

https://dspace.org/

A new actinopterygian fish species from the Late Permian Beaufort Group, South Africa

Bender, Patrick

2001
Bernard Price Institute for Palaeontological Research
http://hdl.handle.net/10539/16361

Downloaded from a DSpace repository. https://dspace.org/

Palaeont. afr., **37**, 25-40 (2001)

A NEW ACTINOPTERYGIAN FISH SPECIES FROM THE LATE PERMIAN BEAUFORT GROUP, SOUTH AFRICA

by

Patrick Bender

Council for Geoscience, Private Bag X112, Pretoria, South Africa.
e-mail: bender@nfi.co.za

ABSTRACT

A new genus and species of actinopterygian (ray-finned) fish, *Bethesdaichthys kitchingi*, is described from the Tatarian, Late Permian, Lower Beaufort Group of South Africa. *Bethesdaichthys* is presently known from three localities, two in the New Bethesda and one in the Victoria West districts of the Karoo region respectively. The fossils were recovered from within the Abrahamskraal Formation *Tapinocephalus* Assemblage Zone at the Victoria West locality, and from an uncertain Formation possibly closely equivalent to the Balfour Formation, within the *Dicynodon* Assemblage Zone at the New Bethesda sites. *Bethesdaichthys kitchingi* is a fusiform fish, up to approximately 300mm in total length, with the skull displaying a moderately oblique suspensorium, and a maxilla with a large sub-rectangular postorbital blade. Furthermore there is a complex of four suborbital bones adjacent to the orbit. The pectoral fin is large relative to body size and the tail is heterocercal with an elongate tapered dorsal body lobe. The anterior midflank scales in particular exhibit a distinctive dermal ornamentation consisting of numerous ganoine ridges. The phylogenetics and interrelationships of *Bethesdaichthys kitchingi* are examined. It appears to exhibit a relatively conservative morphology similar to that found in possibly related Carboniferous taxa such as the South African taxa *Australichthys* and *Willomorichthys*. *Bethesdaichthys kitchingi* is derived relative to stem-actinopterans such as the *Howqualepis* and *Mimia,* and also derived relative to southern African Palaeozoic actinoptyerygians such as *Mentzichthys jubbi,* and *Namaichthys schroederi,* but basal to stem-neopterygians such as *Australosomus, Perleidus* and *Saurichthys.*

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

INTRODUCTION

A new genus and species of Late Permian actinopterygian fish is described here from the Lower Beaufort Group of South Africa, based essentially on well preserved and diagnostic skeletal elements. Taxonomically relevant actinopterygian fossil remains, in particular diagnostic skull remains, have up to now not been described from the Lower Beaufort Group, although incompletely preserved skeletal remains and isolated body scales of fossil fish have been recorded from much or most of the biostratigraphic range (see Broom 1913a, 1913b; Jubb & Gardiner 1975; Woodward 1888, 1889, 1893). Recently, Bender (2000) documented for the first time well preserved and relatively complete actinopterygian remains from the Lower Beaufort Group, tentatively describing several new species, including *Bethesdaichthys kitchingi.*

Bethesdaichthys kitchingi is an actinopterygian fish which belongs to a group of early actinopterygian taxa collectively referred to as "palaeoniscids" (Traquair 1877-1914; Gardiner 1967) or "Palaeoniscomorpha" (Lund *et al.* 1995). It is generally accepted that the palaeoniscids constitute a paraphyletic group of mostly Palaeozoic actinopterygians (Coates 1993), with a global distribution. These palaeoniscids or lower actinopterygians represent the "primitive" or basal members of the Subclass Actinopterygii (Gardiner 1973).

The sedimentary rocks of the Beaufort Group have yielded diverse and important fossils, including macro- and micro-palaeobotanical remains, vertebrate and invertebrate body fossils and traces (Hancox & Rubidge 1997). Analysis of the fossils provides information on the evolution of life in the Permo-Triassic, and has proved significant in unravelling the geological development of the Karoo Basin (Hancox & Rubidge 1997). On the basis of its uniquely large and relatively complete continental Permo-Triassic sedimentary sequence, the Beaufort Group is considered almost as a 'world stratotype' for continental Permo-Triassic age geological and palaeontological research (Smith 1990). The Beaufort Group is particularly renowned for its diversity and range of therapsid fossils, which elucidate the evolutionary transition to mammals (Broom 1932; SACS 1980). The therapsids have been utilized as a basis for an eightfold biostratigraphic subdivision of the Group (Rubidge 1995), with the Lower Beaufort Group comprising six of the eight biozones (Figure 1).

MATERIALS AND METHODS

Three laterally compressed *Bethesdaichthys* specimens were recovered from a *Tapinocephalus* Assemblage Zone locality on the farm Blourug, Victoria West district, Abrahamskraal Formation, Adelaide Subgroup, Lower Beaufort Group. These specimens were contained within a single, thin, buff-coloured, fine

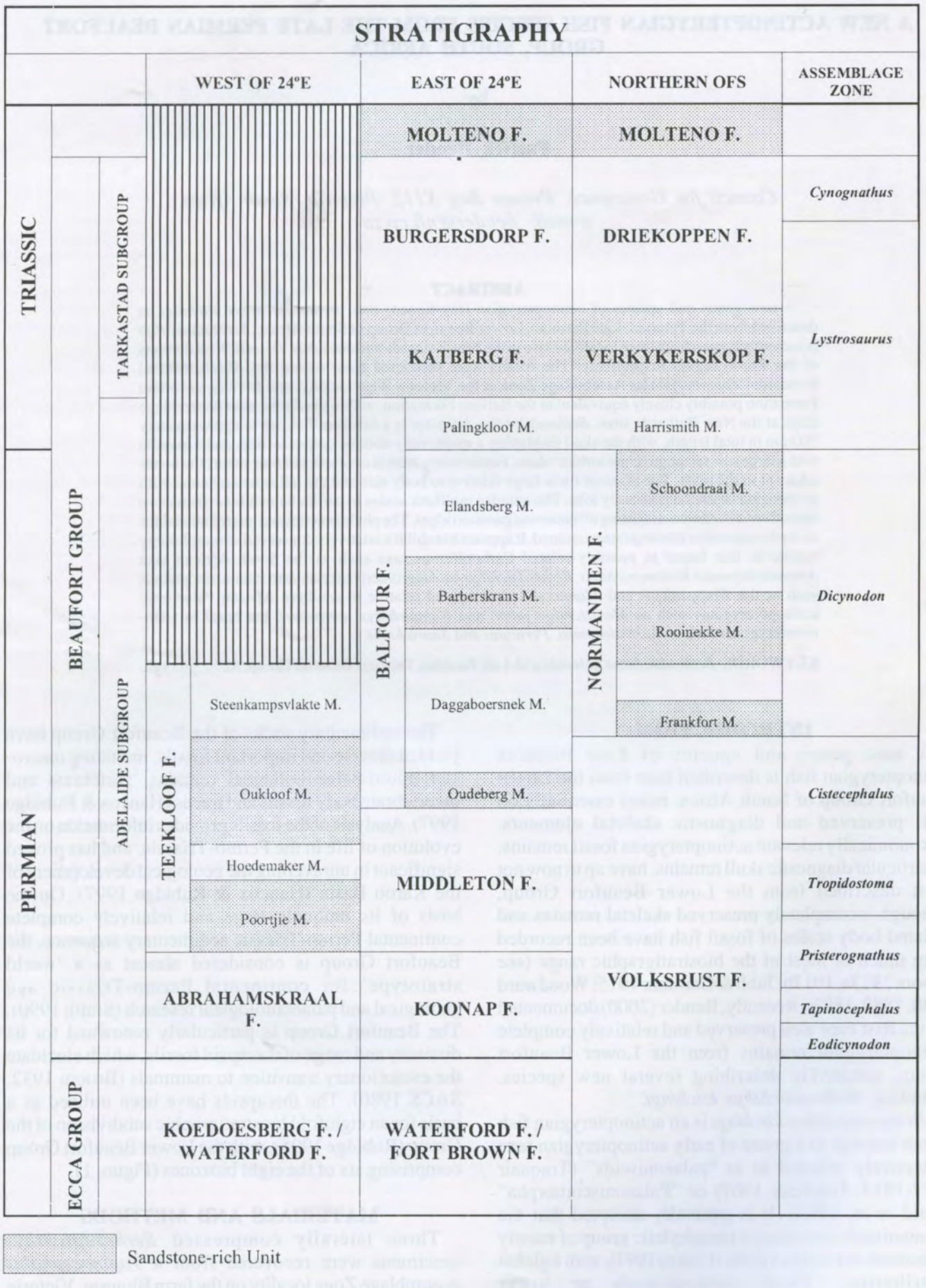


Figure 1. Lithostratigraphic units and Vertebrate Assemblage Zones of the Beaufort Group (after Rubidge *et al.* 1995).

to medium grained sandstone unit, which outcrops over a lateral distance of approximately 70m, and contains numerous specimens of other early actinopterygian species. Until now the exact biostratigraphic zone of the site has been uncertain, but as skull elements of a dinocephalian therapsid were found approximately 15m below the fish site, it appears that the site falls within the *Tapinocephalus* Assemblage Zone.

A total of 15 *Bethesdaichthys* specimens were recovered from a *Dicynodon* Assemblage Zone roadside locality on the farm Wilgerbosch, New Bethesda district, Adelaide Subgroup, Lower 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 at a reservoir also on the farm Wilgerbosch and approximately 35m stratigraphically above the roadside site; preserved in a blue-green siltstone horizon which is situated below a laminated sequence similar in form to that at the roadside site. The formational designation of the Wilgerbosch sites is uncertain (Cole *et al.* in press), but they appear to be situated in roughly the stratigraphic equivalent of the Balfour Formation (see Figure 1).

Most specimens required mechanical and chemical preparation before analysis was possible. Air scribes and an assortment of needles and probes were used initially to remove covering rock matrix, and in certain cases to finely prepare the specimen surface prior to analysis. A dilute 10% solution of acetic acid was on occasions used to soften surrounding matrix. In the case of a number of specimens, analysis was problematical because of the weathered nature of the surface bone and ganoine. In this case preparation of latex rubber casts or peels was found to reveal excellent underlying morphological detail; study and illustration of the casts was facilitated by whitening with ammonium chloride. 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, and for the thin sections, a Zeiss polaroid camera was used. The scanning electron micrographs were made on a Leica Stereoscan 440 at the Council for Geoscience, Pretoria. The phylogenetic analysis was carried out by using the Gardiner and Schaeffer 1989 (cladogram III) as a basis, since this is the most recent comprehensive early actinopterygian phylogenetic analysis. The relevant *Bethesdaichthys* characters were compared to those of the constituent taxa in the Gardiner and Schaeffer (1989) cladogram, thus determining the phylogenetic position of *Bethesdaichthys*. The results of the phylogenetic investigation of *Bethesdaichthys* were illustrated together with a revision of the Gardiner and Schaeffer cladogram III, in which certain nodes and taxa within the cladogram were updated.

SYSTEMATIC PALAEONTOLOGY

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

Derivation of name: Named after the Karoo mountain hamlet, Nieu Bethesda, which is close to the Wilgerbosch site where the first specimen of this taxon was found. Bethesda means "place of flowing waters" (Bible: John, Chap. 5: 2-4), probably appropriate to Late Permian fluvial conditions in the region of the Wilgerbosch fossil fish site. The suffix -'ichthys' is derived from the ancient Greek word for fish.

Diagnosis: A fusiform fish, approximately 300cm in total length. Skull relatively broad, with a moderately oblique suspensorium. Dermopterotic broadens anteriorly and does not suture with the nasal. Dermosphenotic is a crescent-shaped bone. Snout region consists of a small premaxilla, antorbital, narrow rostral and fairly elongate nasal. Jugal is a broad wedge-shaped bone. Maxilla has a large subrectangular postorbital blade. Dentition consists of a median row of large pointed conical teeth and an outer row of numerous smaller pointed teeth. Preopercular with almost right-angled inflexion between the wedge-shaped dorsal, and ventral limbs. There is a complex of four suborbital bones including a large triangular suborbital between the maxilla and the jugal. Opercular is broad and rectangular, subopercular approximately 2/3 of the height of the opercular with an obliquely angled ventral margin. Branchiostegal rays number nine. Distal bifurcation of the fin-rays is visible on the dorsal and caudal fins. Pectoral fin is relatively large and consists of fin-rays which are proximally jointed. Caudal fin is heterocercal with an elongate dorsal body lobe. The anterior rows of flank scales exhibit a distinctive dermal ornament, with up to 14 curved and steeply inclined dorsal ganoine ridges distinct from a series of up to 10 horizontally inclined ventral ridges. A series of enlarged ridge scales is present along most of the dorsal margin. Scale histology shows a laterally continuous, multilayered ganoine layer.

Remarks: Bethesdaichthys is clearly different from any of the other Beaufort Group actinopterygian taxa, based on: fewer than 12-13 branchiostegal rays, the shape of the dermosphenotic, maxilla, preopercular, and opercular in particular, and in the morphology of the suborbitals. *Bethesdaichthys* can be compared to the South African Carboniferous genus *Australichthys* on the basis of maxilla, preopercular and opercular shape and form (see Gardiner 1969), but differs with regard to the dorsal fin shape, size and form.

Type species: *Bethesdaichthys kitchingi* nov.
Derivation of the name: In honour of Mr 'Croonie' Kitching, Nieu Bethesda resident and road builder, who first discovered the Wilgerbosch fossil fish site in about 1928 while constructing a new road over part of the site.

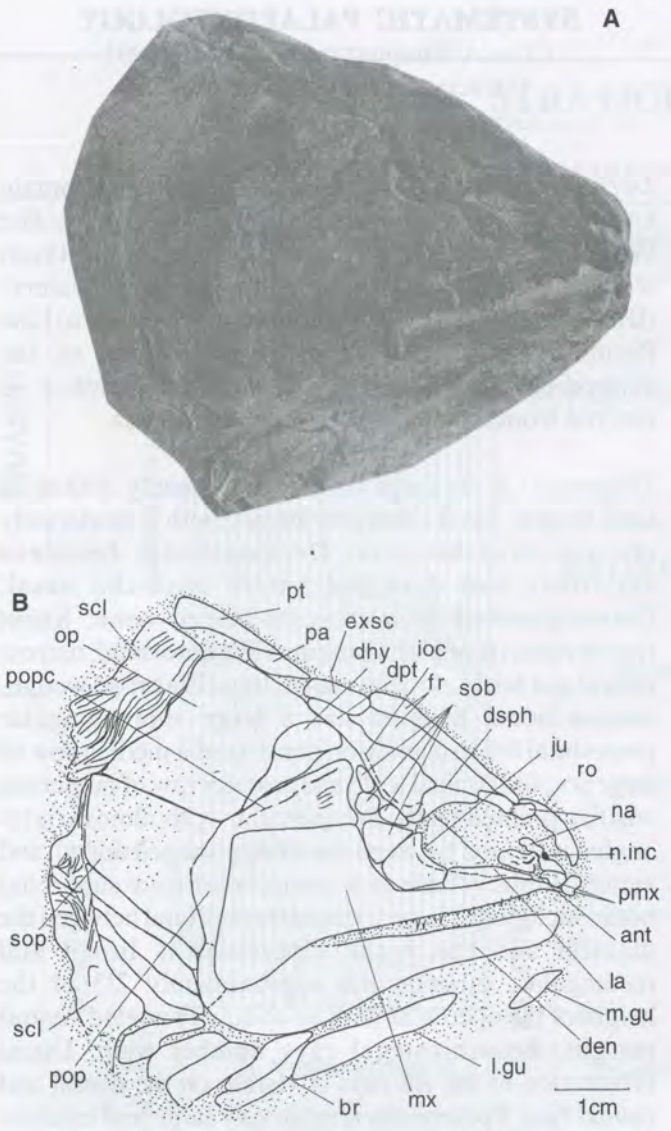


Figure 2. *Bethesdaichthys kitchingi* holotype BP/1/4373/3. A. Lateral view showing the dermal skull region. B. Camera lucida interpretation. (See p. 38 for abbreviations)

Holotype: BP/1/4373/3, in the Bernard Price Institute for Palaeontological Research (BPI), University of the Witwatersrand, Johannesburg. From the Wilgerbosch roadside locality, *Dicynodon* Assemblage Zone, Lower Beaufort Group.

Referred specimens: BP/1/4373/2, 3, 19, 110, 119, 120, 121, 122, 123, 124, 134, 138; BP/1/116, housed at the BPI Palaeontology, Johannesburg. PB/95/6; PB/96/15, housed at the Council For Geoscience, Pretoria; V101, housed at the Victoria West Museum, Victoria West; TM 20, housed at the Transvaal Museum, Pretoria.

Horizon and locality: V101 is from the Blourug locality, *Tapinocephalus* Assemblage Zone, Lower Beaufort Group. TM 20 is from the Wilgerbosch reservoir site, and the rest of the specimens from the Wilgerbosch roadside locality, *Dicynodon* Assemblage Zone, Lower Beaufort Group.

Diagnosis: As for genus.

Remarks: A total of three specimens are recorded from Victoria West, one from the Wilgerbosch reservoir site, and fifteen from the Wilgerbosch roadside locality.

DESCRIPTION

Skull Roof

The skull roof is made up of paired parietals, frontals and extrascapulars, a large dermopterotic and small dermosphenotic located on either side of the frontals. The dermal ornament over the whole of the head region is fairly robust, in the form of mixed short ridges and denticles, which are similar in shape and form to that seen in the cheek region, but more robust. Bones of the skull roof region were studied mainly in specimen BP/1/4373/3 (Figure 2).

Parietals: (Figures 2, 3). The median section of the right parietal is rather poorly preserved in BP/1/4373/3. It is rectangular and approximately one third of the frontal length. Anteriorly it sutures with the frontal and posteriorly with the extrascapulars.

Frontals: (Figures 2, 3). The right frontal is preserved in a somewhat distorted state in BP/1/4373/3. It is relatively long, and narrow although this could be an artifact of preservation. Anteriorly it sutures with the rostral and posteriorly with the parietals.

Dermopterotic: (Figures 2, 3). Most of the right dermopterotic is preserved in BP/1/4373/3. It appears broadest anteriorly and tapers posteriorly. The anterior overlap with the dermosphenotic appears smooth and almost straight vertical. It does not contact the nasal, and is fairly far removed from it. The median section of a broad sensory-line canal is present near the ventral margin.

Dermosphenotic: (Figures 2, 3). The dermosphenotic is small relative to the size of the dermopterotic. It is a narrow, cresentic bone which curves dorsally where it contacts the nasal anteriorly and the dermopterotic posteriorly, and ventrally down under the dermopterotic to form a point at its ventro-posterior extremity. The

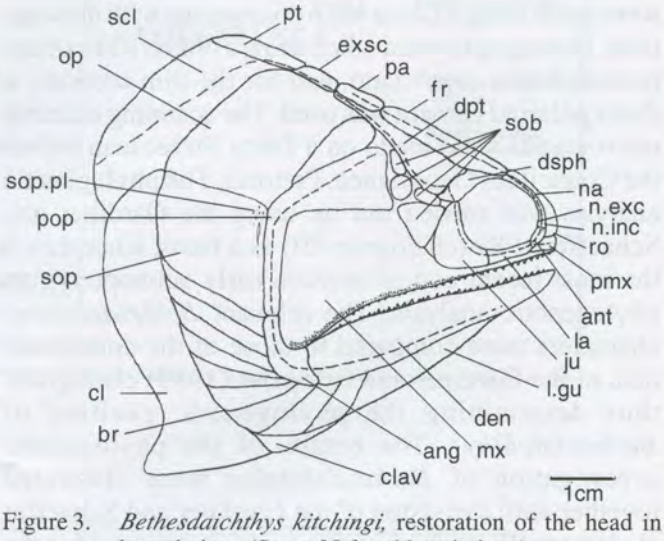


Figure 3. *Bethesdaichthys kitchingi,* restoration of the head in lateral view. (See p.38 for abbreviations)

infraorbital canal can be seen in BP/1/4373/3, close to the ventral margin.

Extrascapulars: (Figures 2, 3). The extrascapulars are not well preserved, but part of a narrow right extrascapular is preserved in BP/1/4373/3.

Snout

The snout region can be seen preserved in a distorted state in BP/1/4373/3 (Figure 2). It consists of a single median rostral, paired premaxillae, an antorbital and a nasal.

Rostral: (Figures 2, 3). The rostral abuts the frontal near the nasal/dermosphenotic suture, and evidently sutures with the premaxillae anteroventrally without being part of the jaw margin.

Premaxillae: (Figures 2, 3). Both premaxillae are preserved in specimen BP/1/4373/3. They are small almost square bones, excluded from the jaw margin, and thus do not contain teeth.

Antorbital: (Figures 2, 3). The single antorbital consists of a fairly narrow rectangular bone which contacts the lachrymal posteriorly. The antorbital contacts the nasal and rostral anteriorly, and the premaxilla anteroventrally. The large distorted opening seen on the dorsal side is part of the well developed infraorbital sensory canal system which has weathered forming a cavity.

Nasal: (Figures 2, 3). The nasal is fractured, with a posterior section in contact with the dermosphenotic broken off from an anterior section in which the incurrent and excurrent nares are visible. It is a narrow bone which is elongate relative to the rostral. It sutures with the dermosphenotic beneath the frontal.

Cheek and Infraorbitals

The cheek region in *Bethesdaichthys* is made up of a large maxillary, preopercular, jugal, lachrymal and a suborbital complex. This region is best noted in specimen number BP/1/4373/3 (Figure 2), although the dermal ornament and various morphological characters can be seen in a number of additional specimens including BP/1/4373/2 and PB/96/15. The dermal ornament consists of numerous, closely aligned, ganoine ridges and denticles (Figure 4).

Jugal: (Figures 2, 3). The jugal is a large crescentic bone which tapers dorsally and anterioventrally. The anterior and posterior margins are evenly curved to accommodate the orbit and maxilla respectively. The dorsal and ventral margins are narrow at the dermosphenotic and lachrymal contacts respectively. A broad infraorbital sensory line canal is present close to the anterior margin and bends almost at right angles in the centre of the bone.

Lachrymal: (Figures 2, 3). The lachrymal is a narrow, elongated, rectangular bone. A large infraorbital sensory line canal is visible over its length. Anteriorly it sutures with the antorbital and posteriorly with the jugal. Ventrally it sutures with the infraorbital limb of the maxilla.

Maxilla: (Figures 2, 3, 4). The maxilla consists of a large, subrectangular, fairly high postorbital blade and an equally long, slender, curved infraorbital blade which appears to form the anterior-most margin of the skull together with the premaxilla. The postorbital blade dermal ornament is well developed in PB/96/15, consisting of robust, well defined ganoine ridges.

Dentition: (Figures 2, 3, 4, 5). Although the dentition is not completely preserved, there appears to be an entire

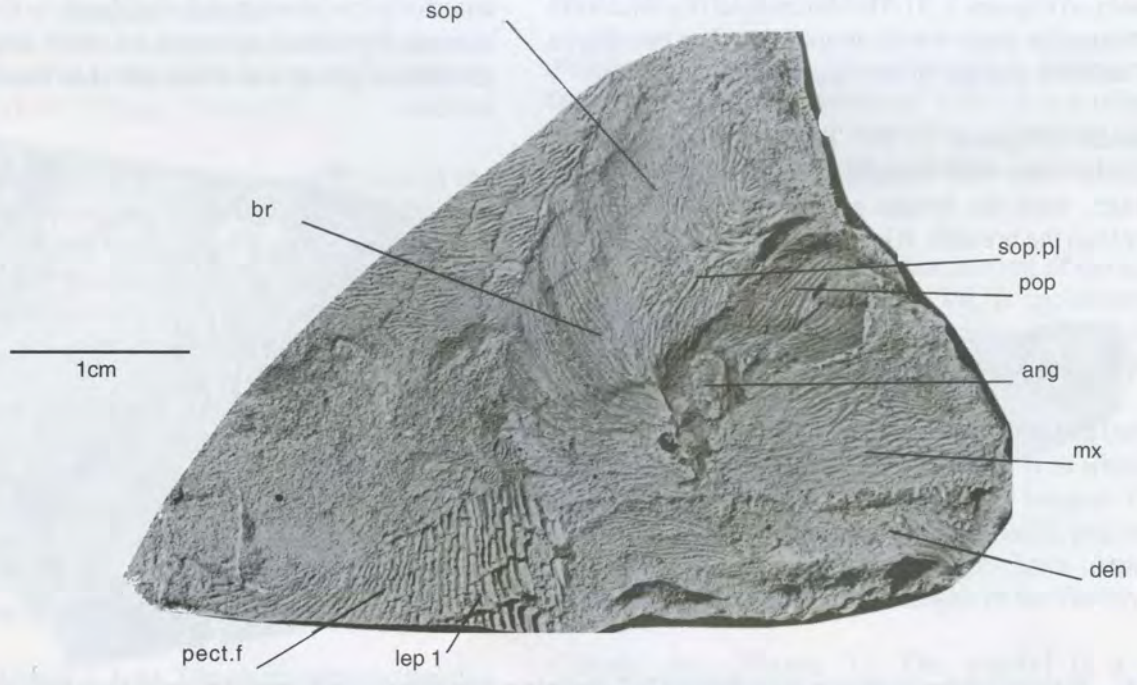


Figure 4. *Bethesdaichthys kitchingi* specimen V101 in lateral view showing pectoral fin, and dermal skull region detail. (See p.38 for abbreviations).

margin of large, pointed conical teeth, up to 2mm in height, arranged in one medial row consisting of more than 20 teeth, in both the maxilla and the mandible. These large teeth are flanked by numerous smaller outer teeth of less than 0.5mm in height; there are also pointed denticles present on the dermal bones of the palate.

Preopercular: (Figures 2, 3, 4). This is a relatively large bone, with a distinctive almost right-angled inflexion at the midline or posterodorsal corner of the postorbital blade of the maxilla. The preopercular consists of a narrow upright posterior limb which is located posterior to the postorbital blade of the maxilla, and a wedge-shaped anterodorsal blade situated above the maxilla. The preopercular canal is situated close to, and parallel to the dorsal margin of the preopercular. The preopercular dermal ornament consists of distinctive vertically inclined ridges ventral to the preopercular canal, and horizontally inclined ridges dorsal to the preopercular canal on the anterior blade, observed in specimens V101(Figure 4) and PB/96/15.

Suborbitals: (Figures 2, 3). Four suborbital bones are present: one large wedge-shaped bone anterior to the maxilla, and three rounded bones in a row anterior to the preopercular, and inclined at an angle parallel to the ventral margin of the dermopterotic.

Operculo-Gular System

The opercular-gular system in *Bethesdaichthys kitchingi* comprises the dermohyal, opercular, and subopercular, the branchiostegal rays, and the gulars. The suspensorium is inclined at an angle of approximately 40-45 degrees to the horizontal in specimen BP/1/4373/3 (the horizontal is taken as the line of the upper jaw margin). The dermal ornament consists of well-developed straight and curved ganoine ridges (Figure 4).

Dermohyal (Figures 2, 3). The dermohyal is a relatively large triangular bone which abuts more than two thirds of the anterior margin of the opercular.

Opercular (Figures 2, 3). This is a large broad rectangular bone with straight margins, slightly longer than high, with the height approximately two thirds greater than the breadth. It is inclined at an angle of c45-50 degrees to the horizontal, and is considerably higher than the adjacent subopercular.

Subopercular (Figures 2, 3, 4). The subopercular is not completely preserved, yet it appears to be slightly narrower than the opercular, and approximately 2/3 of its height. It tapers posteriorly, with the ventral margin terminating in a point at the anteroventral margin. A number of sensory pits and pit canals are visible close to the ventral bone margin (see Figure 3).

Branchiostegal rays (Figures 2, 3, 4, 5). The branchiostegal series was studied in specimens BP/1/4373/2 and BP/1/4373/134. There are nine rectangular branchiostegal rays present, with the most posterodorsal two elements immediately ventral to the subopercular slightly larger than the preceding rays; the posterior few rays are inclined at an angle similar to that of the ventral margin of the subopercular. The dermal ornament consists of ribs of ganoine running the length of the rays.

Gulars (Figures 2, 3). There are three gulars, two large narrow lateral gulars and one short ovate median gular visible in specimen BP/1/4373/134. This configuration is regarded as primitive among lower actinopterygians (Gardiner & Schaeffer 1989).

Lower Jaw

The lower jaw is well-preserved in specimens BP/1/4373/3 (Figure 5) and BP/1/4373/134. Fragments of the dermal ornamentation on the coronoids and prearticular are preserved in specimen BP/1/4373/3, and consist of small, fine denticles.

Dentary (Figures 2, 3, 4, 5). The dentary is a large, elongated bone which tapers anteriorly and has a depth/length ratio of approximately 1:4. The mandibular canal is visible; posteriorly it is close to the ventral border, anteriorly it is present about halfway up the dentary. The dermal ornament consists of well-developed short ganoine ridges and denticles close to the dorsal occlusal surface.

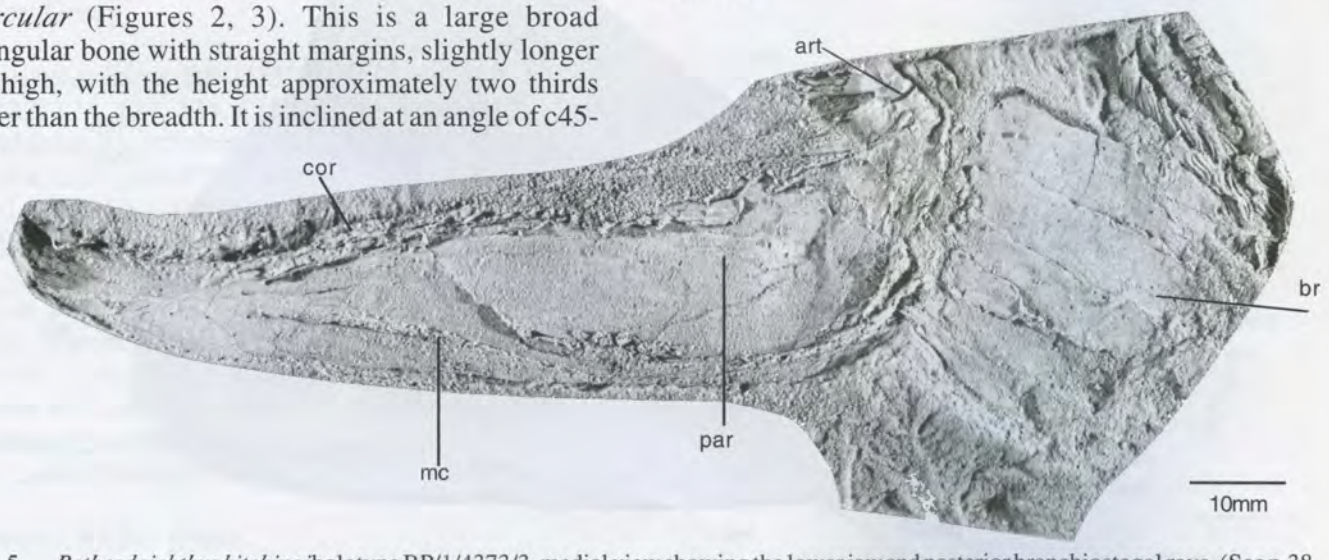


Figure 5. *Bethesdaichthys kitchingi* holotype BP/1/4373/3, medial view showing the lower jaw and posterior branchiostegal rays. (See p.38 for abbreviations.)

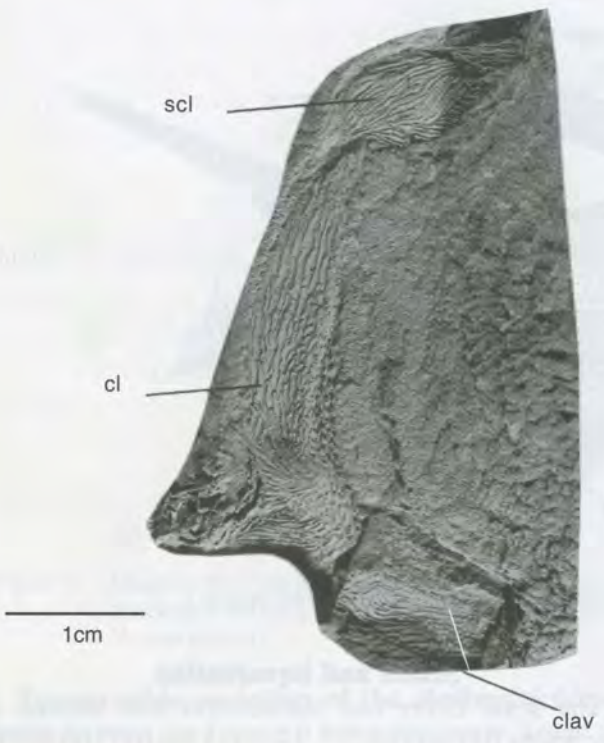


Figure 6. *Bethesdaichthys kitchingi* specimen PB/96/15 in lateral view, showing supracleithrum, cleithrum and clavicle dermal detail. (See p.38 for abbreviations.)

Angular: (Figures 2, 3, 4). The angular, although not completely preserved, seems to be, as in most early actinopterygians, a narrow, elongated crescentic bone which sutures with the posterior margin of the dentary, and abuts the preopercular. An incompletely preserved surangular was noted on specimen BP/1/4373/134.

Articular: (Figure 5). An inclined, angled articular is visible in BP/1/4373/2. A concave fossa is visible in profile, with the condyle of the quadrate also visible.

Pectoral Girdle

None of the bones of the pectoral girdle are completely preserved, but some are partly visible in specimens BP/1/4373/3 and PB/96/15.

Post-temporals: (Figures 2, 3). A dorsal section of the right post-temporal is visible in BP/1/4373/3. It is an elongate bone relative to the adjacent bones of the skull roof, in particular the extrascapular and parietal. The dermal ornament consists of well developed ganoine ridges aligned along the length of the bone.

Supracleithrum: (Figures 2, 3, 6). The supracleithrum is partially preserved in the two study specimens. Evidently it is about half as broad as the adjacent opercular, and longer than it. The distinctive dermal ornament consists of ridges running the length of the bone, and incorporating a dividing ridge which seems to extend the length of the bone.

Cleithrum: (Figures 2, 3, 6). The cleithrum consists of a relatively long, slender slightly curved vertical blade, and a strongly convex ventral expanded region. The pectoral fin embayment on the posterior margin is partially preserved in PB/96/15 and appears to be fairly deep. It has a well developed dermal ornament with wavy ridges running the length of the posterior margin of the vertical blade, and shorter, broader, more horizontally inclined ridges on the anterior margin.

Clavicle: (Figures 3, 6). Most of the right clavicle is preserved in PB/96/15. It is an elongated triangular bone, which has a short posterior contact with the cleithrum. The dermal ornament consists of ridges and denticles horizontally inclined along the length of the bone.

Body and Fins

The complete body is not preserved in any specimens studied, but a composite image of the body shape and form was gained by studying specimens BP/1/4373/3, 37, 134, PB/95/6 and PB/96/15 (see Figure 7). These specimens indicate that *Bethesdaichthys* is a moderately sized, fusiform fish, with a total length of up to approximately 300mm, and a total body length in the region of 200mm. The head length of approximately 67mm in specimen BP/1/4373/3, is contained about four times in the total body length.

Distal fin preservation is not complete in the pectoral, pelvic and anal fins, but all the fins seem to be triangular, composed of numerous closely set fin-rays, with fringing fulcra on the leading edges of the fins. The fin-rays in the dorsal and caudal fins, although generally incomplete towards the distal margins, appear to branch once towards the distal ends of the fin-rays.

Pectoral fin: (Figures 4, 7). An anteroproximal portion of the fin is preserved in specimen V101. Clearly it is a broad based fin, with more than 30 fin-rays preserved. The anteroproximal fin-rays are short and relatively broad, and proximally jointed.

Pelvic fin: (Figure 7). The pelvic fin is preserved in a fragmentary state in specimen V101. It is a relatively large, moderately long based fin, consisting of +42 segmented fin-rays. The fin appears to start at scale row 11-12.

Anal fin: (Figure 7). The anterior portion of the anal fin is preserved in specimen PB/95/6. It apparently is a moderately long based fin which starts approximately at scale row 30-35.

Dorsal fin: (Figure 7). A proximal section of the fin is preserved in specimen BP/1/4373/37. It is triangular, consisting of +26 fin-rays, with the longest fin-ray situated at approximately fin-ray number16, and starts at scale row c35. The fin-ray segments have distinctive striations running the dermal length of the fin-ray.

Caudal fin: (Figure 7). The caudal is a large heterocercal, elongated, triangular fin with a particularly

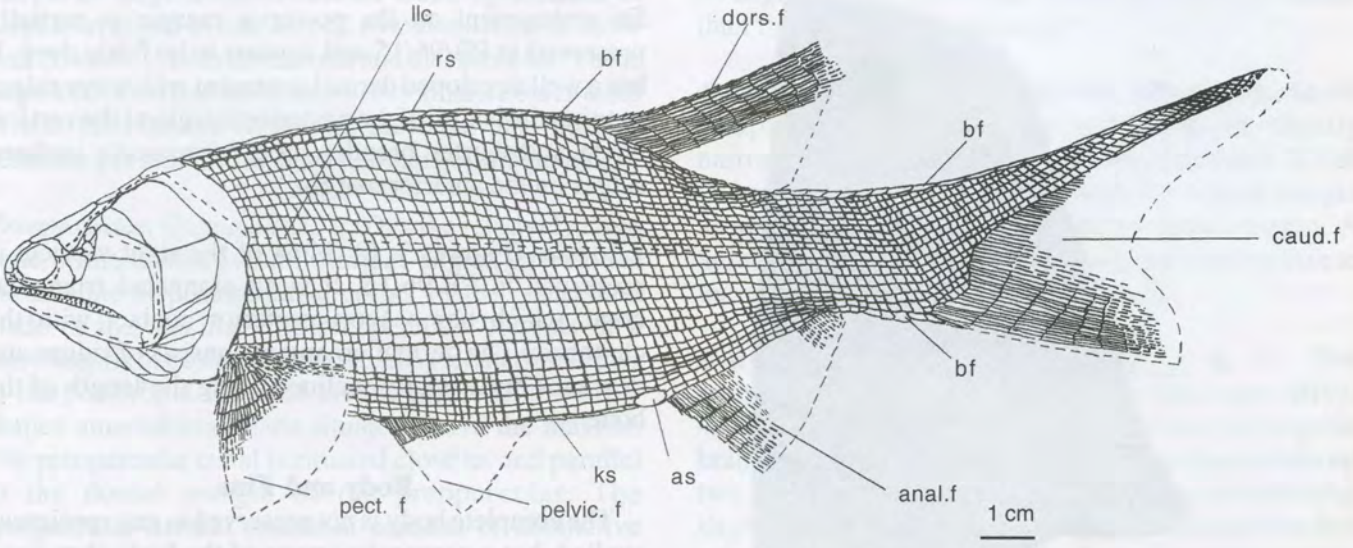


Figure 7. *Bethesdaichthys kitchingi,* restoration of fish in lateral view. (See p.38 for abbreviations.)

extended dorsal hypochordal lobe, which is preserved in somewhat fragmentary state only in specimen PB/95/6. The fin starts on average at scale row 50. The length of the caudal fin (cl) can be expressed as a ratio to total fish length (tfl), cl/tfl = approximately 100:300 = 1:3. The ventral aspect of the tail is not clearly preserved, but the anterior fin-rays on the ventral lobe appear to be relatively long.

Scales and Squamation

The scale cover and squamation was studied in specimens BP/1/4373/2, 3, 19, 37, 134; BP/1/116; PB/95/6; PB/96/15; V101, and TM 20. *Bethesdaichthys* exhibits rhombic scales (the largest, midflank scales are on average approximately 6x5mm in size), with strong peg and socket articulation between the dorsal and ventral margins of the scales, an anterodorsal angle or process to the scale, and each scale row overlapping the row posterior to it (Figure 8).

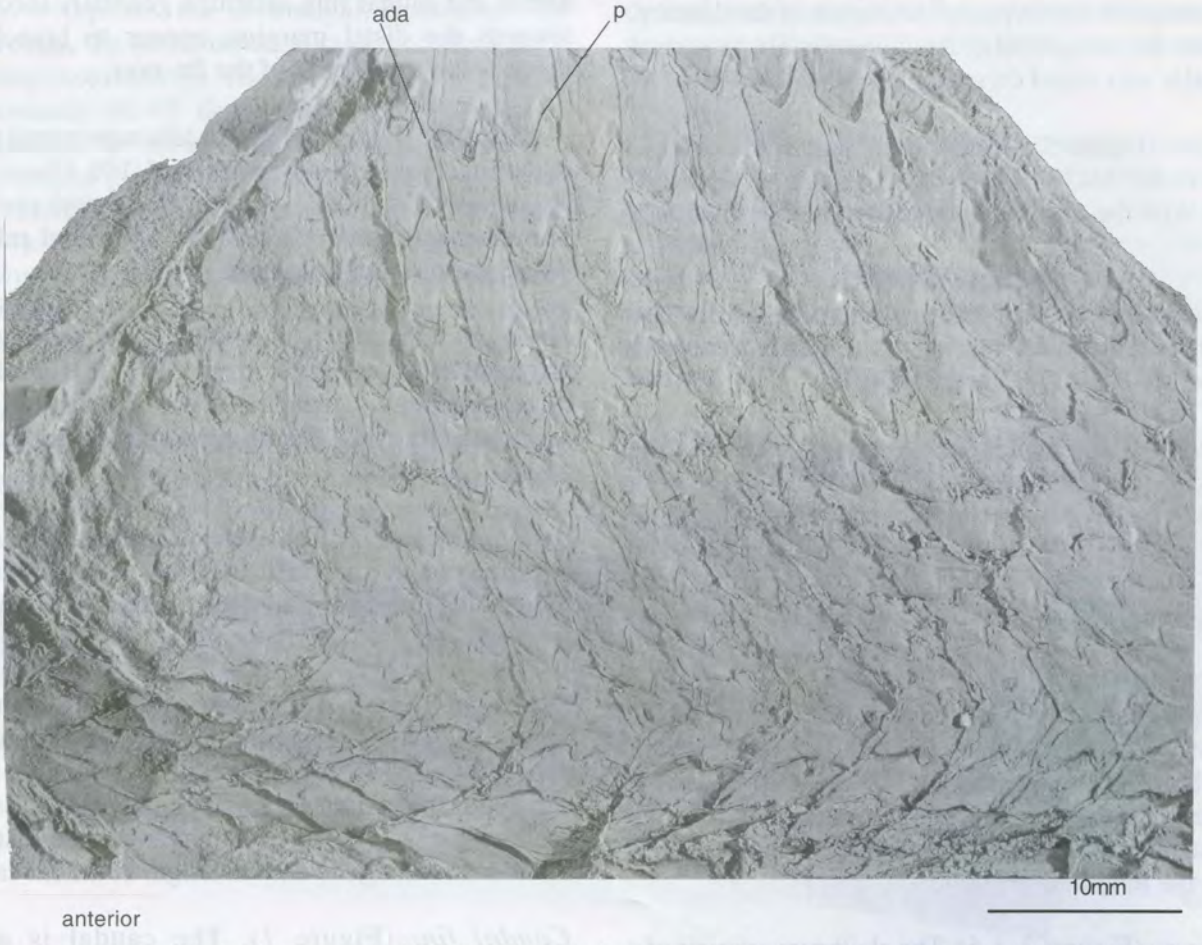


Figure 8. *Bethesdaichthys kitchingi* specimen BP/1/4373/2, medial view of midflank scales, showing peg and socket articulation, and anterodorsal angle.

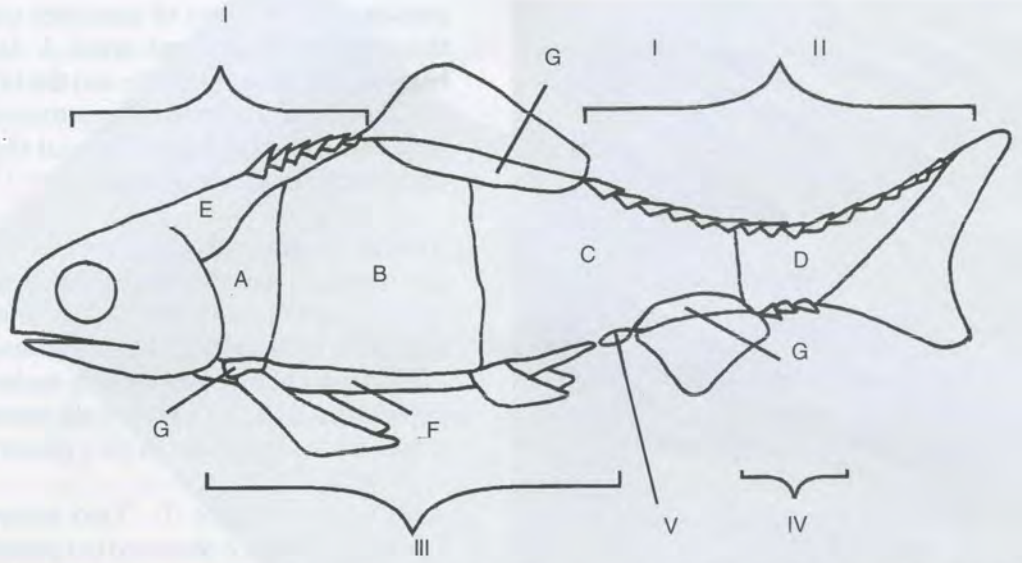


Figure 9. Diagram showing the various areas of scale cover in lower actinopterygian fishes (after Esin 1991). A, B, C, D, E, F, and G are areas of the scale cover on the lateral surfaces of the body; I - ridge scales; II - basal fulcra; III - keel scales; IV- basal fulcra; V- anal scale(s).

Topographic variation of the *Bethesdaichthys* scale cover (see Figure 9 for scale cover Areas and designations of scale types).

Area A: (Figures 10, 11). Scales in this area are situated anterior to the insertion of the pelvic fin. Well preserved scales are seen towards the posterior margin of Area A. The scales are almost rectangular, with a height (h) to length (l) ratio of approximately 2:1. They exhibit steeply inclined anterior and posterior margins, a well developed anterodorsal angle and a smooth anterior depressed field overlap surface anterior to the free field region. The dermal ornament is particularly prominent in this area and consists of elongated ridges, and shorter denticles of ganoine. The free field can basically be separated into two vertically adjacent and distinctive, but interlocking regions. The dorsal free field section consists of numerous (10-14) ridges, most of which are steeply inclined and are not continuous over the entire free field width. Of the posteriorly situated ridges, c5-7 terminate in posterior denticles. Some of the centrally situated dorsal free field ridges sometimes display a 'semi-circular layout' (this was also found to occur in area B). The ventral free field section, situated below the above-mentioned dorsal free field, consists of 8-10 horizontal ridges basically parallel to the ventral border, which terminate in c3-5 posterior denticles. There is a large smooth field anteriorly overlapped by the preceding scale on all the flank scale areas (A to C).

Area B: (Figure 11). The scales in area B are situated between the pelvic fin and the insertion of the dorsal fin. They are almost square, with a h/l ratio of approximately 3:2. The free field, as in area A, can be separated into two vertically adjacent but interlocking regions. In the dorsal free field section, 6-9 posteriorly situated ridges terminate in posterior denticles; in the ventral section of the scale 6-8 horizontally orientated ridges terminate in c3 posterior denticles. The ridges of the free field appear to be less prominent than in area A.

Area C (Figure 12). Scales in this area can be seen in PB/95/6 and PB/96/15. The scales in this area are longer than high, with a h/l ratio of approximately 2:3. The free field consists of 4-7 curved dorsal ridges, and 5-7 horizontally inclined ventral ridges. There are c3 prominent posterior denticles along the posterior scale margin.

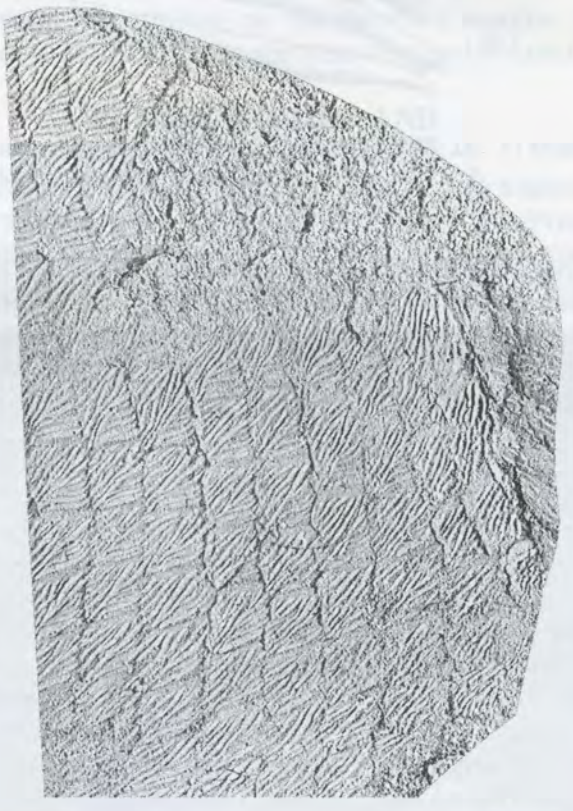


Figure 10. *Bethesdaichthys kitchingi* specimen V101 in lateral view, showing dermal scale detail from Area A.

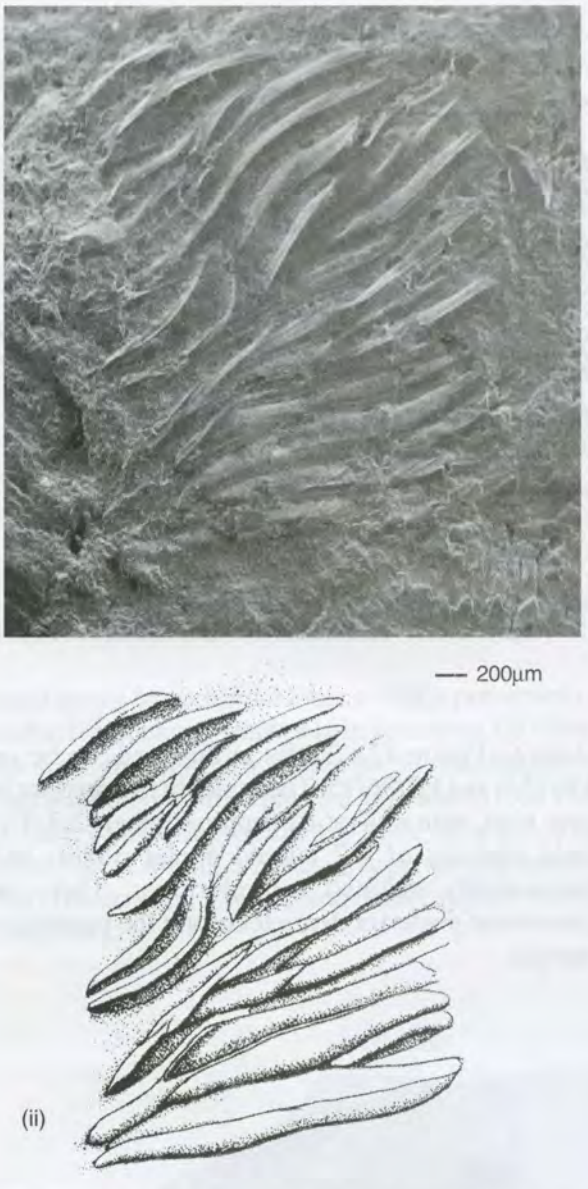


Figure 11 (i). SEM of *Bethesdaichthys kitchingi* specimen BP/1/4373/2b, showing dermal scale scale detail from Area A/B. (ii). Line drawing interpretation.

Area D: Scales in this area are not distinctive, but can be seen in BP/1/4373/37. Caudal scales are small and diamond-shaped, with a h/l ratio of approximately 1:2. The free field consists of approximately 2-3 faint curved dorsal ridges and 2-3 curved ventral ridges, separated by a faint diagonal ridge, and terminating in an entire margin.

Area E: Scales in this area are generally not well preserved and therefore have not been figured, they can be seen in specimens BP/1/4373/19, 37, 134. Scales of this area appear in *Bethesdaichthys* to occur along almost the entire dorsal margin, immediately ventral to the ridge scales. The scales are small and reduced compared to adjacent area A and B scales, with a h/l ratio of almost 1:1. They are triangular, consisting of c4 curved dorsal and c5 curved ventral ridges which taper posteriorly almost to a point.

Area F: Scales in this area are not completely preserved but can be seen in specimen BP/1/4373/134. This area consists of c7-9 rows of narrower scales compared to those found in adjacent areas A and B, and occurs between the pectoral girdle and the insertion of the anal fin. They have a h/l ratio of approximately 1:2. The free field consists of c4-5 curved dorsal and c5 ventral ridges terminating in almost a point.

Area G: Scales in this area are incompletely preserved and therefore have not been figured, they can be seen in specimen BP/1/4373/134. Scales of this area are found in regions of the pelvic, dorsal and anal fins, and consist of c5-8 rows of tiny overlapping scales with a h/l ratio of approximately 1:3. The free field consists of c7 diagonal ridges which terminate in c3-4 posterior denticles.

Anal scales (Figure 7). Two enlarged, paired anal fulcral scales were observed in specimen PB/95/6, with a h/l ratio of approximately 1:2. The free field consists of c16 diagonally orientated ridges which terminate in a rounded apex and c3-4 posterior denticles.

Ridge Scales (Figures 7, 12). Ridge scales, although not entirely preserved, were observed in specimens BP/1/4373/37 and PB/96/15. They are enlarged and roughly triangular in shape, with a h/l ratio of approximately 2:3. Ridge scales appear to be present along the entire dorsal margin anterior to the dorsal fin, the free field consisting of c24 dermal ganoine ridges. Approximately 7-9 ridge scales are present posterior to the dorsal fin and anterior to the caudal fin, the free field consisting of a fainter ornament, and the scale more rounded than the anterior ridge scales.

Keel scales (Figure 7). Not well preserved, but fragmentary scales can be seen in specimens BP/1/4373/19 and 134. Keel scales occur between the pectoral girdle and the anal fin insertion. They appear to be paired, and are elongated, enlarged, triangular scales, with a h/l ratio of approximately 1:2. The free field consists of c4-5 ridges dorsally, separated by a diagonal ridge from c5 ventral ridges.

Basal fulcra

- Dorsal fin, basal fulcra (BP/1/4373/37)(Figure 7). Approximately 3-5 small triangular basal fulcra occur immediately anterior to the dorsal fin.
- Caudal fin, dorsal basal fulcra (PB/95/6)(Figure 7). A row at least 16 acutely triangular basal fulcra is situated above the caudal fin.
- Caudal fin, ventral basal fulcra (BP/1/4373/37)(Figure 7). A row of more than 4 triangular basal fulcra is situated immediately anterior to the insertion of the caudal fin.

Squamation

The scale rows are close to vertical on the flanks, tilted slightly anterodorsally at an angle of approximately 70 degrees to the horizontal (Figures 7, 8, 12). The caudal inversion is just posterior to the insertion of the caudal fin (Figure 7).

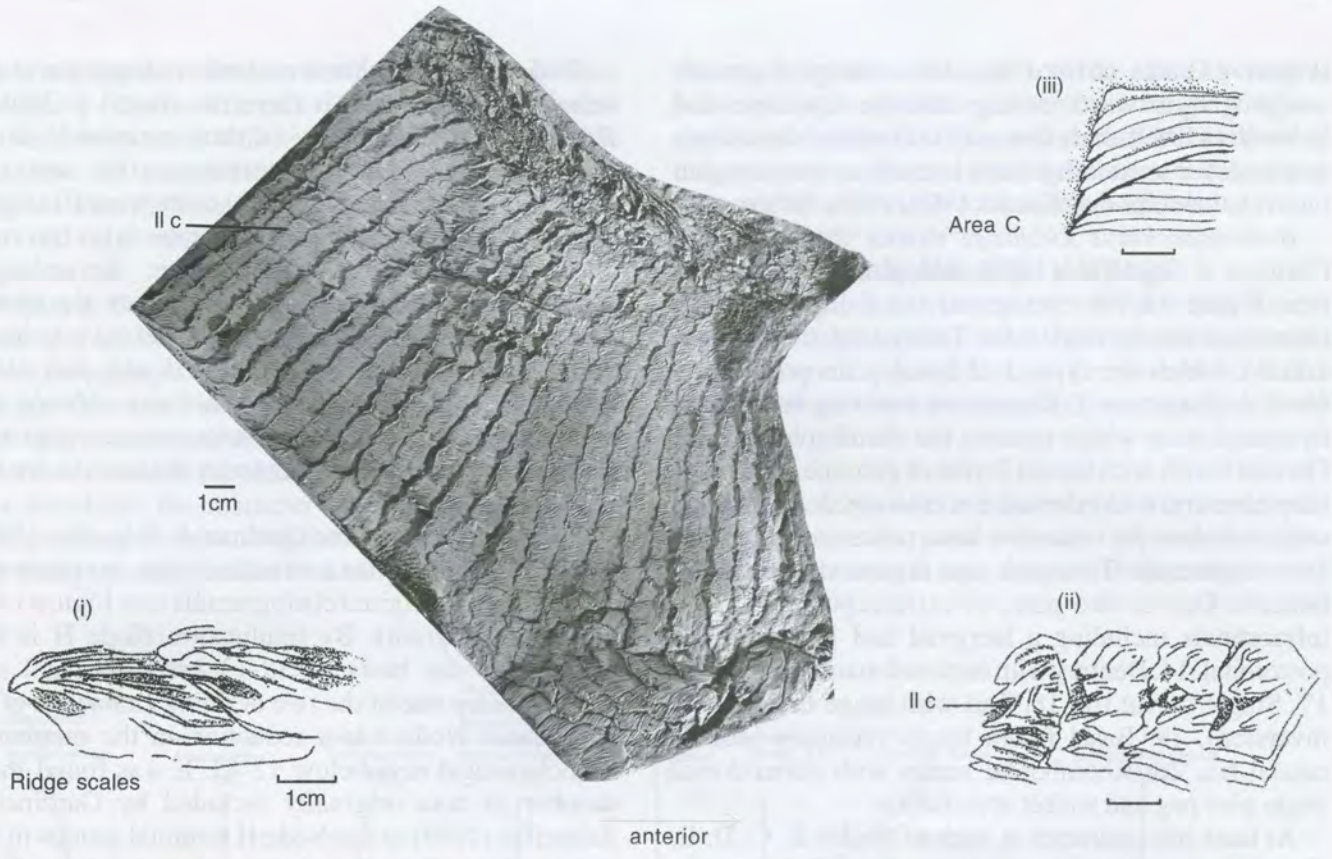


Figure 12. *Bethesdaichthys kitchingi* specimen PB/96/15 in lateral view showing dermal scale morphology. (i). Camera lucida interpretation showing ridge scales. (ii). Camera lucida interpretation showing lateral-line scales in Area B. (iii). Line drawing interpretation showing scale detail from Area C.

Scale counting data:

- Scale rows to pelvic fin (V101; BP/1/4373/19): 11, 11-12.
- Scale rows to dorsal fin (BP/1/4373/124): 35.
- Scale rows to anal fin (BP/1/4373/37): 30-35.
- Scale rows to caudal fin (BP/1/4373/124): 50.
- Scale rows to caudal inversion (BP/1/4373/124): 54.

Number of scales in a single scale column:

- In front of pelvic fin (BP/1/4373/134): 18-20.
- In front of anal fin (BP/1/4373/37): 22-25.
- In front of dorsal fin (BP/1/4373/37): 22-25.
- In front of caudal fin (BP/1/4373/37): 18-20.
- In front of the caudal inversion (BP/1/4373/37): c15.

Scale histology

The general histological structure of the scale can be seen in Figure 13. The scale consists of a basal layer of lamellar bone, overlain by a dentine layer containing an upright, branched plexus of dentine tubules. This layer is in turn overlain by a relatively thick (compared to the overall thickness of the scale), continuous multilayered 'ganoine' or enamel-like layer (see Richter & Smith, 1995, for discussion of the term ganoine). This type of scale histology, in particular the multilayered 'ganoine' is present in most lower actinopterygians, including *Polypterus* and *Lepisosteus* (Richter & Smith 1995).

Laterosensory System

The laterosensory canal system was studied in specimens BP/1/4373/19, 134 and PB/96/15 (Figure 12). It consists of a well developed canal system, which is carried by a single row of flank scales over the entire length of the body (c7 scale rows ventral to the dorsal margin, in front of the pelvic fin region). The lateral line scale consists of an enlarged posterior aperture situated approximately midway on the posterior margin. A number of slit-like canal pores were observed in Area B.

PHYLOGENETICS AND INTERRELATIONSHIPS

The preservation of the specimens is of such a nature that essentially dermal characters only are preserved, and thus the comprehensive lower actinopterygian phylogenetic analysis of Gardiner & Schaeffer (1989)

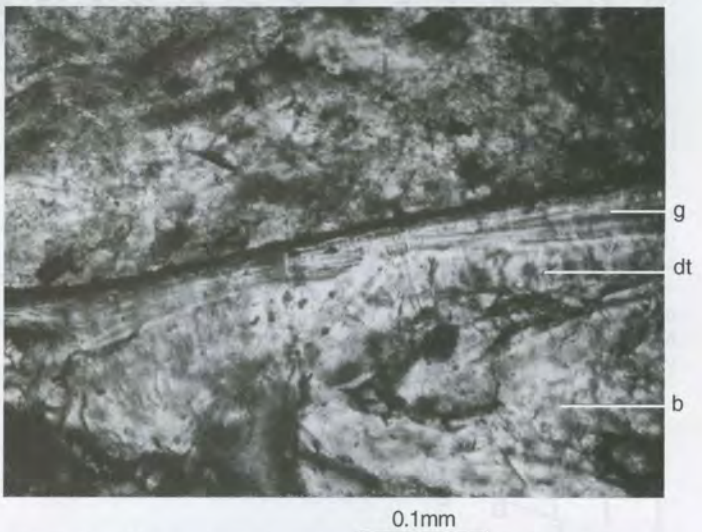


Figure 13. Thin-section photograph of *Bethesdaichthys kitchingi* specimen BP/1/4373/110, showing the structure of the scale layers. (See p.38 for abbreviations)

(Figure 14) was utilized as a basis for phylogenetic analysis. It is worth noting that the Gardiner and Schaeffer (1989) analysis is still utilized by researchers as a basis for examining lower or early actinopterygian interrelationships (see Coates 1993, 1998, 1999).

Bethesdaichthys kitchingi shares the following Gardiner & Schaeffer (1989) cladogram III characters (see Figure 14 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 the study taxon: 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.

Bethesdaichthys shares no further characters at any subsequent nodes and is therefore rooted at Node I. *Bethesdaichthys kitchingi* is thus contained on the *Bobasatrania-Dorypterus* transformation series of the Gardiner & Schaeffer (1989) cladogram III (Figure 14), which is a side-branch separate from the main chondrostean-neopterygian lineage. Accordingly, *Bethesdaichthys* 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.*

Re-examination of the Gardiner & Schaeffer (1989) Node H terminal taxa revealed that revision was required of the original cladogram III (see Figure 15 for revised cladogram). By implication Node H is also defined on the basis of 12-13 branchiostegal rays present, since one of the two defining characters of the subsequent Node I is a reduction in the number of branchiostegal rays below 12-13. It was found that a number of taxa originally included by Gardiner & Schaeffer (1989) in the Node H terminal groups in fact had less than 12-13 branchiostegal rays, and should be rooted at Node I, together with *Bethesdaichthys kitchingi.*

The following group of taxa comprising those analysed by Gardiner & Schaeffer (1989), and including *Bethesdaichthys,* are thus rooted at Node I: *Aetheretmon, Australichthys, Cycloptychius, Phanerosteon, Rhadinichthys canobiensis, Strepheoschema* and *Willomorichthys.*

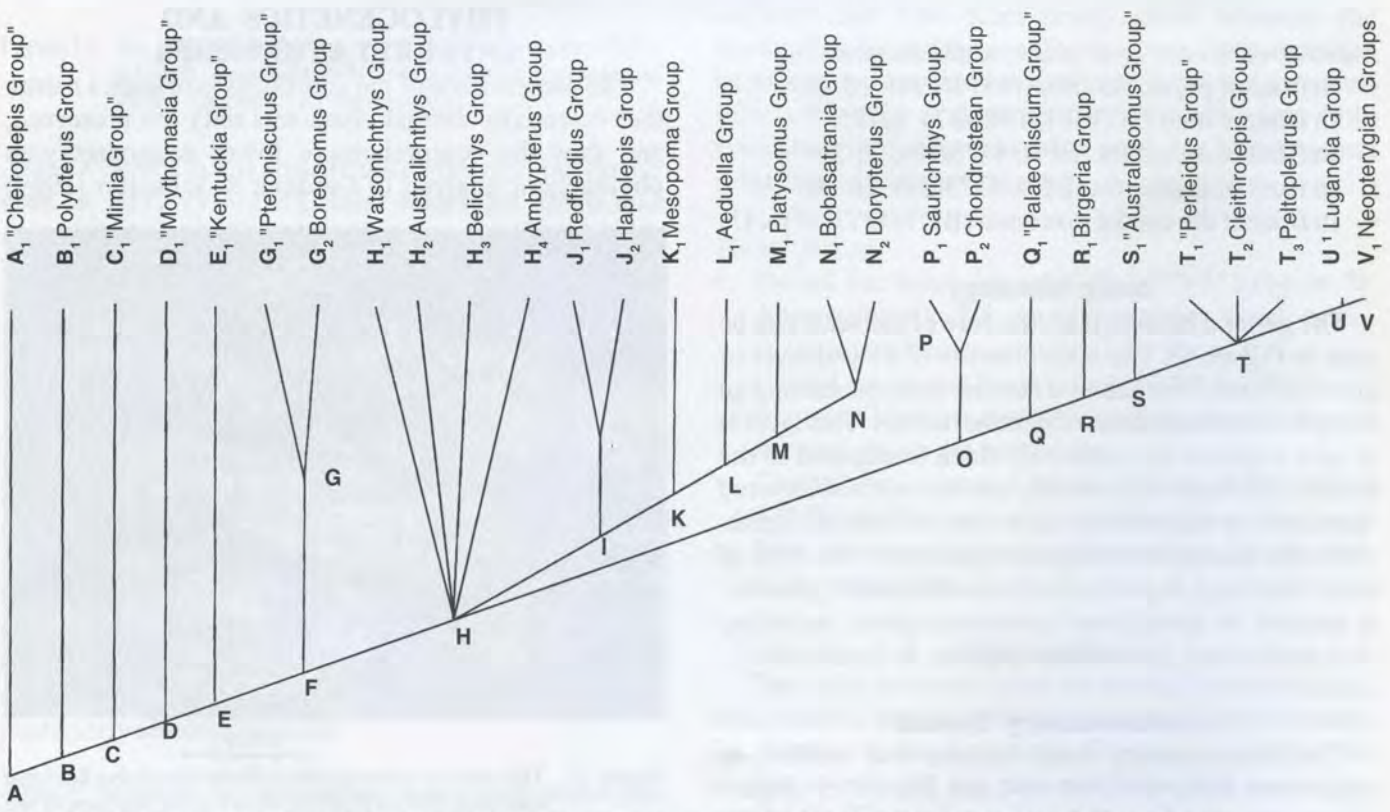


Figure 14. Cladogram for selected major groups of lower actinopterygians from Gardiner & Schaeffer (1989) cladogram III.

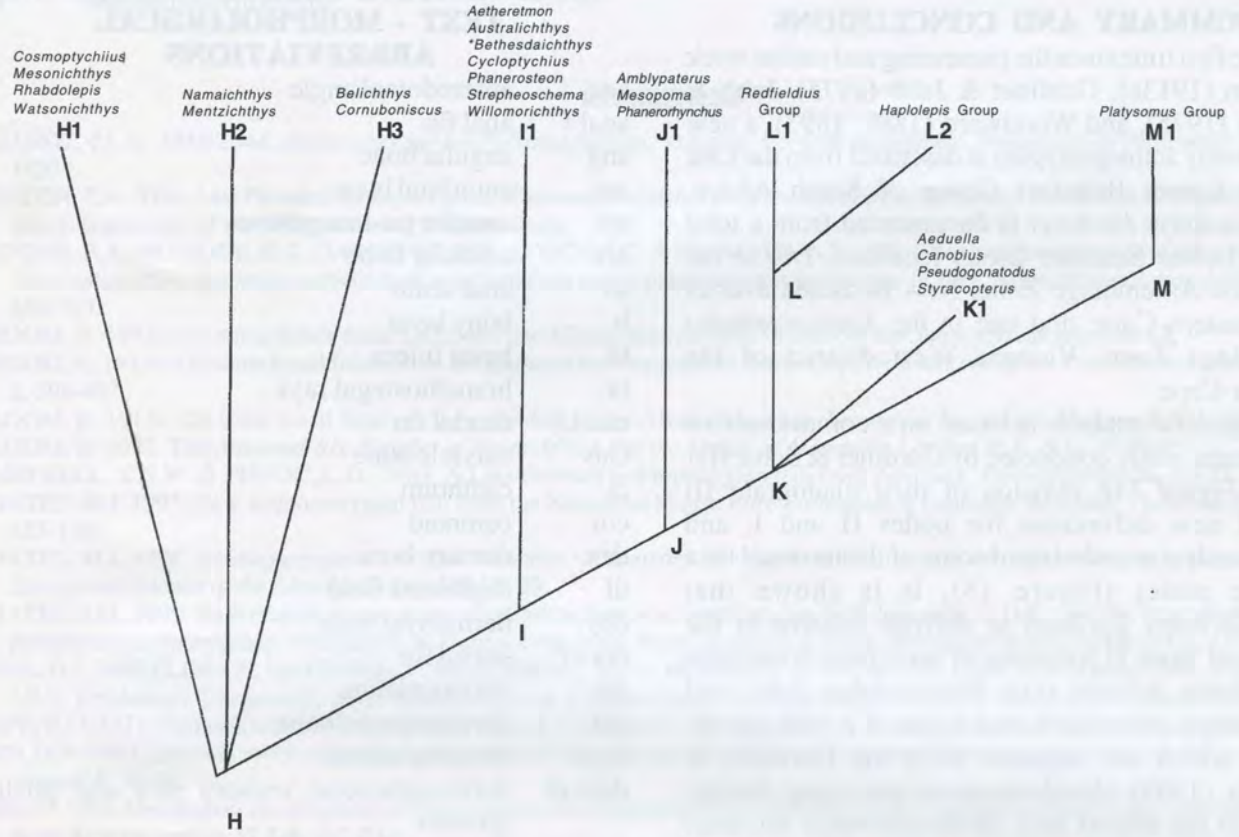
Rooted together with *Bethesdaichthys* at Node I are the Early Carboniferous South African forms *Australichthys* and *Willomorichthys,* with the other taxa also all essentially Carboniferous taxa. This suggests that *Bethesdachthys* as a Late Permian form is relatively unspecialised or morphologically conservative.

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 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.

Bethesdaichthys kitchingi

Stem-actinopteran characters: subopercular shorter than opercular; unspecialized marginal dentition; maxilla with elongate postorbital blade; jaw articulation posterior to parieto-extrascapular suture; elongate body lobe of the tail.

Stem-neopterygian characters: dermopterotic present; premaxillary and antorbital separate; less than 12-13 branchiostegal rays; suborbitals present.



List of nodal characters for Figure 15

NODE H. Dermopterotic present; at least 12-13 branchiostegal rays.
- H1. Dermopterotic with anterior narrowing, in contact with nasal.
- H2. Dermopterotic overlapping T-shaped dermosphenotic, not contacting nasal.
- H3. Dermopterotic widely separated from nasal; cresent- or sickle-shaped dermosphenotic.

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 infraobital 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; andible deep posteriorly, tapering markedly towards premaxillo-antorbital.

* Indicates the study taxon

Figure 15. Revision of the Gardiner & Schaeffer (1989) cladogram III, including study taxon.

Specialized characters: very broad pectoral fin; high but relatively broad postorbital blade of the maxilla.

What these study taxon character sets show is that *Bethesdaichthys* has an almost equal mix of stem-actinopteran and stem-neopterygian characters, and thus a 'fairly equal' distribution of primitive and derived lower actinopterytgian characters.

The earlier, more traditionally based lower actinopterygian studies of Gardiner (1967) and Schaeffer (1973), are perhaps useful in briefly encapsulating the interrelationships of the study species: *Bethesdaichthys kitchingi* appears to be related to members of the 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

For the first time since the pioneering and earlier work of Broom (1913a), Gardiner & Jubb (1975), Jubb & Gardiner (1975), and Woodward (1889, 1893), a new taxon of early actinopterygian is described from the Late Permian Lower Beaufort Group of South Africa. *Bethesdaichthys kitchingi* is documented from a total of three Lower Beaufort Group localities, two in the *Dicynodon* Assemblage Zone, New Bethesda district of the Eastern Cape, and one in the *Tapinocephalus* Assemblage Zone, Victoria West district of the Northern Cape.

Phylogenetic analysis is based on a comprehensive phylogenetic study conducted by Gardiner & Schaeffer (1989) (Figure 14); revision of their cladogram III revealed new definitions for nodes H and I, and consequently a re-ordering of some of the terminal taxa at these nodes (Figure 15). It is shown that *Bethesdaichthys kitchingi* is derived relative to the unresolved 'node H polytomy of taxa' (which includes the southern African taxa *Mentzichthys jubbi* and *Namaichthys schroederi*), and is part of a 'side-group' of taxa which are separate from the Gardiner & Schaeffer (1989) chondrostean-neopterygian lineage leading to the teleost taxa. *Bethesdaichthys kitchingi* exhibits a similarly conservative unspecialised basic skull morphology comparable to that found in various Carboniferous taxa such as *Australichthys, Cycloptychius* and *Willomorichthys.* It 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 *Bethesdaichthys kitchingi* is part of a group of taxa which are found in Britain, Europe and South Africa and thus are not confined to one region. *Bethesdaichthys kitchingi* is morphologically conservative when compared with Late Permian actinopterygian taxa such as *Ebenaqua richiei* from the Late Permian Rangal Coal Measures, Blackwater, central Queensland, Australia, or *Aeduella* and *Dorypterus* from the Permian of Europe and England respectively.

Bethesdaichthys kitchingi is part of a Lower Beaufort Group, Late Permian (Tatarian) high latitude freshwater ichthyofauna which consists essentially of extinct lower actinopterygian taxa (Bender 2000). This ichthyofauna is made up of the following taxa: *Atherstonia scutata, Atherstonia minor, Atherstonia seeleyi, Bethesdaichthys kitchingi, Caruichthys ornatus, Elonichthys whaitsi, Namaichthys digitata,* and *Pteronisculus meiringi.*

In terms of its biostratigraphic implications, *Bethesdaichthys kitchingi* has been documented from the *Tapinocephalus* Assemblage Zone and the *Dicynodon* Assemblage Zone, thus indicating a biostratigraphic range spanning five Assemblage Zones and all of the Late Permian Lower Beaufort Group apart from the basal *Eodicynodon* Assemblage Zone.

ABBREVIATIONS USED IN FIGURES AND TEXT - MORPHOLOGICAL ABBREVIATIONS

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
dsph.pl	dermosphenotic sensory pits and pit-line 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
l.gu	lateral gular bone
llc	lateral-line canal
ll.p	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 pit-line grooves
p	peg
pa	parietal bone
par	prearticular
pcl	postcleithrum
pect.f	pectoral fin
pelvic f	pelvic fin
pmx	premaxilla bone
pop	preopercular bone
popc	preopercular sensory canal
pop.pl	preopercular sensory pits and pit-line 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 pit-line grooves

ACKNOWLEDGEMENTS

As this article was part of a PhD study, I would like to thank project supervisors Professor Bruce Rubidge and Dr John Long, also Professor James Kitching, for their invaluable support and advice over a number of years. I would also like to thank Dr Michael Coates for his invaluable comment and advice. Thanks to my employers, the Council for Geoscience, and a number of its members, including the directors for their support; appreciation is also expressed to colleagues at the BPI Palaeontology, Wits University for their support and assistance. Thanks also to: Mr and Mrs Esterhuizen and Clive Kingwell of the farm Blourug and Lionel de la Harpe at Wilgerbosch, for their hospitality, help and enthusiasm; Rochelle Vlok curator at the Victoria West Museum; Geoscience Museum Artist Anke Raath for assistance with the diagrams; and Bernice McLean for field assistance and close friendship.

REFERENCES

AGASSIZ, J.L.R. 1833-1844. *Recherches sur les Poissons fossiles.* Volumne 1-5 with supplement. Imprimere de Petitpierre. Neuchatel, 1420.

BENDER, P.A. 2000. *Late Permian Actinopterygian (Palaeoniscid) fishes from the Lower Beaufort Group, South Africa.* Unpublished. PhD thesis. University of the Witwatersrand, Johannesburg.

BENDER, P.A., RUBIDGE, B.S., GARDINER, B.S., LOOCK, J.C. & BREMNER, A.T. 1991. The stratigraphic range of the palaeoniscoid fish *Namaichthys digitata* in rocks of the Karoo Sequence and its palaeoenvironmental significance. *South African Journal of Science* **87**, 468-469.

BROOM, R. 1913a. On some fishes from the Lower and Middle Karroo Beds. *Annals of the South African Museum* **12,** 1-5.

BROOM, R. 1913b. On some fossil fishes from the diamond bearing pipes of Kimberley. *Transactions of the Royal Society of South Africa* **3,** 399-402.

BROOM, R. 1913c. On some fossil fishes in the collection of the Albany Museum. *Records of the Albany Museum* **2,** 391-393.

BROOM, R. 1932. The *Mammal-like Reptiles of South Africa and the Origin of Mammals.* London, H.F. & G. Witherby.

CAMPBELL, K.S.W. & PHUOC, L.D., 1983. A Late Permian actinopterygian fish from Australia. *Palaeontology* **26,** 33-70.

COATES, M.I. 1993. New actinopterygian fish from the Namurian Manse Burn Formation of Bearsden, Scotland. *Palaeontology* **36** (1), 123-146.

COATES, M.I. 1998. Actinopterygians from the Namurian of Bearsden, Scotland, with comments on early actinopterygian neurocrania. *Zoological Journal of the Linnean Society* **122,** 27-59.

COATES, M.I. 1999. Endocranial preservation of a Carboniferous actinopterygian from Lancashire, U.K., and the interrelationships of primitive actinopterygians. *Philosophical Transactions of the Royal Society of London, Biological Sciences* **354**(1382), 435-462.

COLE, D.I., NEVELING, J., HATTINGH, J., REDDERING, J.S.V., BENDER, P.A. & CHEVALLIER, L.P. In press 2001. (Compiled by J.S.V. Reddering). The geology of the Middleburg area. *Explanation of sheet 3124 (Middleburg), Council for Geoscience, South Africa.*

COPE, E.D. 1871. Contribution to the ichthyology of the Lesser Antilles. *Transactions of the American Philosophical Society* **14,** 445-483.

ESIN, D.N. 1990. The scale cover of *Amblypterina costata* (Eichwald) and the palaeoniscid taxonomy based on isolated scales. *Palaeontological Journal* **2,** 90-98.

ESIN, D. 1995. Ontogenetic development of the squamation in some palaeoniscoid fishes. *Bulletin du Museum national d' Histoire naturelle Paris* 4e serie section **17 1-4,** 227-234.

GARDINER, B.G. 1967. Further notes on palaeoniscoid fishes with a classification of the Chondrostei. *Bulletin of the British Museum (Natural History), Geology* **14** (5), 143-206.

GARDINER, B.G. 1969. New palaeoniscoid fish from the Witteberg Series of South Africa. *Zoological Journal of the Linnean Society* **48,** 423-452.

GARDINER, B.G. 1973. Interrelationships of teleostomes. **In:** Greenwood, P.H., Patterson, C. & Miles, R.S. (eds.), *Interrelationships of Fishes,* 105-135. London & New York, Academic Press.

GARDINER, B.G. 1993. Osteichthyes: Basal Actinopterygians. **In:** Benton, M, *The Fossil Record* **2,** 611-619. London, Chapman Hall.

GARDINER, B.G. & JUBB, R.A. 1975. A new palaeoniscid from the Lower Beaufort Series of South Africa. *Annals of the South African Museum* **67** (12), 441-445.

GARDINER, B.G. & SCHAEFFER, B. 1989. Interrelationships of lower actinopterygian fishes. *Biological Journal of the Linnean Society* **97,** 135-187.

HANCOX, J.P. & RUBIDGE, B.R. 1997. The role of fossils in interpreting the development of the Karoo Basin. *Palaeontologia africana* **33,** 41-54.

JUBB, R.A. & GARDINER, B.G. 1975. A preliminary catalogue of identifiable fossil fish material from southern Africa. *Annals of the South African Museum* **67** (11), 381-440.

LE ROUX, F.G. & KEYSER, A.W. 1988. Die geologie van die gebied Victoria-Wes. *Explanation of Sheet 3122 (Victoria West) Geological Survey, South Africa.*

LUND, R., POPLIN, C. & McCARTHY, K. 1995. Preliminary analysis of the interrelationships of some Palaeozoic Actinopterygii. **In:** Levièvre, H., Wenz, S., Blieck, A., & Cloutier, R. (Edms), *Premiers Vertébrés et Vertébrés Inférieurs Geobios M S* **19,** 215-220.

LUND, R. & POPLIN, C. 1997. The Rhadinichthyids (Paleoniscoid Actinopterygiaans) from the Bear Gulch Limestone of Montana (USA, Lower Carboniferous). *Journal of Vertebrate Paleontology* **17**(3), 466-486.

POPLIN, C. & VERAN, M. 1996. A Revision of the actinopterygian fish *Coccophalus wildi* from the upper Carboniferous of Lancashire. **In:** Milner, A.R. (ed.), *Studies on Carboniferous and Permian Vertebrates.* Special papers in Palaeontology **52,** 7-30.

RICHTER, M. & SMITH, M.M. 1995. A microstructural study of the ganoine tissue of selected lower vertebrates. *Zoological Journal of the Linnean Society* **114,** 173-212.

RUBIDGE, B.S., JOHNSON, M.R., KITCHING, J.W., SMITH, R.M.H., KEYSER, A.W. & GROENEWALD, G.H. 1995. An introduction to the biozonation of the Beaufort Group. **In:** Rubidge, B.S. (ed.), *Biostratigraphy of the Beaufort Group (Karoo Supergroup).* South African Committee for Stratigraphy, Biostratigraphic Series **1,** 1-2.

RUBIDGE, B.S. 1995 (ed.), *Biostratigraphy of the Beaufort Group (Karoo Supergroup).* South African Committee for Stratigraphy, Biostratigraphic Series **1,** 1-46.

SOUTH AFRICAN COMMITTEE FOR STRATIGRAPHY (S.A.C.S.). 1980. *Stratigraphy of South Africa, Part 1* (compiled by Kent, L.E.), *Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia, and the Republic of Bophuthatswana, Transkei and Venda.* Handbook of the Geological Survey of South Africa 8.

SCHAEFFER, B. 1973. Interrelationships of chondrosteans. **In:** Greenwood, P.H., Miles, R.M. & Patterson, C. (eds.), *Interrelationships of Fishes,* 207-226. London & New York, Academic Press.

SMITH, R.M.H. 1990. A review of stratigraphy and sedimentary environments of the Karoo Basin of South Africa. *Journal of African Earth Sciences* **10** (1/2), 117-137.

WOODWARD, A.S. 1888. On two new lepidotoid ganoids from the early Mesozoic deposits of Orange Free State, South Africa. *Quarterly Journal of the Geological Society of London* **44,** 138-143.

WOODWARD, A.S. 1889. On *Atherstonia,* a new genus of palaeoniscid fishes from the Karroo Formation of South Africa. *Annals and Magazine of Natural History* **4** (6), 239-242.

WOODWARD, A.S. 1891. *Catalogue of the Fossil Fishes in the British Museum (Natural History), London* 2. London: British Museum.

WOODWARD, A.S. 1893. Further notes on fossil fishes from the Karroo Formation of South Africa. *Annals and Magazine of Natural History* **12**(6), 393-398.