basic skull morphology comparable to that found in various Carboniferous taxa such as *Australichthys, Cycloptychius* and *Willomorichthys,* and thus appears to be a relatively primitive Late Permian taxon comparable to taxa which have their origins in the Early Carboniferous. Phylogenetic analysis indicates that *Kompasia delaharpei* is part of a group of taxa (Node I terminal taxa), which are found in Britain, Europe and South Africa and thus are not confined to one region. *Kompasia delaharpei* is morphologically conservative when compared with Late Permian actinopterygian taxa such as *Ebenaqua richiei* from the Late Permian Rangal Coal Measures, Blackwater, central Queensland region of Australia, or *Aeduella* and *Dorypterus* from the Permian of Europe and England respectively.

ABBREVIATIONS USED IN FIGURES AND TEXT - MORPHOLOGICAL ABBREVIATONS

ada	anterodorsal angle
anal f	anal fin
ang	angular bone
ant	antorbital bone
apl	anterior pit-line groove
art	articular bone
as	anal scale
b	bony layer
bf	basal fulcra
br	branchiostegal rays

caud.f caudal fin
clav clavicle bone
cl cleithrum
cor coronoid
den dentary bone
df depressed field
dhy dermohyal bone
dors.f dorsal fin
dpl dermopalatine
dpt dermopterotic bone
dsph dermosphenotic bone
dsph.pl dermosphenotic sensory pits and pitline grooves
dt dentine layer
ent entopterygoid
exsc extrascapular bone
fr frontal bone
frf fringing fulcra
g ganoine layer
ioc infraorbital sensory-line canal
ju jugal bone
ks keel scale
la lachrymal bone
l.gu lateral gular bone
llc lateral-line canal
ll.pl pit-line for main lateral-line
mc mandibular sensory-line canal
mx maxilla bone
na nasal bone
n.exc excurrent or posterior naris
n.inc incurrent or anterior naris
op opercular bone
op.pl opercular sensory pits and pitline grooves
p peg
pa parietal bone
par prearticular bone
pcl postcleithrum bone
pect.f pectoral fin
pelvic f pelvic fin
pmx premaxilla bone
pop preopercular bone
popc preopercular sensory canal
pop.pl preopercular sensory pits and pitline grooves
pt post-temporal bone
ro rostral bone
rs ridge scale
scl supracleithrum bone
sob suborbital bones
soc supraorbital sensory-line canal
sop subopercular bone
sop.pl subopercular sensory pits and pitline grooves

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