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A new deep-bodied Late Permian actinopterygian fish from the Beaufort Group, South Africa

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A new genus of actinopterygian (ray-finned) fish, *Blourugia seeleyi* is described from Late Permian (Tatarian) fluvio-lacustrine, siltstone-dominated deposits within the lower Beaufort Group of South Africa. It was originally provisionally assigned to the globally known genus *Atherstonia* by Woodward (1893), but indications are that the genus is distinct from *Atherstonia* on the basis of its deep-bodied form and the associated skull characters; thus *Blourugia seeleyi* is placed in Gardiner & Schaeffer's (1989) *Platysomus* Group. The new genus is characterized by a uniquely shaped prominent high triangular posterior blade of the maxilla, dermosphenotic triangular shaped, pointed marginal teeth, 8–10 branchiostegal rays, flank scales that exhibit a well-developed dermal ornamentation consisting of numerous transverse ganoine ridges, and the presence of a dermopterotic that contacts the nasal. *Blourugia* appears to be a primitive deep-bodied form, basal to lower actinopterygian deep-bodied forms such as *Adroichthys, Amphicentrum, Cheirodopsis, Paramesolepis* and *Platysomus.* As a member of Gardiner & Schaeffer's *Platysomus* Group, it is therefore derived relative to stem-actinopterans such as *Howqualepis, Mimia* and *Moythomasia,* and also derived relative to earlier southern African Palaeozoic actinopterygians such as *Atherstonia scutata, Mentzichthys jubbi, Namaichthys schroederi* and the newly/recently described lower Beaufort Group taxa *Bethesdaichthys kitchingi* and *Kompasia delaharpei,* but basal to stem-neopterygians such as *Australosomus* and *Saurichthys.*

Keywords: *Blourugia,* deep-bodied palaeoniscid, Late Permian, Tatarian, Beaufort Group, Actinopterygii.

INTRODUCTION

The type specimen of the proposed new genus of deep-bodied actinopterygian fossil fish, *Blourugia seeleyi,* was originally provisionally assigned by Woodward (1893) to *Atherstonia seeleyi* based on a single incomplete specimen from Klipfontein, Fraserburg district (*Dicynodon* Assemblage Zone), Northern Cape, South Africa. Subsequently Jubb & Gardiner (1975), in their preliminary catalogue of South African fossil fish, referred a number of specimens from Blourug, Victoria West district (*Tapinocephalus* Assemblage Zone) to *A. seeleyi.*

Actinopterygian fishes are bony fishes particularly characterized by the morphology of the fins that are supported by stiff bony spines (Patterson 1982; Romer 1966). They constitute the largest group of living fishes, with a least 29 000 living species (M. Gomon, pers. comm.). 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 (Patterson 1982).

Blourugia seeleyi gen. nov. belongs to a group of early actinopterygian taxa which, owing to uncertain phylogenetic position, are usually grade-classified as 'palaeoniscids' (see Coates 1998), or consigned to the paraphyletic 'palaeonisciforms' (Coates 1999).

These 'palaeoniscid' early actinoptgerygians are generally characterized by thick, ganoine-covered scales articulated by interlocking peg and socket joints, a heterocercal tail, and a maxilla with an extended postorbital blade attached to the cheek (Gardiner & Schaeffer 1989). 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 *et al.* 1995), consist of mostly Palaeozoic, globally distributed actinopterygians (Coates 1993). The work of Patterson (1982), Gardiner (1984), Coates (1998, 1999), Gardiner & Schaeffer (1989), Poplin & Lund (2000), Cloutier & Arratia (2004) and Gardiner *et al.* (2005) showed that these 'palaeoniscids' include stem-taxa related to the Actinopterygii, Actinopteri, Chondrostei and Neopterygii. 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), but a fair number of fossil actinopterygian fish specimens have also been collected (Jubb & Gardiner 1975; Bender 1998, 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 ten lower Beaufort Group actinopterygian species are now known, including *Blourugia seeleyi* gen. nov., and the recently described *Kompasia delaharpei, Bethesdaichthys kitchingi* and *Westlepis kempeni* (Bender 2001, 2002). Fossil fish are relatively rare, but where present are useful biostratigraphic indicators, and have palaeoenvironmental and global correlative potential (Bender *et al.* 1991; Hancox & Rubidge 1997).

MATERIALS AND METHODS

More than 27 laterally compressed *Blourugia* gen.nov. specimens were recovered by the author from a *Tapinocephalus* Assemblage Zone locality on the farm Blourug, Victoria West district (Abrahamskraal Formation,

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Adelaide Subgroup), Beaufort Group (referred to by Jubb & Gardiner 1975). Ten specimens were collected from a *Dicynodon* Assemblage Zone locality on the farm Wilgerbosch, New Bethesda district (Adelaide Subgroup). The formational designation of the Wilgerbosch site is uncertain (Cole *et al.* 2003) but appears to be situated in roughly the stratigraphic equivalent of the Balfour Formation. The specimens at Blourug are contained in a single, thin (on average 10 cm thick), buff-coloured, fine- to medium-grained, sandstone 'fish-bearing' unit, and occur over a lateral distance of 70 m. The fish are generally laterally compressed, occur throughout the unit, and tend to be preserved as fairly complete specimens. They are generally concentrated in areas or 'pockets' within the fish-bearing unit, with over 150 well-preserved specimens collected in total. The specimens at the Wilgerbosch roadside site were derived from a greenish mudstone/siltstone/fine-grained sandstone horizon, 4.5–13 cm in thickness. Over 350 specimens have been collected from an area of approximately 10 m^2. As with Blourug, the fish are generally laterally compressed, and occur throughout the unit. Examination of the geology at the two study localities and the nature of the fossil fish deposits, indicates that the fishes were deposited in riverine overbank-type environments, preserving the fossils at the Blourug and Wilgerbosch roadside study localities in isolated 'palaeoponds'.

A number of the referred specimens required mechanical and chemical preparation (see Bender 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 polarized 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 *Blourugia seeleyi* gen. nov., are investigated using the Gardiner & Schaeffer cladogram III as a basis (Gardiner & Schaeffer 1989), since this is the most recent comprehensive early actinopterygian phylogenetic analysis (Coates 1999).

SYSTEMATIC PALAEONTOLOGY

Class Actinopterygii Woodward 1891
Infraclass Actinopteri Cope 1871

***Blourugia* gen. nov.**

Type species. Blourugia seeleyi (Atherstonia seeleyi) Woodward 1893.

Derivation of name. Named after the paratype locality, privately owned farm 'Blourug'. Blourug means 'blue ridge' in Afrikaans, probably the most commonly used language of the region.

Diagnosis

Medium-sized, deep-bodied fish up to 200 mm in total length with a terminal mouth and almost upright suspensorium. Dermopterotic is a fairly broad, elongated bone, which contacts the nasal as does the triangular dermosphenotic. Premaxilla (or premaxillo-antorbital) is rectangular and is partially excluded from the jaw margin by the maxilla. Jugal is elongated and broad, the lachrymal is relatively short and narrow. Maxilla has a prominent, high triangular postorbital blade. Dentition consists of a median row of larger conical teeth surrounded by more numerous smaller teeth, also present are marginal peg-like teeth. Preopercular is a single large upright triangular to wedge-shaped bone. Two rounded suborbitals and a broad elongated dermohyal are present. Opercular is broad, rounded and articulated on the subopercular. Subopercular is broader and slightly higher than the opercular, and tapers ventrally. Suspensorium is upright. There are 8–10 branchiostegal rays. All the fins are large. Pectoral fin is very elongate with the fin-rays closely jointed over the entire length of the fin. Distal bifurcation is present on at least some of the fins. Heterocercal caudal fin has an elongated body lobe. Flank scales exhibit a well-developed dermal ornamentation consisting of numerous transverse ganoine ridges. Enlarged ridge scales present along the entire dorsal margin. Scale histology consists of a laterally continuous, multilayered ganoine layer, overlying dentine basal bony layers.

Remarks and comparisons

This genus was originally described as *Atherstonia seeleyi* by Woodward (1893), who indicated that the fish was only provisionally referred to the genus *Atherstonia* because of the extremely fragmentary nature of the holotype. Subsequently, Jubb & Gardiner (1975), on the basis of additional well-preserved specimens from Blourug, Victoria West, confirmed the generic and specific designation. Most recently the author recovered ten deep-bodied specimens from Wilgerbosch, which are now also assigned to *Blourugia seeleyi.* Indications from the present study are that the genus is distinct from *Atherstonia,* because of the following characteristics: its deep-bodied form; dermopterotic which contacts the nasal; no antorbital; reduced triangular postorbital blade of the premaxilla; upright wedge-shaped preopercular; high, broad subopercular, which tapers ventrally and is higher and broader than the opercular and branchiostegal rays reduced below the primitive 12–13.

On the basis of its deep-bodied form and the associated skull characters, which are found in deep-bodied lower actinopterygian taxa (such as the triangular postorbital blade of the maxilla, upright triangular preopercular, upright suspensorium), *Blourugia seeleyi* can be placed in the *Platysomus* Group of Gardiner & Schaeffer (1989). *Blourugia* has marginal conical teeth, and an absence of crushing toothplates, which suggests it is comparable with taxa such as *Platysomus superbus* and *Paramesolepis tuberculata,* and distinct from the deep-bodied forms with crushing toothplates such as *Amphicentrum crassum* and *Adroichthys tuberculatus* (see Coates 1988; Gardiner 1969; Moy-Thomas & Dyne 1938) for reference to comparative taxa). The presence of a dermopterotic that contacts the nasal in *Blourugia seeleyi* appears to distinguish it from

other *Platysomus* Group taxa. This character is however present in an undescribed Late Permian deep-bodied form from the Bowen Basin, Australia (Bender 1999).

Blourugia seeleyi Woodward 1893

Derivation of name. Named after Professor H.G. Seeley, who discovered the holotype. Although the generic designation is emended, the species name *seeleyi* is retained (see Woodward 1893).

Holotype. P.8613 in the Natural History Museum, London (NHM). The locality is Klipfontein, SW of Fraserburg, Nieuwveldt Range, W Cape, *Dicynodon* Assemblage Zone, Lower Beaufort Group (Jubb & Gardiner 1975).

Paratypes. AK/76/7 and PB/96/5, housed at the Council for Geoscience, Pretoria. The locality is Blourug, Victoria West district, *Tapinocephalus* Assemblage Zone, Lower Beaufort Group.

Referred specimens. V63 and V64 housed in the Victoria West Museum, Victoria West; BPI/1/4373/27,28a,29,30,31, 34,35,36, housed at the BPI Palaeontology, Johannesburg; AK/76/2,3,4,5,6,8; PB/95/5; PB/96/1–4, 6, 8, 9,10,11,13a, housed at the Council for Geoscience, Pretoria.

Horizon and locality. V63, V64, AK/76/2–8, PB/96/1–4, 6, 8, 9, 10, 11, 13a are from Blourug, *Tapinocephalus* Assemblage Zone, Lower Beaufort Group. BPI/1/4373/27, 28a, 29, 30, 31, 34, 35, 36, and PB/95/5 are from the Wilgerbosch roadside locality, *Dicynodon* Assemblage Zone, Lower Beaufort Group.

Diagnosis

Only one species.

Remarks and comparisons

Blourugia seeleyi is the most abundant species at Blourug with in excess of 20 specimens recorded, and10 specimens recorded from Wilgerbosch.

DESCRIPTION

Skull roof

The skull roof region was analysed on the basis of specimens PB/96/4, 5, 9, AK/76/1,7 (see Figs 1–3). It is made up of broad paired parietals, frontals, extrascapulars, and a dermopterotic and dermosphenotic on either side of the frontals. All of the bones of the skull roof are ornamented with well-developed dermal ganoine ridges and denticles. The sensory line system appears to be well developed, with a canal, pits and pit-lines visible.

Parietals (Figs 1, 3 & 4). Most of the left parietal is preserved in PB/96/5 (Fig. 1B, pa) and is a relatively large, broad and subrectangular to ovate, slightly greater than half as long as the frontal. It tapers anteriorly to where it sutures with the frontal bone, posteriorly it is overlapped by the extrascapular. The posterior section of the supraorbital canal terminates in a triradiate canal system.

Frontals (Figs 1, 3 & 4). The frontals (Fig. 1B, fr) are elongate, forming approximately one third of the total length of the skull roof, meeting the median rostral and the nasals anteriorly. The supraorbital canal is marked by as a prominent series of pits in specimen number PB/96/9 (Fig. 3). Dermal ornament consists of a distinctive anteroposteriorly aligned pattern of ribs and denticles except at the posterior margin where they are aligned dorsoventrally.

Dermopterotic (Figs 1–4). The dermopterotic (Fig. 1B, dpt) is a prominent, elongate bone, which is broad posteriorly, tapering anteriorly over the dermosphenotic where it contacts the nasal. It is approximately the combined length of the parietal and the frontal. The infraorbital canal is situated low down on the lateral surface of the bone, towards the ventral margin, where a line of pits and pit-lines appear to trace the passage of the canal dermally. A cluster of pit-lines are present above the dermohyal. The infraorbital canal curves dorsally above the dermosphenotic, and then turns ventrally to enter the dermosphenotic towards the anterior margin. The nasal contact is unusual in deep-bodied lower actinopterygian forms since in most other deep-bodied forms the dermopterotic terminates against the dermosphenotic and is thus separated from the nasal by the dermosphenotic.

Dermosphenotic (Figs 1–4). This bone (Fig. 1B, dsph) is damaged in all of the study specimens in which it is visible but appears to be a fairly large relative to the other bones making up the orbital region, roughly triangular bone, which contacts the nasal anteriorly, underlying the dermopterotic along its entire dorsal margin. The infraorbital canal is visible on the dermal surface as a series of pits and pit canals, which enter the dorsal bone margin from the dermopterotic approximately midway along the margin, and curve ventrally close to the anterior margin before exiting at the narrow ventral margin.

Extrascapulars (Figs 1, 2 & 4). The left extrascapular (Fig. 1B, exsc) is well preserved in PB/96/5 (Fig. 1) and is an elongate, narrow bone overlapping the posterior margin of the skull. It is situated between the parietal and the post-temporal, overlying the post-temporal. The lateral line canal extends along the ventral border, where a number of sensory pits are visible. Dermal ornamentation consists of horizontally inclined ridges, which are distinct from those of the post-temporal in that the ridges are smaller and narrower.

Snout

The snout region is distorted and incomplete but is visible in specimens AK/76/7, PB/96/9, PB/98/3 and appears to consist of a median rostral bone, paired premaxillae and a nasal on either side of the rostral.

Premaxilla (or premaxillo-antorbital) (Figs 2 & 4). The premaxilla (Fig. 2B, pmx) is seen in medial view, poorly preserved in AK/76/7. It appears to be a rectangular bone and seems to be part of the upper jaw margin, at least anteriorly, and does not appear to bear teeth. The rostral bone is situated anterior to the premaxillae and is thus excluded from the jaw margin. Posteriorly the premaxilla sutures with the lachrymal and the nasal.

Nasal (Figs 2 & 4). Narrow and elongate, the nasal (Fig. 2B, na) forms the anterior dorsal margin of the orbit. It contacts the tapered anterior margins of the dermopterotic and the dermosphenotic above the posterior

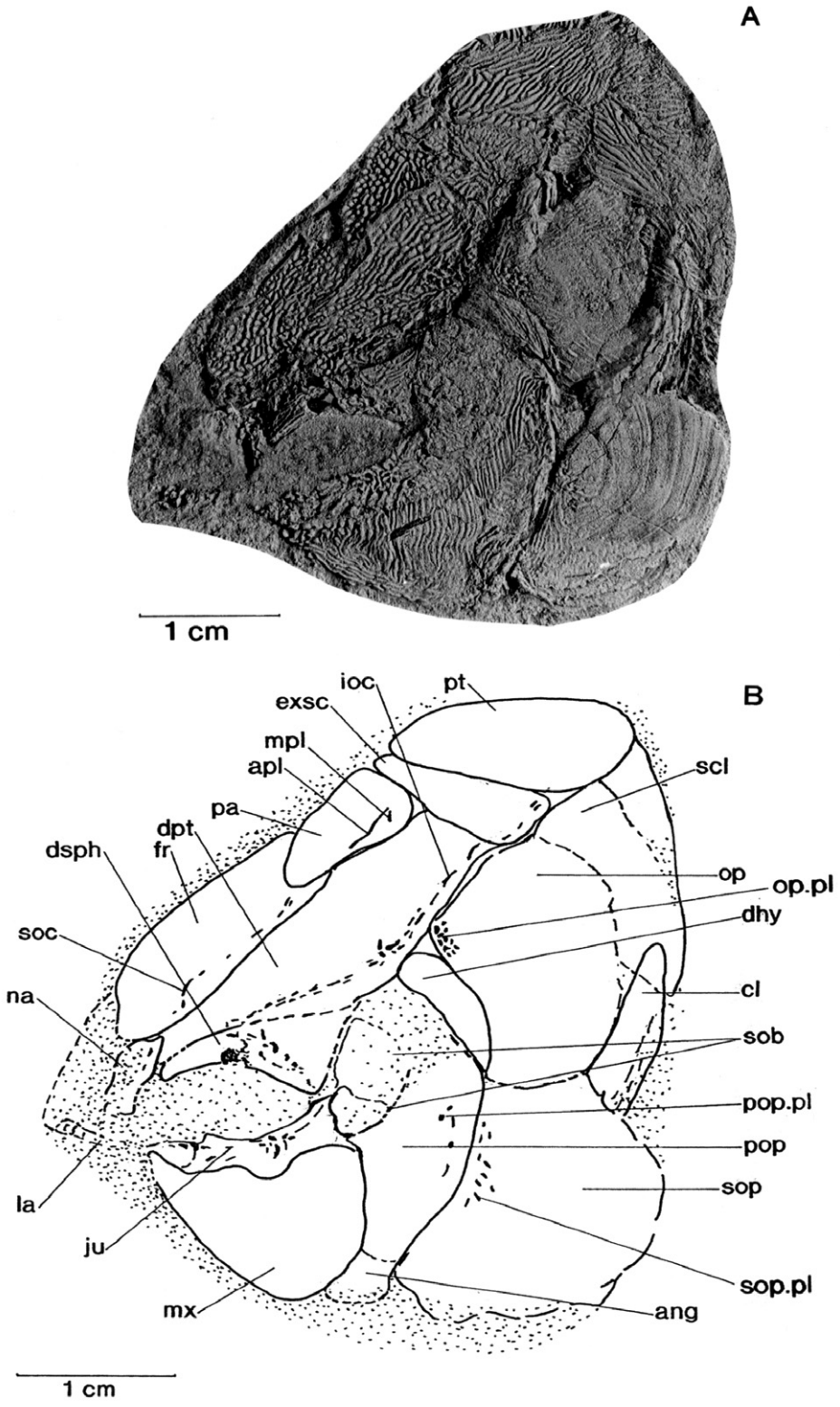


Figure 1. *Blourugia seeleyi* paratype PB/96/5. **A**, Photograph in lateral view showing skull region dermal detail. **B**, Camera lucida reconstruction.

dorsal margin of the orbit. Ventrally the nasal contacts the lachrymal. A single, rounded posterior naris is clearly visible in specimen AK/76/7, situated approximately a third of the distance up from the ventral border; the anterior naris is faintly visible on the inner margin.

Rostral (Figs 2 & 4). The rostral (Fig. 2B, ro) is poorly preserved, but appears to be a single median bone. In AK/76/7 its ventral margin appears to contact the premaxilla some distance above the jaw margin, and is thus removed from the jaw articulation.

Cheek and infraorbitals

The infraorbital region is not well preserved but is visible in specimens PB/96/2, PB/96/5, and AK/76/7, consisting of a large jugal and slightly smaller lachrymal, The cheek region consists externally of a prominent maxilla, preopercular, suborbital complex, an inner palato-quadrate and dermal bones of the mouth, and is best represented in specimens PB/96/5 and AK/76/7.

Jugal (Figs 1, 3 & 4). A large, elongate, crescentic bone (Fig. 1B, ju), which forms most of the posterior margin of

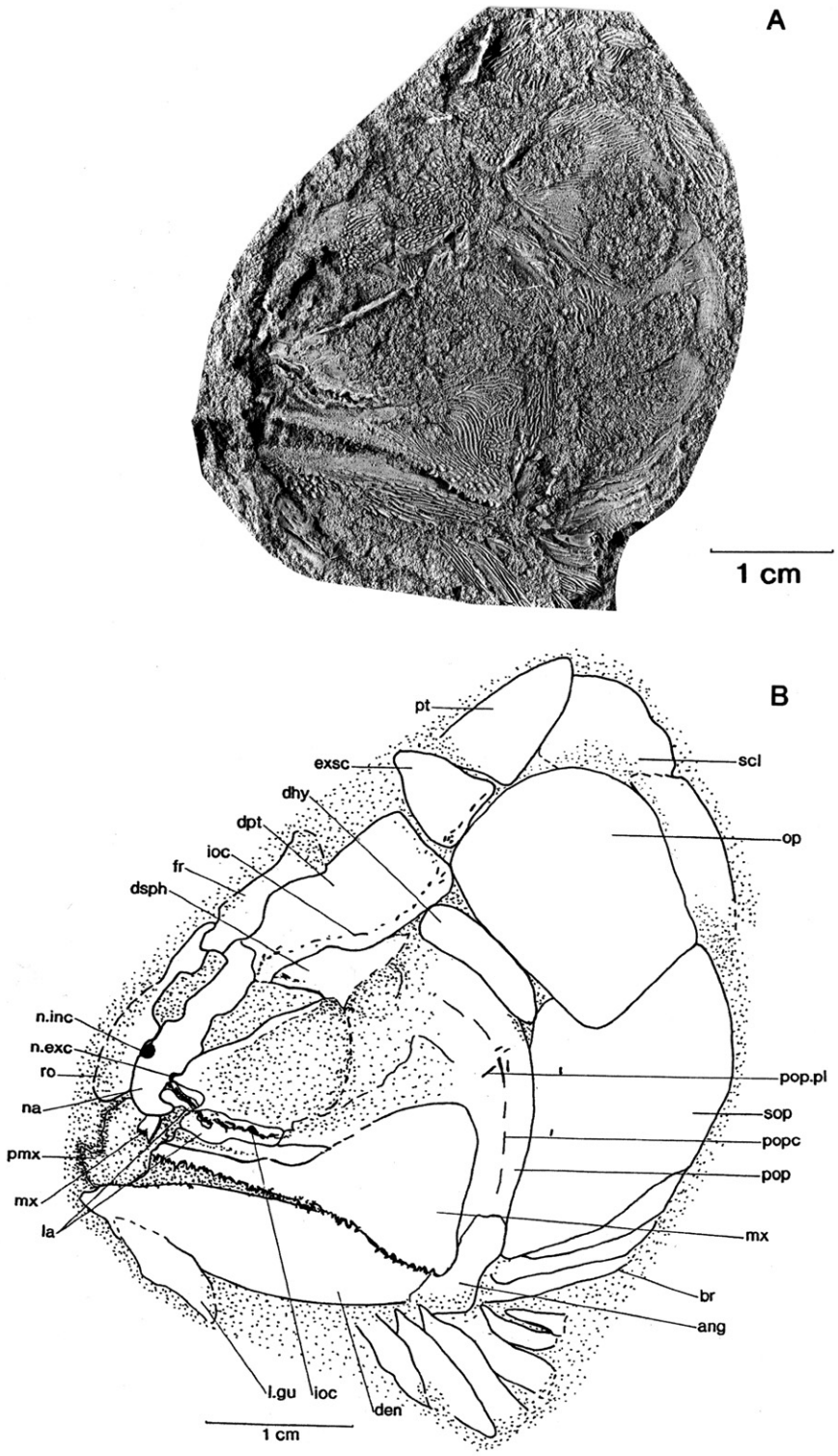


Figure 2. *Blourugia seeleyi* paratype AK/76/1. **A**, Photograph in lateral view showing cheek and snout region detail. **B**, Camera lucida reconstruction.

the orbit, and contacts the dermosphenotic dorsally and the lachrymal ventrally. A well-developed infraorbital canal, with associated posteroventral branchlets, is visible in specimen PB/96/2. A series of pits associated with the infraorbital canal are also visible. Dermal ornament in the form of ridges can be seen towards the dorsal margin of the bone.

Lachrymal (Figs 1–4). The lachrymal (Fig. 2B, la) can be seen in median view in specimen AK/76/7, although it is fractured and somewhat distorted. It is slightly narrower than the jugal and shorter with a broad well-developed infraorbital canal present. Anteriorly it sutures with the premaxilla and the nasal, ventrally it borders the infraorbital blade of the maxilla.

Maxilla (Figs 1–4 & 6). The maxilla (Fig. 2B, mx) consists of a triangular postorbital blade, which is high and rounded dorsally, and a tapered sub-infraorbital blade, which is approximately half of the total maxilla length which appears to be fairly robust. Anteriorly the maxilla appears to suture with the premaxilla, which forms the terminal margin of the skull. The dermal ornament on the postorbital blade is well developed and consists of

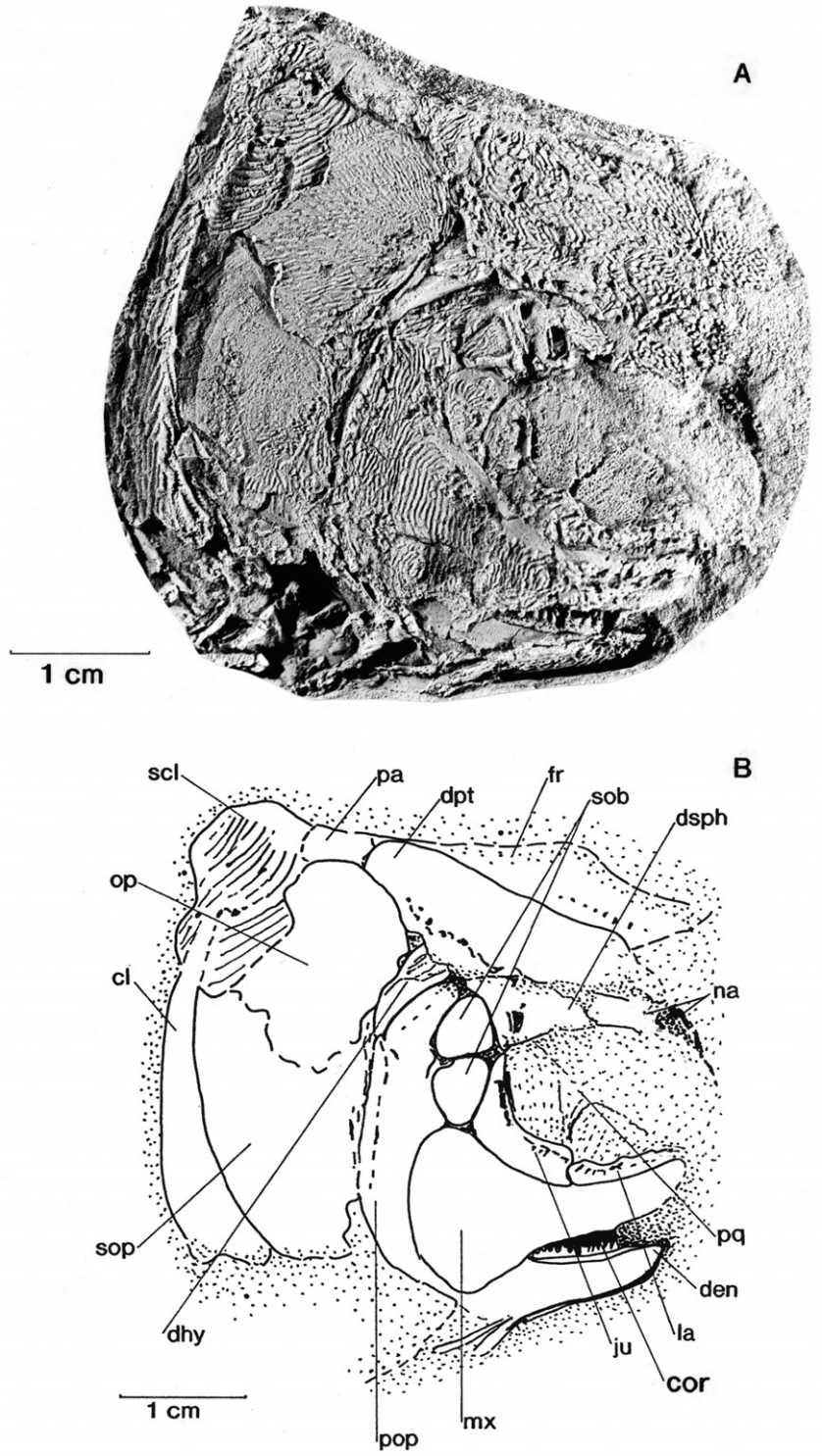


Figure 3. *Blourugia seeleyi,* specimen PB/96/9. **A**, Photograph in lateral view showing suborbital complex in particular. **B**, Camera lucida reconstruction.

numerous vertical or slightly inclined ridges on the body of the blade, and laterally orientated ridges close to the jaw margin.

Dentition (Figs 2 & 4). The occlusal margin of both the maxilla and the mandible consists of a single row of large conical medial teeth (*c.* 1 mm in height) surrounded, at least in certain areas of the jaw margins, by smaller marginal teeth. The dentition pattern seems to be a mixture of the primitive dental pattern and the apparently more advanced type that occurs in *Platysomus* (Poplin & Heyler 1993), characterized by a single row of marginal peg-like teeth. Also present are tooth-like rows of denticles on the dermal bones of the palate (Fig. 8) and the coronoids of the mandible (Fig. 3).

Preopercular (Figs 1–4). The preopercular (Fig. 3B, pop) consists of a single, upright, bar-like, sickle-shaped bone situated between the opercular and subopercular posteriorly, and the suborbitals and maxilla anteriorly. It tapers to form a blunt, rounded ventral margin; the dorsal half of the bone is slightly curved to fit over the posterior margin of the maxilla and contact the suborbitals. The sensory canal system consists of a preopercular canal and a horizon-

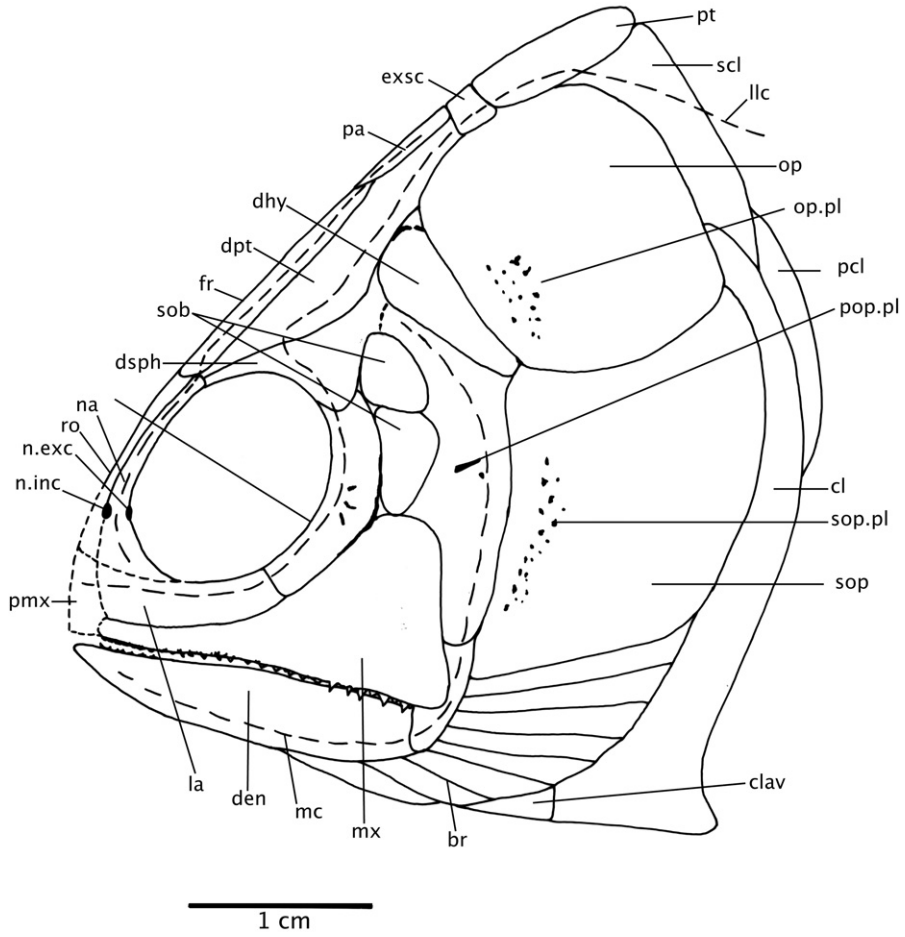


Figure 4. *Blourugia seeleyi,* restoration of the head in lateral view.

tally aligned pit-line groove, which is situated at approximately the inflexion point of the bone; immediately ventral to this a vertical pit-line extends into the preopercular canal. Above the upper horizontal pit-line the preopercular canal continues up to end midway along the dorsal limb and close to the dorsal margin. A series of pits are present close to and also parallel to the posterior margin. The dermal ornament is well developed, and consists of a series of vertically aligned ridges.

Suborbitals (Figs 1, 3 & 4). The suborbital complex (Fig. 3B, sob) consists of two vertically aligned wedge-shaped suborbital bones with rounded margins, situated between the preopercular posteriorly, and the dermosphenotic and the jugal anteriorly.

Palatoquadrate and the dermal bones of the mouth. Portion of the palatoquadrate (Fig. 3B, pq) was observed in specimen PB/96/9. Dermopalatine teeth are visible along the lateral margin of the palatoquadrate in specimen V63 (Fig. 8, ent).

Operculo-gular system

The opercular-gular system is well preserved in a number of specimens, and comprises the dermohyal, opercular, subopercular, branchiostegal rays and the gular plates. The suspensorium is inclined at an angle of approximately 70° to the horizontal. The dermal ornament consists of well-developed ganoine ridges.

Dermohyal (Figs 1, 2, 3 & 4). The dermohyal (Fig. 1B, dhy) is a relatively large, broad, roughly triangular bone, which extends approximately two-thirds of the length of the adjacent opercular.

Opercular (Figs 1–4). The opercular (Fig. 2B, op) is an almost square bone with rounded margins, which is slightly higher than broad and inclined at an angle of *c.* 60° to the horizontal. It is slightly shorter than the subopercular, overlapping and articulating with the subopercular, so that the anterior margin of the subopercular extends dorsally between the dermohyal and the opercular. A series of pits extend along the anterior margin.

Subopercular (Figs 1–4). The largest bone in the skull (Fig. 2B, sop), it is subrectangular with a diagonal length almost as long as the skull roof. The subopercular is dorsally broader than the opercular, and slightly taller. A series of sensory pits are visible along the anterior margin.

Branchiostegal rays (Figs 2, 4 & 6). The branchiostegal ray series (Fig. 2B, br) is not completely preserved in any specimen but appears to consist of 8–10 elongate rays. The posterior-most three are angled diagonally upwards towards the mid-flank region. The dermal ornament consists of ridges running the length of the bones.

The *gulars* are not clearly preserved in any of the study specimens, a lateral gular fragment is preserved in AK/76/7 (Fig. 2B, l.gu).

Lower jaw

The lower jaw was studied in specimens AK/76/7 and PB/96/9. It appears to be well ossified and moderately deep. The dermal ornament is clearly developed in the

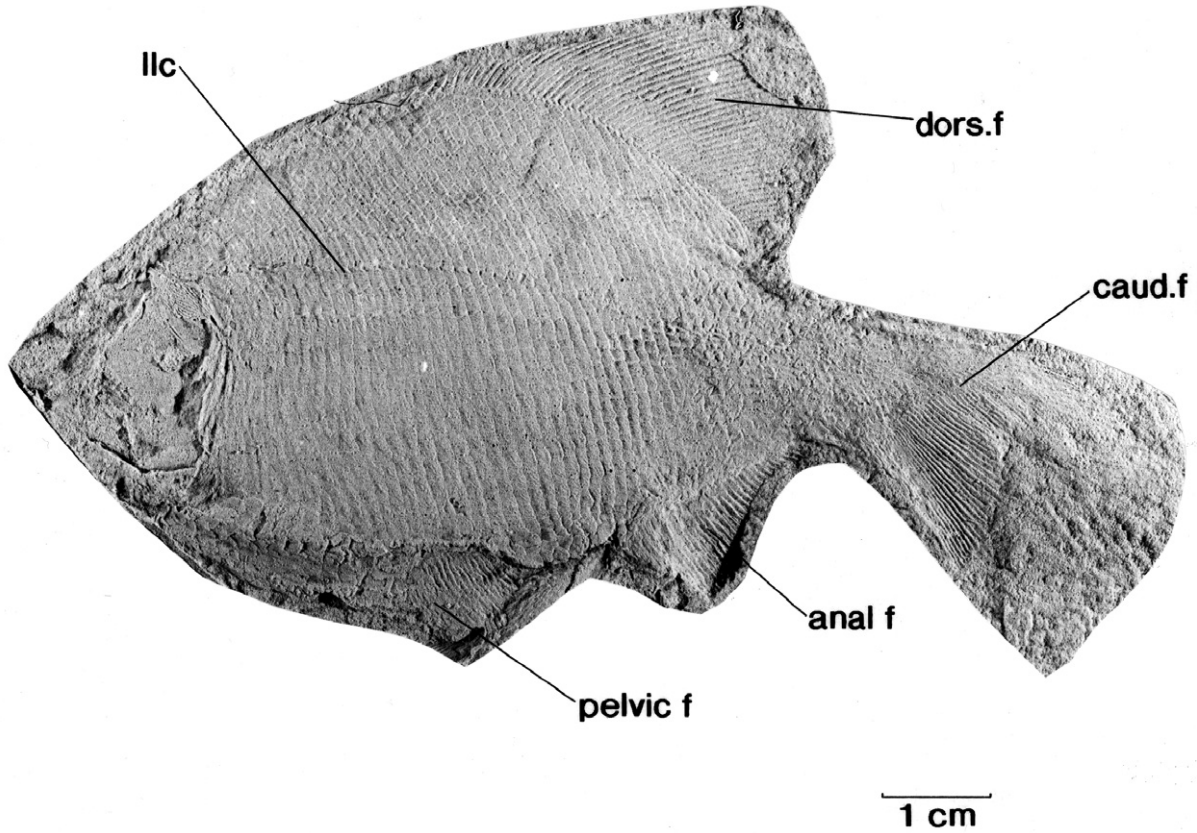


Figure 5. Photograph of *Blourugia seeleyi* specimen AK/76/2 in lateral view, showing the body and fins.

form of narrow, laterally orientated ganoine ridges and short broader denticles. In PB/96/9 a coronoid fragment containing teeth is visible (Fig. 3).

Dentary (Figs 2–4). The dentary (Fig. 2B, den) is fairly Hrobust and deepest in its centre, tapering anteriorly. The depth/length ratio is approximately 1:3.5 (PB/96/9), which indicates a fairly deep dentary relative to fusiform taxa such as *Atherstonia scutata,* and comparable in this regard to other deep-bodied taxa such as *Paramesolepis.* A prominent mandibular sensory line is partially preserved in specimen PB/96/9, represented by a pit-line, usually present on the angular.

Angular (Figs 1, 2 & 4). This bone has a high posterior blade that articulates dorsally with the ventral margin of the preopercular; anteriorly it sutures with the posterior margin of the dentary. In specimen AK/76/7 (Fig. 2) the dentary canal can be seen close to the dorsal margin of the angular where it continues up into the preopercular.

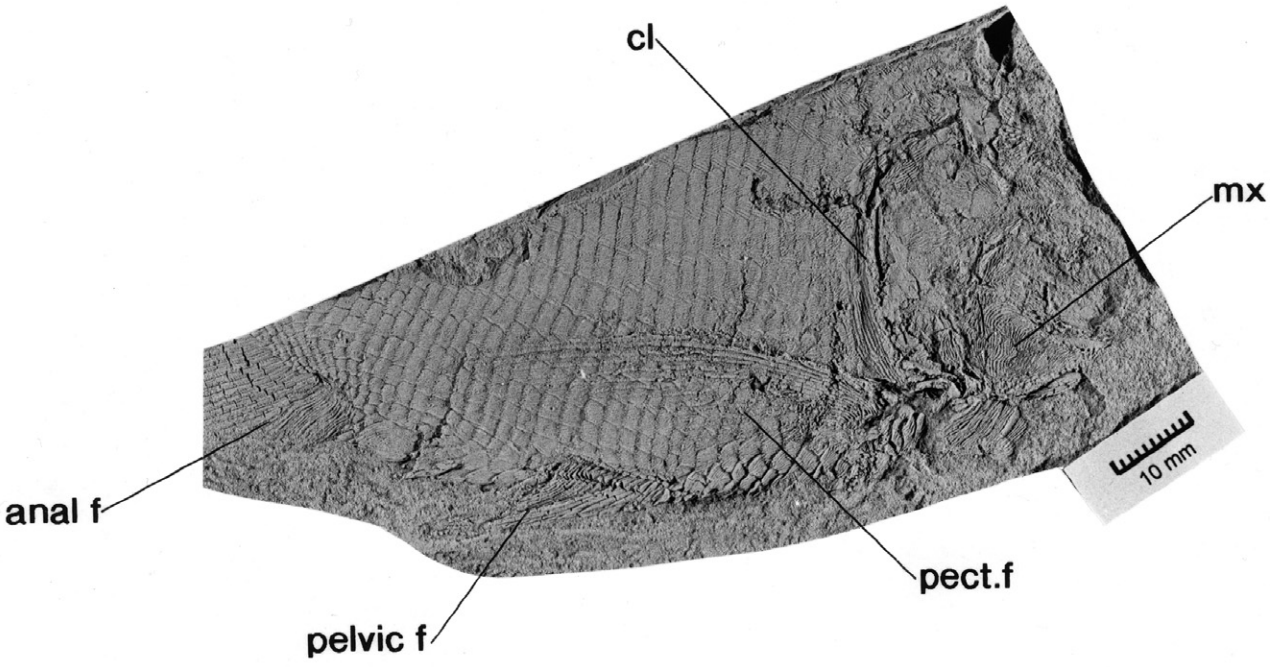


Figure 6. Photograph of *Blourugia seeleyi* specimen PB/96/1 in lateral view, showing pectoral fin and skull region detail.

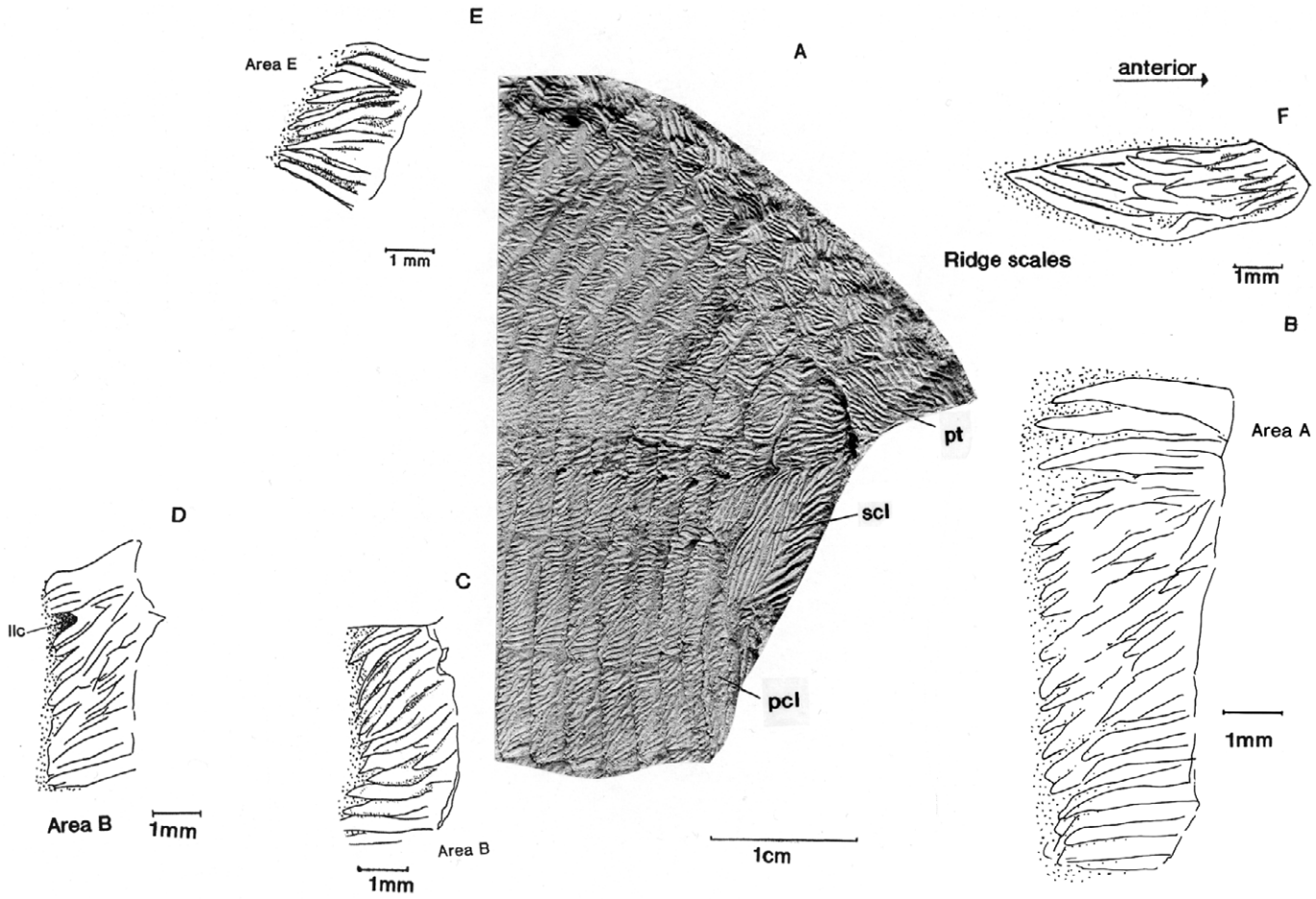


Figure 7. *Blourugia seeleyi* specimen PB/96/13a in lateral view, photograph and camera lucida reconstructions showing scale morphology detail.

Pectoral girdle

The pectoral girdle was studied in specimens PB/96/1 and 5, and consists of paired post-temporals, and a cleithrum, postcleithrum and a supracleithrum on either side of the skull.

Post-temporals (Figs 1, 2, 4, 7 & 8). The left post-temporal (Fig. 1B, pt) is well preserved in PB/96/5 (Fig. 1). It is a large, triangular bone that tapers dorsoventrally towards the posterior margin. It has a straight anterior margin which overlaps the extrascapular The lateral-line canal can be seen close to the ventral margin, where it enters the supracleithrum approximately halfway along the ventral margin of the post-temporal. The lateral-line canal is preceded by a number of pits at the anteroventral border. Dermal ornament consists of ridges horizontally aligned along the length of the bone, and parallel to the inclined dorsal margin.

Supracleithrum (Figs 1–4, 7 & 8). Well preserved (Fig. 1B, scl), but some of the margins are incomplete in a range of specimens. Large with a broad dorsal end where it is overlapped by the post-temporal bone (this overlap is particularly noticeable in Fig. 7), tapering to where it contacts the cleithrum. The lateral-line canal, with associated sensory pits, enters approximately halfway along the posterior margin and exits approximately halfway along the dorsal margin. The dermal ornamentation consists of well-developed ridges, which generally are aligned along the length of the bone, but are horizontally inclined towards the ventral margin (see in Fig. 7).

Postcleithrum (Figs 4 & 7). A narrow, elongated post-cleithrum (Fig. 7A, pcl) bone is visible in specimen PB/96/13a, situated at the posteroventral margin of the supracleithrum. It has well-developed horizontal ridges that constitute the dermal ornamentation, similar to those found on adjacent flank scales, but more robust.

Cleithrum (Figs 1, 3, 4, 6 & 8). The cleithrum (Fig. 3B, cl) consists of a slender, elongated vertical blade and a expanded ventral region anterior to the pectoral fin insertion area. It is almost upright in attitude with a slightly curved tapered dorsal blade, and a horizontally inclined ventral blade, which is not clearly preserved. The dermal ornament on the dorsal blade consists of more than five dermal ridges orientated along the length, and on the anterior surface a series of robust 'studs' or denticles.

Body and fins

The body is on average less than twice as long as it is deep, giving *Blourugia seeleyi* a deep-bodied shape (Figs 5, 8 & 9). The total fish length ranges from approximately 115 mm in AK/76/2 (Fig. 7), to 200 mm in V63 (Fig. 8). The total body length ranges from about 80 mm in AK/76/2, to 125 mm in V63. The head length is contained almost six times within the total body length.

The fins are large compared to those of other deep-bodied lower actinopterygians; all apart from the pectoral fin are triangular. All fins have a number of short fin-rays at the fin insertion immediately anterior to the main body of the fin, with fringing fulcra present on the leading

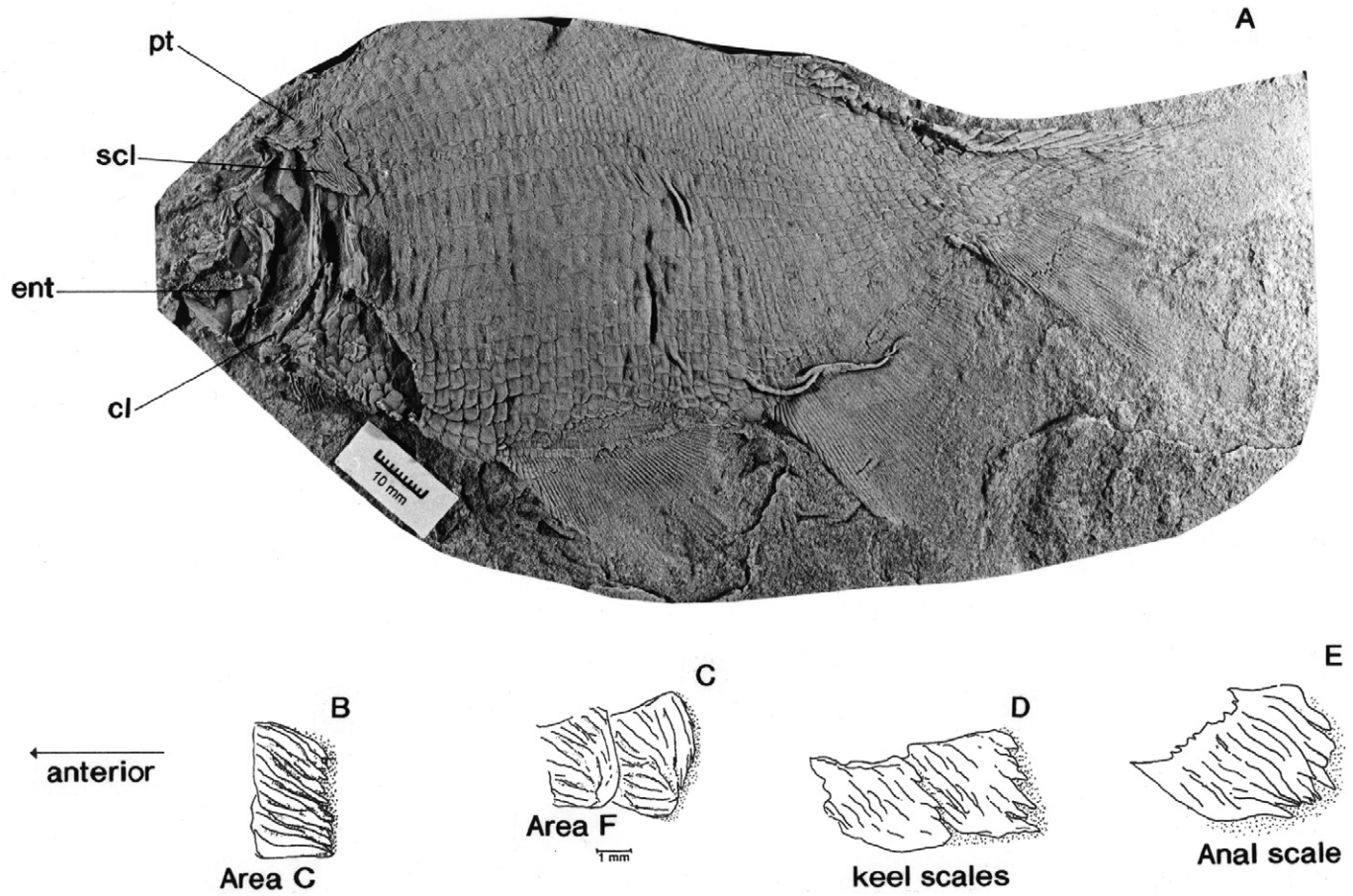


Figure 8. *Blourugia seeleyi* specimen V63 in lateral view, showing body and scale detail.

edges. Fin-rays are numerous and closely articulated throughout their length with unpaired fins and the pelvic fins exhibiting distal birfurcation. The presence of a prominent dermal ornamentation in the form of a rib running lengthways is particularly visible on the pectoral and dorsal fins but also present on the other fins.

Pectoral fin (Figs 6 & 9). Clearly visible (Fig. 6, pect.f) , re-curved over the body in PB/96/1 (Fig. 6), appearing to extend back to the vicinity of the anal fin insertion (scale row *c.* 25), although the distal margin is not preserved it is obviously a very elongate fin. Part of the first or marginal fin-ray is preserved and seems to be a thick, elongate bone. The fin-rays are closely articulated or jointed, apparently throughout the fin length (proximally and distally), with a fin-ray segmentation count of 25–30 close to the leading edge.

Pelvic fin (Figs 5, 6, 8 & 9). The pelvic fin (Fig. 5, pelvic f) is well preserved in V63 (Fig. 8) although the distal margin is not clearly visible. It is a large fin with a fin-ray number of *c.* 50–52. Fin base length is approximately 32 mm in specimen V63, which is particularly long compared to other deep-bodied lower actinopterygians. The fin starts in most specimens at scale row 7, and is located about halfway between the pectoral girdle and the insertion of the anal fin. The fin-rays are up to 30 mm long, with the longest located at the 14th fin-ray.

Anal fin (Figs 5, 6, 8 & 9). This fin (Fig. 5, anal f) is fairly well preserved in V63 (Fig. 8), although the distal margin is not clearly visible. It is a large fin with a fin base length of *c.* 40 mm in specimen V63. This fin starts in most specimens at scale row 26, and comprises more than 60 fin-rays. The fin-rays are up to *c.* 30 mm long, with the longest at the 9th fin-ray.

Dorsal fin (Figs 5 & 9). The dorsal fin (Fig. 5, dors.f) is situated in the anterior half of the body opposite the pelvic fin; it is incompletely preserved in specimen AK/76/2. It is a relatively large fin with a fin-base length of approximately 35 mm and the fin inserted on average at scale row 24. The fin is made up of more than 32 fin-rays, with the longest fin-ray more than 20 mm and the 12th fin-ray from the anterior fin margin. A series of *c.* 7 shorter fin-rays are situated anteriorly on the dorsal fin, preceding the first full length fin-rays of the dorsal fin.

Caudal fin (Figs 5, 8 & 9). The caudal fin (Fig. 5, caud.f) is heterocercal, with an elongated dorsal hypochordal lobe; the longest fin-ray is situated at the 8th fin-ray and is *c.* 45 mm long. The fin starts on average at scale row 41. Caudal fin length (cl) to total fish length (tfl) ratio in specimen V63, cl/tfl = approximately 80:200 mm = 1:2.5, which is relatively large for deep-bodied lower actinopterygians. There is a visible cleft in the tail between the dorsal and ventral lobes situated at approximately the 16th fin-ray.

Scales and squamation

The scale cover and squamation was studied in specimens V63, PB/96/2, 13a and AK/76/2 (see Figs 5–9). The scales are rhombic and have peg and socket articulations, with particularly the mid-flank scales anterior to the pelvic fin elongated and large. The flank scales, particularly in scale cover Areas B to D, undergo a size reduction dorsally

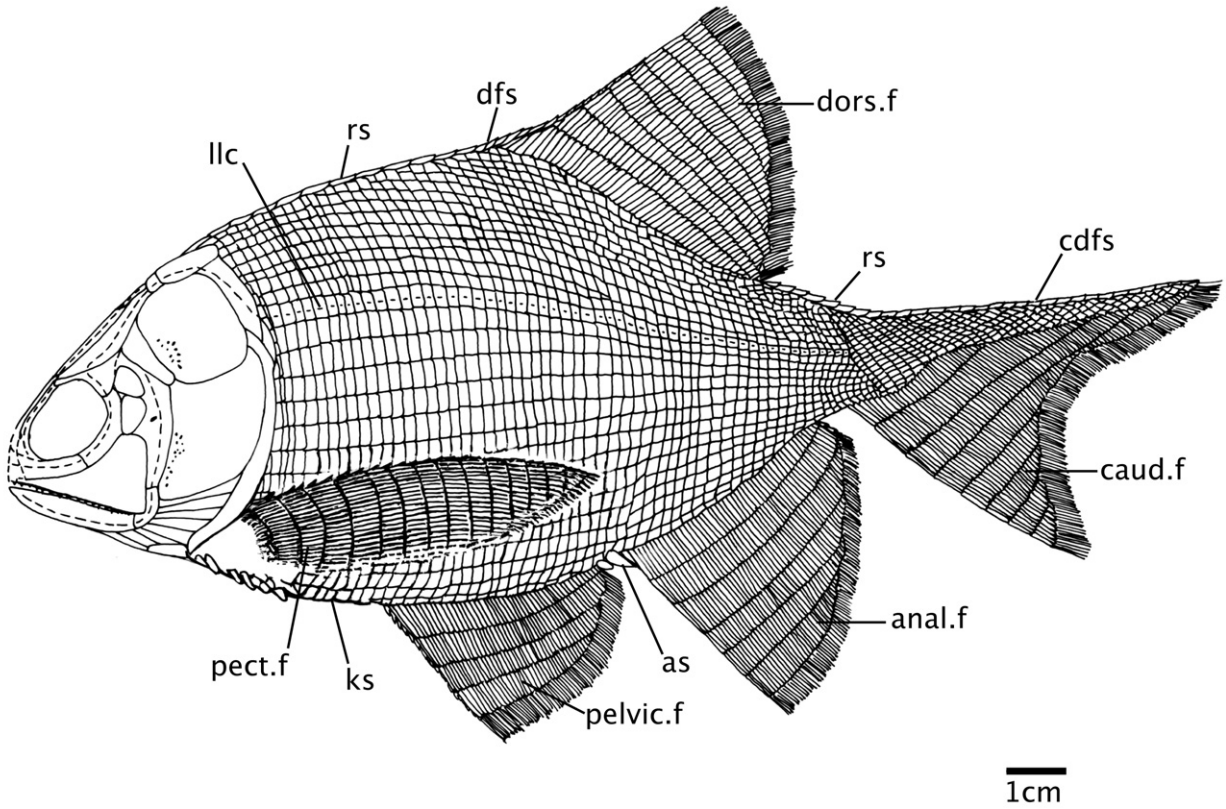


Figure 9. *Blourugia seeleyi,* restoration of fish in lateral view.

and ventrally from the mid-flank region outwards. In PB/96/18 the medial scale morphology was observed, showing a prominent rostrodorsal process or antero-dorsal angle present, this character is typical to the palaeoniscids but absent in deep-bodied forms with specialized squamation such as *Amphicentrum, Platysomus* and the bobasatraniids (Coates 1988; Traquair 1879).

Topographic variation of the *Blourugia seeleyi* scale cover (after Esin 1991)

Area A (Figs 7–9). Area A appears to be a small area immediately behind the pectoral girdle, consisting of 5–7 rows of scales. The scales are elongate rectangular, with a height to length ratio of about 3:1. The anterior and posterior scale margins are steeply inclined. The dermal ornamentation on the free field consists of *c.* 16–18 horizontally inclined ridges, most of which terminate in a posterior denticle.

Area B (Figs 7–9). Scales of this area are situated between the pelvic and dorsal fin insertions. As in Area A, they are also elongate rectangular, with a height to length ratio of about 3:1. The anterior and posterior scale margins are also steeply inclined, as in Area A. The free field consists of *c.* 13–16 horizontally to diagonally inclined ridges in the dorsal two-thirds of the scale, which terminate in *c.* 13 posterior denticles. This dorsal series of dermal ridges is separated from a group of ventral ridges, by a diagonal series of ridges running ventroposteriorly. Below the diagonals there are *c.* 8–12 generally horizontally inclined ventral ridges, some of which can be traced into ridges of the abovementioned dorsal series. The ventral *c.* 5 ridges terminate in posterior denticles.

Area C (Figs 8 & 9). The scales in this region are rectangular, becoming square as they taper progressively off in size towards the caudal fin. The height to length ratio is approximately 2:1 near the Area B region, and almost 1:1 close to the caudal region area D border. The free field consists of *c.* 8–15 diagonally to horizontally inclined ridges that terminate in *c.* 4–12 posterior denticles.

Area D (Figs 5, 8 & 9). Scales in the caudal region are reduced, rectangular to diamond-shaped posteriorly with a h/l ratio of approximately 2:3. A series of *c.* 2–4 faint diagonal ridges and grooves are visible on the free field. In the scales near Area C, 1–2 posterior denticles are visible, with the posterior margin becoming entire further back in area D.

Area E (Figs 7, 8 & 9). Area E is a narrow area consisting of approximately 3–4 rows of reduced scales, situated above Areas A and B. The scales are inclined at a steeper angle than the scales of areas A and B, giving them an almost triangular appearance; however, the h/l ratio of approximately 3:2 is indicative of a rectangular shape. The free field consists of *c.* 4–6 prominent enamel ridges in the upper third to quarter of the scale, and then ventrally in the lower three-quarters to two-thirds of the scale there are *c.* 6–8 sub-horizontal ridges. Posterior denticles are not well preserved but there appear to be *c.* 7–10.

Area F (Figs 6, 8 & 9). This area, situated between the pectoral girdle and the insertion of the anal fin consists of 2–4 rows of scales, reduced in size relative to the scales from areas A and B, with a rounded posteroventral margin. The h/l ratio is almost 1:1. The dermal ornament on the free field consists of c. 8 ganoine ridges, which are more diagonally orientated across the body of the scale than in any of the previous areas, terminating in *c.* 4 posterior denticles.

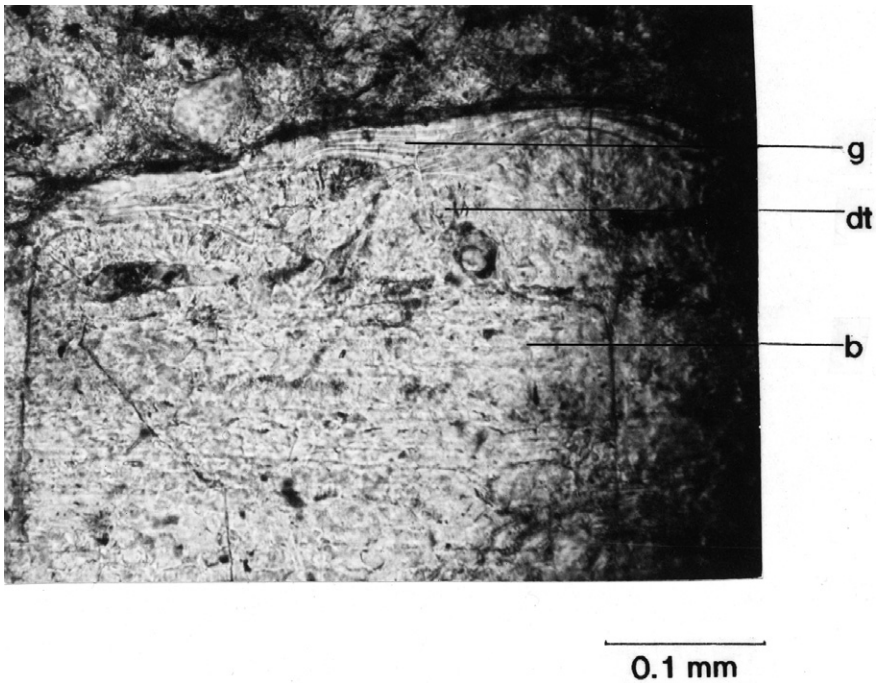


Figure 10. Thin-section photograph of *Blourugia seeleyi* specimen BP/1/4373/35, showing the morphology of the scale layers.

Areas G (Figs 6, 8 & 9). This area consists of *c.* 3–6 rows of very small, slightly elongated, overlapping scales in the regions of the dorsal, pelvic and anal fins. The free field dermal ornamentation consists of *c.* 2–4 diagonal ridges that terminate in *c.* 2 posterior denticles.

Anal scales (Figs 6, 8 & 9). There appears to be one enlarged, ovate anal scale preceding the insertion of the anal fin. The dermal ornamentation is similar to that found on the keel scales.

Ridge scales (Figs 5, 7 & 9). A row of *c.* 12 enlarged triangular ridge scales precede the dorsal fin, with an h/l ratio of approximately 1:3. A row of *c.* 4–5 poorly preserved, enlarged ridge scales are present behind the dorsal fin. The free field ornamentation consists of *c.* 10–12 well-developed parallel ridges along the length of the scales.

Keel scales (Figs 6, 8 & 9). A marginal row of *c.* 10 poorly preserved, enlarged, triangular scales is present between the pectoral and pelvic fins. A further *c.* 5 enlarged, triangular scales are present along the ventral margin between the pelvic and anal fins. The dermal ornament consists of ganoine ridges aligned parallel to the ventral margin.

Basal fulcra

Dorsal fin, basal fulcra (Figs 5 & 9). A series of *c.* 5 small, triangular scales are situated between the ridge scales and the short fin-rays, which constitute the insertion of the dorsal fin.

Caudal fin, dorsal basal fulcra (Figs 8 & 9). A series of *c.* 12–14 elongated and enlarged, acute, triangular scales are situated above the caudal fin.

Caudal fin, ventral basal fulcra (Figs 8 & 9). There appear to be 2–3 triangular scales preceding the insertion of the caudal fin.

Squamation

The scale row configuration can be seen in a number of specimens, including V63 (see Figs 5–9). Scale rows have a slightly sinusoidal arrangement, which can be seen immediately posterior to the pectoral girdle. There is a marked caudal inversion approximately four fin-rays back from the caudal fin insertion.

Scale counting data

Scale rows to pelvic fin (BP/1/4373/36, V63, V64, AK/76/2, PB/96/1, PB/96/8, BP/14373 27):	*c.* 7, 7,7, 7, 7, 8, –.
Scale rows to dorsal fin:	*c.* 25, –, 24, 23, –, 24, 25.
Scale rows to anal fin:	–, 26, *c.* 27, 26, *c.* 25, 26, –.
Scale rows to caudal fin:	*c.* 41, 41, 41, –, –, 42, +40.
Scale rows to caudal inversion:	*c.* 49, 49, 47, –, –, –, +47.

Number of scales in a single scale column:

In front of pelvic fin (V64, PB/96/8, BP/1/4373/27):	*c.* 18, *c.* 22.
In front of anal fin:	*c.* 25, *c.* 27, –,.
In front of dorsal fin:	*c.* 28, *c.* 26, –.
In front of caudal fin:	*c.* 17, –, 17.
In front of caudal inversion:	*c.* 12, *c.* 12, –.

Scale histology

The histological structure of the scale of *Blourugia seeleyi* is shown in Fig. 10. The bottom, bony layer constitutes more than half of the scale thickness. The middle dentine layer appears to laterally overlap in a number of places, but still fairly laterally extensive, with upright branched dentine tubules in a laterally continuous plexus. The ganoine layer is multilayered, and varies in thickness laterally. The scale structure is different to that in *Platysomus,* in which there are only two layers, a compact basal bony layer and upper bone layer (Aldinger 1937). The configuration of the ganoine and dentine layers is similar to the elonichthyid type, and possibly more similar to *Gonatodus* and *Pseudogonatodus* with respect to their variation of

thickness in the ganoine layer. It is certainly very different to the *Playsomus* type of scale histology, indicating that, although deep-bodied, *Blourugia seeleyi* may not be related to *Platysomus.* Clearly more detailed analysis of the scale structure, in relation to that in other taxa, is needed.

Laterosensory system

The laterosensory canal system (Fig. 5, llc) was studied in specimens V63 (Fig. 8), PB/96/2, 13a (Fig. 7) and AK/76/2 (Fig. 5). It consists of a well-developed canal system carried by a single row of flank scales over the entire body length (*c.* 6–7th scale row ventral to the dorsal margin in front of the pelvic fin). The lateral line can be seen as a prominent rounded ridge that underlies the dermal manifestation of the canal. The lateral-line scales (see Fig. 7) consist of an enlarged posterior aperture situated on the posterior scale margin. A number of slit-like canal pores were observed in the mid-flank region in specimen PB/96/2. Sensory line pits were observed on the suboperculum and the operculum?

PHYLOGENETIC POSITION OF *BLOURUGIA* GEN. NOV.

Phylogenetic analyses of the study taxon was carried out using cladistic methods, on the basis that most recent comprehensive lower actinopterygian phylogenies utilize cladistics to analyse interrelationships (Gardiner 1984; Gardiner & Schaeffer 1989; Coates 1999; Poplin & Lund 2000; Cloutier & Arratia 2004; Gardiner *et al.* 2005)). The comprehensive lower actinopterygian phylogenetic analysis of Gardiner & Schaeffer (1989) (see Bender 2001, fig. 14) was used as a basis for phylogenetic analysis, since their analysis largely utilizes 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. In addition, the Gardiner & Schaeffer (1989) analysis is probably the most comprehensive phylogenetic basis for examining lower actinopterygian interrelationships, although, as indicated by Cloutier & Arratia (2004), a number of the taxa are based on poorly known characters.

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 (Bender 2001, fig. 14) 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 characterized 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 Lower Beaufort Group taxon *Kompasia*), and the other to the Neopterygian Groups. According to Gardiner & Schaeffer, both transformation series are rooted to the *Watsonichthys–Amblypterus* complex. The stem-group neopterygians are defined by Gardiner & Schaeffer 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 *Blourugia* gen. nov. 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) indicated that the stem-neopterygians diverged earlier than indicated by Gardiner & Schaeffer (1989), and on that basis *Blourugia* could be termed a stem-neopterygian.

Blourugia seeleyi shares the following Gardiner & Schaeffer (1989) cladogram III characters (Bender 2001, fig. 14: 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. 6. Dermosphenotic in contact with nasal bone. 8. One or two pairs of extrascapulars. 9. Two infraorbitals including a lacrymal and jugal, and no postorbital. 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, I, K, L and M is shared by *Blourugia*: Node B Acrodin crown on all teeth and separated from the collar enamel of the tooth shaft. Node C. Fringing fulcra on leading rays of all fins. Node D. Supra-angular on mandible. Node E. The presence of suborbital bones. Node H. 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. Node K. Suspensorium more or less vertical. Preopercular reduced and sickle-shaped. Node L. Snout blunt and rounded. Node M. Body deep and laterally compressed; flank scales deepened.

Blourugia seeleyi shares no further characters at any subsequent nodes and is therefore rooted at Node M, and is thus contained in the *Bobasatrania–Dorypterus* transformation series of the Gardiner & Schaeffer (1989) cladogram III (Bender 2001, fig. 14), which is a side-branch separate from the main chondrostean–neopterygian lineage. Accordingly, *Blourugia* 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 *Moytho-*

masia, but basal to stem-neopterygian taxa such as *Australosomus, Birgeria, Palaeoniscum* and *Perleidus.*

Bender (2001, 2002) suggested that a revision was required of the original Gardiner & Schaeffer (1989) cladogram III, in particular revision of all the nodes contained on the *Bobasatrania–Dorypterus* side-branch, including the *Platysomus* Group node (Bender 2001, fig. 15). Recently significant new cladistic analyses of lower actinopterygians have included taxa on the *Bobasatrania–Dorypteryus* side branch (Cloutier & Arratia 2004; Gardiner *et al.* 2005), although no Carboniferous or Permian deep-bodied taxa have been incorporated. For this reason these analyses have not been utilized within the framework of the present study. Node M is unchanged from the original Gardiner & Schaeffer 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 that 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 a with peg-and-socket articulation and anterodorsal angle, and shares the stem-neopterygian presence of a dermopterotic, and suborbitals.

The *Blourugia* characters can be summarized as follows:

- *Blourugia seeleyi stem-actinopteran characters*: elongate body lobe of the tail; large pelvic fin.
- *Blourugia seeleyi stem-neopterygian characters*: dermopterotic present; less than 12–13 branchiostegal rays; suborbitals present; subopercular taller than opercular; preopercular upright and sickle-shaped; maxilla postorbital blade reduced.
- *Blourugia seeleyi specialized characters*: elongate pectoral fin jointed throughout.

What these study taxon character sets show is that *Blourugia* displays more stem-neopterygian than stem-actinopteran characters. On the basis of the earlier, more traditionally based lower actinopterygian studies of Gardiner (1967) and Schaeffer (1973), *Blourugia seeleyi* appears to be related to members of a group of mostly Carboniferous forms that 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 deep-bodied early actinopterygian is described from the Late Permian lower Beaufort Group of South Africa. *Blourugia seeleyi* is part of a Beaufort Group, Late Permian (Tatarian) high-latitude, freshwater ichthyofauna which consists essentially of extinct lower actinopterygian taxa. Phylogenetic analysis is based on a comprehensive phylogenetic study conducted by Gardiner & Schaeffer (1989), revised by Bender (2001, fig. 15) which reveals that *Blourugia,* as a deep-bodied lower actinopterygian form belongs to Gardiner & Schaeffer's (1989) Platysomus Group. On the basis of its marginal dentition and no crushing toothplates, *Blourugia* is more closely allied to *Platysomus* and similarly dentitioned deep-bodied taxa; and basal to the stem-neopterygians such as *Australosomus, Palaeonisum* and *Perleidus.* The platysomid-like deep-bodied lower actinopterygians form a speciose group, including Permo-Carboniferous taxa from Australia, China, England, Europe, North America, Russia, Scotland and South Africa. *B. seeleyi* has a deep body and deepened flank scales, marginal dentition and no crushing toothplates and thus is contained within the *Platysomus* Group, and can be more closely allied to the 'platysomid-like' taxa such as *Platysomus* on the basis of its marginal dentition and absence of crushing toothplates, but basal to more advanced lower actinopterygian deep-bodied forms such as *Bobasatrania, Ebenaqua* and *Dorypterus,* in which the maxilla is free from the cheek bones.

It is a privilege to participate in this volume honouring the late James Kitching who was indeed a constant source of inspiration. Thanks are due to the referees for their time, commitment and invaluable input, and to the journal editors for all their efforts; as this article was part of a Ph.D. study, I would like to thank project supervisors Bruce Rubidge and John Long for their invaluable support and advice over a number of years. I would also like to thank Mike Coates and the late James Kitching for their invaluable comments and advice: James Kitching forever willing to share his considerable knowledge of the Karoo and its fossil treasures, Mike Coates for providing essential fish-morphology guidance to me throughout the duration of the Ph.D. study. Thanks to my employers, the Council for Geoscience, including the directors and other colleagues, for their support; appreciation is also expressed to colleagues at the BPI Palaeontology, Wits University, for their support and assistance. Thanks also to Lionel de la Harpe at Wilgerbosch, and JP and Hester Steynberg at Ganora, for their hospitality, help and enthusiasm; Geoscience Museum Artist Anke Raath, and artists Marinda Smith and Mike Tobias, for providing the diagrams; and last but not least Bernice McLean for invaluable field assistance.

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
cdbf	caudal fin dorsal basal fulcra
clav	clavicle bone
cl	cleithrum
cor	coronoid
cvbf	caudal fin basal fulcra
dbf	dorsal fin basal fulcra
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 scalela – lachrymal
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 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 bone
ssoc	supraorbital sensory-line canal
sop	subopercular bone
sop.pl	subopercular sensory pits and pit-line grooves

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