TAPHONOMY OF ACANTHODIANS FROM THE DEVONIAN BUNGA BEDS (LATE GIVETIAN/EARLY FRASNIAN) OF NEW SOUTH WALES

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Several articulated, but incomplete, acanthodians from the Bunga Beds (late Givetian/early Frasnian) of the southern coast of New South Wales are tentatively identified as ischnacanthids. Heads are missing from all three prepared specimens. They exhibit the following characters: two dorsal fin spines; long, slender scapulocoracoids; slender, relatively deeply inserted, unpaired fin spines; minute scales with a fairly smooth, flat, crown; and an increase in size of normal body scales towards the tip of the tail. The fish are preserved in black, finely laminated shales, which were probably deposited as deep water, lacustrine sediments. The rarity, burial conditions, and headless state of the Bunga Beds acanthodians indicate that they might have died in shallow water, sunk to the bottom, refloated by gas-induced buoyancy, with the heads lost while drifting out to deeper waters, where the bodies finally sank to a scavenger-free, anaerobic substrate.

KEY WORDS: Acanthodians, ischnacanthids, taphonomy, Bunga Beds, Givetian/Frasnian.

INTRODUCTION

Most descriptions of Devonian acanthodian fish are based on specimens generally interpreted to have been preserved after a mass mortality. The classic Devonian localities that have yielded articulated acanthodians are in the Welsh Borderland, and the Caithness region and Midland Valley of Scotland. These include: Turin Hill (Angus, Scotland), with finely bedded, calcareous and micaceous shales of the Lower Old Red Sandstone; Achanarras (Scotland), with lacustrine, calcareous laminites of the Middle Old Red Sandstone; and siltstone lenticles in the Lower Old Red Sandstone (Lochkovian Ditton Group) in Wayne Herbert quarry, south-west Herefordshire. The first of these localities, at Turin Hill, is part of the Lower Devonian Arbuthnott Group, interpreted as lacustrine deposits (Mykura, 1991). The fish from the Middle Devonian Achanarras beds, “...were preserved following mass mortalities induced by algal blooms, mixing of waters by storms and lake overturn” (Trewin, 1986, p. 21). The fish at Wayne Herbert, are thought to be fluvial species trapped by the drying up of the body of water in which they lived (Miles, 1973).

Devonian acanthodians have also been described from a lagoonal deposit in the Lower Devonian Delorme Formation, Northwest Territories, Canada, again interpreted as a mass mortality deposit (Bernacsek and Dineley, 1977). Acanthodians from the Frasnian lacustrine black shales of Mt Howitt, Victoria, have also been interpreted as a mass mortality deposit, perhaps caused by gaseous volcanic infusions (Long, 1982).

The fish described here were collected from the late Givetian/early Frasnian Bunga Beds (Figure 1), which Fergusson et al. (1979) interpreted as lacustrine flyschoid deposits. The Bunga Beds fauna is impoverished, and includes a shark Antarcilamna prisca, a
Figure 1 Locality map of collection sites of Bunga Beds acanthodians; CPC16996 was collected from site A; CPC30433, 33499 and 33500 were collected from site B.

holoptychoid rhipidistian, disarticulated acanthodian remains and abundant plants (Young in Fergusson et al., 1979; Young, 1982).

TAPHONOMY OF ACANTHODIANS

Few taphonomic studies of Devonian acanthodians have been reported, although Long (1982) gives a brief comparison of the burial histories of four Late Devonian fish localities in Victoria, including the Mt Howitt assemblage. A comprehensive study by Zangerl and Richardson (1963) on the palaeoecology of the Pennsylvanian (Carboniferous) Mecca and Logan Quarry black shales includes descriptions of acanthodiiform remains. Most descriptions of articulated acanthodians from Devonian deposits are based on very well preserved fish. However, a greater number of acanthodian species are known only from isolated scales, spines and/or teeth.

To determine the natural post-mortem disintegration pattern of Devonian acanthodians requires comparisons with the disintegration of modern fishes and other vertebrates,
consideration of skeletal architecture (both internal and external), and a survey of the state of preservation of well articulated acanthodians from various lithologies. Schäfer (1972) carried out detailed investigations of the death, disintegration and burial of modern marine fishes, and showed that temperature is the most important factor determining the fate of a carcass (see also Elder and Smith, 1988). Low temperatures tend to retard decay of soft tissues and bacterial proliferation. At high temperatures the rate of decomposition of gut contents is accelerated, generating gases faster than they can escape from the carcass. A corollary of this is that the propensity to refloat also depends on body shape; i.e. the greater the surface area to volume ratio, the faster gas can escape. Carcass buoyancy may also be controlled by the presence or absence of gut contents. Temperature, then, affects the sequence and rate of disintegration of the carcass: the pattern of disintegration differs depending on whether the carcass remains lying on the substrate, or is floating at the surface. Most fish carcasses undergo some transport between death and burial, if only by sinking to the substrate. If fermentation of gut contents does cause refloating, the duration of post-mortem drift will depend on size (Schäfer, 1972).

It is difficult to find an enlightening modern analogue for acanthodians; the dermal skeleton is perhaps generally comparable to that of modern (neoselachian) sharks, but much of the internal skeleton of acanthodians was bony rather than cartilaginous. From the evidence provided by fossil remains, it appears that the integument and scales of acanthodians maintained integrity better that those of sharks after death. Compared with shark scales, which may be shed in life, non-shedding acanthodian scales generally have a much more robust, deep base, with many bundles of Sharpey's fibres anchoring the scales in the integument. Isolated patches of acanthodian scales are often preserved in their original arrangement (Woodward, 1906). Allowing for these differences, sharks are still the closest modern fish to an acanthodian in form and structure.

Schäfer (1972) observed the following pattern of disintegration for the carcass of the shark, Galeorhinus galeus: the carcass sank to the bottom ventral side down, subsequently refloated (with the head and tail hanging down), then sank back to the substrate; pieces of skin fell off and decomposed, leaving heaps of placoid scales; the abdominal cavity broke open; after 20 days, some of the rays of the paired and unpaired fins remained, along with jaw cartilages and oral teeth, and scattered heaps of placoid scales; the vertebrae had rolled away. A similar sequence involving refloating of the carcass occurred with many other modern fish observed. Schäfer's observations of the disintegration of the sea scorpion, Myxoccephalus scorpius, noted that in some instances the neurocranium was missing, as the skull resurfaced more frequently than other parts, and drifted away.

In considering the skeletal structure of acanthodians, it is convenient to separate them into the three orders - Climatiiformes, Ischnacanthiformes and Acanthodiiformes. All three orders have similar squamation, but differ in the robustness of the jaw and fin spine attachments. In Climatiiformes and Ischnacanthiformes (and also some of the more primitive Acanthodiiformes), the palatoquadrate cartilage did not articulate with the endocranium. In most Acanthodiiformes (e.g. Acanthodes and Howittacanthus Long, 1986) there are two otic articulations between the palatoquadrate and the braincase (Long, 1986a). Climatiiformes and Acanthodiiformes have tighter articulation between the palatoquadrate and mandible than Ischnacanthiformes. Climatiiformes (except culmacanthids) have the internal scapulocoracoid fused to the pectoral fin spine, unlike all other acanthodians; the climatiids' other fin spines have only a short inserted portion, while on all other acanthodians they are more deeply inserted.

Taking into account this information, it is possible to speculate on the taphonomic processes likely to have affected the preservation of acanthodians. If temperatures are low, most fish would probably remain on the substrate and, in the absence of scavengers
or currents, might be preserved in a well articulated state. If the temperature were higher, and the fish had gut contents, the carcass might refloat; this would have been less likely for slender, fusiform/anguilliform acanthodiiformes than for deeper bodied fish. Hecht (1933), in his experiments on the rate and order of decay of dead fish, noted that although fusiform fish carcasses refloated, those of eels stayed on the bottom. If an acanthodian carcass refloated, the lower jaw would be likely to disarticulate first, particularly in ischnacanthids with their weaker jaw articulation. Both jaws would probably detach from the endocranium in Ischnacanthiformes and Climatiiformes, whereas the otic articulations of Acanthodiiformes would be expected to hold the jaws and braincase together for a longer period. The remains of the head might be next to detach, perhaps aided by tearing in the region of the gills, with release of gas, and subsequent sinking of the carcass.

The state of preservation of fossil acanthodians thus would be expected to depend on the mobility between the skeletal parts. It should be assumed that most collections result from biased sampling of fossils, as well-preserved specimens were inevitably collected first. This is probably true of older museum collections, which often comprise much material sold to the museums by professional collectors. A survey of specimens from sites mentioned earlier, for which some details (often minimal) have been published (e.g. Woodward, 1891; Watson, 1937; Miles, 1973; Bernacsek and Dineley, 1987; Long, 1983), indicates that the Devonian fossil record of acanthodians appears to conform with the hypothetical disintegration schedules described earlier. The more advanced Acanthodiiformes Acanthodes and Howittacanthus are often preserved with heads still attached, reflecting the tighter articulation of the skeletal elements of the head, and perhaps also a lower propensity to refloat post-mortem. Climatiiformes and Ischnacanthiformes are more often found without the head, or with only some parts thereof intact. Ischnacanthiformes are often preserved with the lower jaw missing; they have the weakest jaw articulation of acanthodians. As a corollary to this, several ischnacanthids are described from isolated dentigerous jaw bones (e.g. Long, 1986b): the lack of ossification of most of the internal skeleton was undoubtedly also a contributing factor to this mode of preservation.

SYSTEMATIC PALAEONTOLOGY

Class Acanthodii

Order Ischnacanthiformes?

Family Ischnacanthidae?

Ischnacanthis? gen. et sp. indet. (Figures 2–8)

1979 ‘acanthodian species ... may be a diplacanthid or an ischnacanthid, ...’, Young in Fergusson et al., p. 102

1986 ‘articulated acanthodians ... provisionally identified as ischnacanthids ...’, Long, 1986a, p. 1


1994 ‘diplacanthid? gen. et sp. indet.’, Davis, p. 65

Diagnosis

Ischnacanthis? acanthodians with relatively deeply inserted fin spines, and longitudinally striated base of insertion; exserted portion with four or five smooth, equally wide ribs per side; anterior dorsal fin spine shorter than posterior dorsal fin spine. Pelvic fin spines
short and straight. Scapulocoracoid high and slender. Body scales range from 0.05 to 0.3 mm wide, with relatively smooth, flat crown; scale size increases towards tip of tail.

Remarks
The headless state of the specimens precludes precise classification. However, the features common to all three prepared specimens (somewhat fusiform body, relative proportions of fin spines, shape of scales, increase in scale size towards the tip of the tail, and zonation of caudal squamation) indicate conspecificity. These features, plus the presence of two dorsal fin spines and the lack of fusion of the scapulocoracoids to the pectoral fin spines, indicate the fish are probably ischnacanthid acanthodians.

Material
Four specimens (CPC 16996, 30433, 33499, 33500 - the latter unprepared) lacking heads, and antero-ventral part of body including pectoral fins and spines. The fish are preserved in dark, finely laminated shales, which have been deformed by lateral compression. The fish are reposited in the Commonwealth Palaeontological Collection, Canberra (CPC); AMNH refers to specimens from the American Museum of Natural History, New York.

Locality and Age
Bunga Beds, Boyd Volcanic Complex, Lachlan Fold Belt; late Givetian/early Frasnian, Middle/Late Devonian. The specimens were collected near Bunga Beach, on the north side of Bunga Head northeast of Bega, New South Wales, Australia: GR 2353E 59494N Murrah 1:50000 topographical sheet, approximately 36°35'S 150°06'E (Fergusson et al., 1979; see Figure 1). CPC16996 was collected in 1974 or 1977, while the other three specimens were collected in 1979, downhill from CPC16996, and along strike at a similar, horizon (G.C. Young, pers. comm., 1995).

Description
CPC16996, preserved in part and counterpart (Figures 2, 3), is a laterally compressed, articulated fish, lacking the head and ventral anterior trunk region. The preserved portion is 78 mm long and 23 mm deep at the level of insertion of the posterior dorsal fin spine. The ratio of distance between anterior and posterior dorsal fins (APL) to estimated body depth (BD) at level of anterior dorsal fin spine, hereafter designated APL:BD, is 0.97. Fragments of two dorsal fin spines, the anal, and a fragment of a pelvic fin spine are preserved; the anal and posterior dorsal fin spines are inserted approximately opposite one another. As noted by Young (pp. 102, 103 in Fergusson et al., 1979), the anterior dorsal fin spine is slightly shorter than the posterior dorsal. The spines range from 17 mm (anal) to 22 mm (posterior dorsal) in length. Although not well preserved, the spines are fairly straight, with four or five longitudinal ribs of uniform width, visible on each side (Figure 3a, b). The inserted section of the spine (Figure 3b) bears 10 to 12 narrow, closely spaced, longitudinal striations on each side (Young, in Fergusson et al., 1979). A sediment cast of the scale cover from the right side of the body has been preserved in the part (Figure 3c). A lateral line runs above mid-flank (Figure 2a, b); there are no special scales lining it. The normal body scales increase in size towards the tail. Scales from the main lobe of the tail (Zone Z1 cf. Miles, 1970) are 0.3 mm square, while those from the central flank at a level approximately midway between
Figure 2 Incomplete ischnacanthid? gen. et sp. indet. CPC16996 from the Bunga Beds, south coast of New South Wales, in part (a) CPC16996a, showing the external view of the squamation of the right side, and counterpart (b) CPC16996b, with the impression of the right side. Stippling indicates areas with scale impressions; light lines indicate general direction of scale rows; scale bar = 5 mm. Abbreviations used in figures 2, 4, 6: af: anal fin spine; adf: anterior dorsal fin spine; c: coprolite; ll: main lateral line; pdf: posterior dorsal fin spine; pf: pelvic fin spine; sc: scapulocoracoid.

the dorsal fin spines are 0.1 mm square. The scales have smooth, diamond-shaped crowns (Figure 3c), but poor preservation precludes histological examination. Fin webs with minute scales (less than 0.1 mm long) are present on all three preserved spines (Figure 3d).

Specimen CPC30433 (Figures 4, 5), previously figured in Rich and Rich (1993, plate 58), has left and right sides preserved. The specimen is 53 mm in length, and 12 mm deep at the level of the posterior dorsal fin spine. The trunk is not as deep as CPC16996 (APL : BD ratio 1.3). The head and pectoral fins are missing, but the scapulocoracoids (Figure 5b, c), both dorsal fin spines, and the pelvic and anal fin spines are preserved. The ornamentation of the fin spines is the same as on CPC16996, the inserted portion of the anal fin spine on CPC30433 (Figure 5d) having seven well preserved narrow,
Figure 3 Incomplete ischnacanthid? gen. et sp. indet. CPC 16996 from the Bunga Beds, (a) counterpart CPC16996b, mostly preserved as an impression of the right side above a possible coprolite (labelled c), (b) anterior dorsal fin spine and part of squamation, CPC16996b, (c) part of squamation from the caudal lobe of the tail on CPC16996a (arrow indicates rostral direction), and (d) broken anal fin spine, with part of fin web squamation preserved, CPC16996b. Scale bar = 5 mm in (a), 1 mm in (b and d), and 0.1 mm in (c).
Figure 4 Incomplete ischnacanthid? gen. et sp. indet. CPC30433 from the Bunga Beds, (a) CPC30433a, with right side preserved, and (b) CPC30433b, with left side preserved. Scale bar = 5mm.

parallel striations. Fin webs are preserved on the anterior and posterior dorsal, and anal, fin spines. The pelvic fin spines are straight and short (length 6 mm) versus a length of 11 mm for the anal fin spine. Both dorsal fin spines are incomplete. The scapulocoracoids are incomplete (Figure 5b, c), but are high, slender bones, with the dorsal region of the scapula somewhat flattened laterally (Figure 5b, right element), becoming narrower centrally, then flaring out in the ventral section. Pectoral fin spines are not preserved, and presumably these were not fused to the scapulocoracoids.

The lateral line runs approximately mid-flank (Figure 5a), and normal body scales increase in size towards the tail tip (Figure 5e). The scales are small, the largest about 0.3 mm in length (Fig. 8d, e), and the smallest scales of the fin webs with length less than 0.05 mm. Preservation of the posterior dorsal fin web (Figure 5a) indicates a ventral notch.

The third specimen, CPC33499, (Figures 6, 7) is preserved as left and right sides and is smaller (length 40 mm), and more slender than the other specimens (APL : BD ratio 1.7). Anterior and posterior dorsal, anal, and pelvic fin spines are preserved, the anterior dorsal fin spine present only on the counterpart. As on CPC30433, the pelvic
Figure 5 Ischnacanthid? gen. et sp. indet. CPC30433, from the Bunga Beds (a) part CPC30433a, with left side preserved. (b) anterior region of CPC30433a, showing both scapulocoracoids, (c) left? scapulocoracid in CPC30433b, (d) part of inserted portion of the anal fin spine, and bases of surrounding squamation, on CPC30433a, and (e) tail of CPC30433a with well articulated squamation (scale bases showing). Scale bar = 5 mm in (a), 1 mm in (b-e).
fin spines are straight and short. The tail squamation of CPC33499 is very well preserved, with clear zonation (Figure 7a-c); the scales increase in size towards the tail tip. Following Miles’ (1970) zonation plan: Z1 continues to the tip of the tail, with Z2 and Z2” tapering out before the tip, Z3 and Z4 form one continuous zone; the subsidiary zone Z3” is not present.

Discussion

Precise identification of the Bunga Beds acanthodians is precluded by the lack of heads and poor preservation of scales on the specimens. However, as noted earlier, the features shared by all three prepared specimens indicate they are probably conspecific. Climatiiformes and Ischnacanthiformes have two dorsal fin spines. The presence of apparently smooth-crowned scales, two dorsal fin spines, and scapulocoracoids apparently not fused to the pectoral fin spines, would once have led to classification of the Bunga Beds fish as "Ischnacanthus sp.", because all Climatiiformes were thought to have the scapulocoracoid fused to the pectoral fin spine. However, Long (1983) established the new family Culmacanthidae (Order Climatiiformes, Suborder Diplacanthoidae) for the new species Culmacanthus stewarti that, like ischnacanthids and the Bunga Beds fish, has pectoral fin spines not fused to the scapulocoracoid, whereas in the family Diplacanthidae they are fused. The only synapomorphy of ischnacanthiforms is the dentigerous jaw bones, although Long (1986b) proposed that Acanthodopsis, which has dentigerous jaw bones,
Figure 7 Bunga Beds ischnacanthid gen. et sp. indet. CPC33499, (a) tail on CPC33499b, with well-articulated squamation, (b) tip of the tail on CPC33499a (scale bases showing), (c) dorsal scale rows between the posterior dorsal fin spine and the tail, on CPC33499b, and (d) pelvic fin spines on CPC33499a. Scale bar = 1 mm on (a,b,d) and 0.1 mm on (c).
might be an acanthodiiform. A comparison of the features of the Bunga Beds acanthodians with those of the groups to which they might be assigned (i.e., Order Ischnacanthida, or Order Climatiida, Suborder Diplocanthonoidea, Family Culmacanthidae), follows:

**Body shape**

The relative depth of the body of the Bunga Beds acanthodians is variable, with the APL:BD ratio 0.97 for the largest fish CPC16996, 1.3 for the medium-sized CPC30433, and 1.7 for the smallest, CPC33499. The average ratio for several specimens of the fusiform ischnacanthid, *Ischnacanthus gracilis* (AMNH7773, 7775, 7776) is 1.5, on Watson’s (1937, figure 10) reconstruction of a ‘medium-sized’ *I. gracilis* (i.e., length 15 cm) it is 1.8, and on assigned to three Canadian specimens *I. gracilis* (Bernacsek and Dindey, 1977, pl. 6) the ratio is 1.0, 1.2 and 1.2, while that for the deep-bodied *Culmacanthus stewarti* is 0.91, as measured on the holotype (Long, 1983, figure 1A). No clearcut conclusions can be drawn from these widely varying values, but they can be interpreted in several ways: 1.) CPC16996 is a different species from the other two Bunga Beds fish, 2.) the differences are due to presence/absence of gut contents, and distortion due to gas distension, or 3.) the ratio varies with the ontogeny of the fish.

**Fins and fin spines**

The partial preservation of the fin webs makes it impossible to state categorically that the webs were notched proximally, like those of *Culmacanthus*, or not (as in *Ischnacanthus*). The anal, and both dorsal fins have remnant fin webs on all three Bunga Beds fish. Watson (1937) found no evidence of a fin web on the anterior dorsal fin of *I. gracilis*, but several Canadian examples have this feature (Bernacsek and Dineley, 1977), and *Culmacanthus* has fin webs on all spines. The ornament of the fin spines in CPC16996 and 30433 closely resembles that of the form taxon *Striacanthus sicaeformis* Hills 1931, and also the fin spines of *Culmacanthus*. The ischnacanthids *I. gracilis* and *Poracanthodes menneri* Valiukevicius, 1992, have spines with longitudinal ribs, with the anterior rib usually markedly wider than the others. AMNH7773, however, has fin spines with five longitudinal ribs of equal width. The number of ribs comprising the fin spine ornament depends on the spine position, and on the age of the fish (Valiukevicius, 1992, p. 205). Gross (1971, abb. 25) illustrated the increasing depth with age of spines of the ischnacanthid *Gomphonchus sandelensis*. No description has been given of the ornament of the inserted base of the spines for any of the articulated ischnacanthids *Ischnacanthus*, *P. menneri*, or *Uraniacanthus* Miles, 1973. One of the pectoral fin spines of the specimen of *I. gracilis* figured in Bernacsek and Dineley (1977, pl. 5) shows striations on the inserted segment similar to those on the Bunga Beds fish. The position of the fin spines is similar on all Bunga Beds fish, on *Ischnacanthus*, and also on *Culmacanthus*. The fin spines on the Bunga Beds specimens have a similar ratio of inserted to total spine length as the spines on *Ischnacanthus*; pelvic fin spines on CPC30433 and CPC33499 are short and straight, like those of *Ischnacanthus*; and the Bunga Beds fish and *I. gracilis* have anterior dorsal fin spines which are shorter than the posterior spines (AMNH7773 and 7776; Watson, 1937, fig. 10): on *Culmacanthus stewarti*, the anterior spine is larger than the posterior one.

**Squamation**

Unfortunately, the scales of the Bunga Beds acanthodians are poorly preserved. The “scales” on CPC16996 are actually sediment casts. The scales of all three prepared
specimens have similar morphology, with a relatively smooth, flat crown, a fairly deep neck, and a moderately vaulted base (Figure 8d, e). The broad, long crown overhangs the base posteriorly. There are no specialized scales along the lateral lines, which are distinguishable only by slight change in direction of the scale rows, and by the impression of a ridge on the mold. The size of the normal body scales increases from anterior to posterior. There are no enlarged scales at the bases of the fin spines, nor along the anterior edge of the hypocaudal lobe of the tail (Zone Z3”, Miles, 1970). Both culmacanthids and ischnacanthids can have enlarged scales at the bases of the fin spines and along the edge of the hypocaudal lobe, so this feature is not helpful in classifying the Bunga Beds specimens. The increase in size of the scales towards the tail tip is distinctive and represents a feature not previously recorded in acanthodians. At least one specimen of *I. gracilis* (AMNH7773) shares this feature. The squamation pattern of the tail is preserved on all three Bunga Beds fish (Figure 8a-c) and there is no apparent differentiation on the caudal fin web, so this is designated as Zone Z3, rather than Z3 + Z4. There is also no differentiation between these two zones on the caudal fin web of *I. gracilis*. Watson (1937) stated that the hypocaudal lobe of the tail on the specimens of *I. gracilis* (and also the acanthodiiform *Mesacanthus mitchelli*) from Turin Hill, has a peculiar recurved hook. This feature might be an artifact of preservation, perhaps the result of the row of enlarged scales stiffening the anterior edge of this lobe, while the main fin web (with its minute scales) might have become slightly shrivelled and distorted. Some specimens of *I. gracilis* (AMNH7773, 7775, 7776), also from Turin Hill, lack this feature.

![Figure 8](image_url)

*Figure 8* Tail squamation on Bunga Beds acanthodians (a) CPC16996 (b) CPC30433 (c) CPC33499: (d) lateral view, and (e) basal view of scale from zone Z1, CPC30433. Scale bar = 5 mm on (a-c), and 0.1 mm on (d,e).
Watson (1937, p. 81) described the shoulder girdle of *I. gracilis* as a "...single element on each side", however, Denison (1979, pp. 7, 8) described an angulate, external surface of the scapula, and a separate procoracoid. Bernacsek and Dineley (1977, p. 12) found no evidence of separate procoracoids in the Canadian material. On *Culmacanthus* and CPC30433 the scapular blade is quite high and slender, but the scapular blade on *I. gracilis* can also be similarly shaped (Bernacsek and Dineley, 1977, pl. 5).

In summary, the Bunga Beds acanthodians share more characters with *I. gracilis* than with *Culmacanthus*, as they are not deep-bodied (a diagnostic character of culmacanthids), anterior dorsal fin spines are shorter than posterior spines, scales appear smooth crowned, and increase in size towards the tail tip. Young (1989) acknowledges "the small number of reliable characters available to define the major groups". Unfortunately, it appears that as more taxa are described, the divisions between groups become less clear. As no heads (and thus no jaws) were preserved, and the scales only poorly preserved, the fish can only be tentatively identified as ischnacanthids.

TAPHONOMY

All three described specimens are headless, but the preserved fin spines and squamation retain original articulation. The simplest taphonomic scenario would be that the fish, being mid to surface water feeders (probably with an air bladder), died and sank to the bottom. However, this hypothesis does not account for the lack of heads, jaws, or pectoral fin spines. It is more probable the fish died in shallow water, possibly during a mass mortality (precluding scavenging, thus preserving the carcass intact). Distension of the body, caused by fermentation of the gut contents, led to refloating of the carcasses,
but the closely articulated, well-anchored acanthodian squamation prevented tearing of the abdominal integument (as usually occurs in modern fish). Tearing and gas release probably occurred in the region of the gills, with the weakly articulated head separating from the trunk. The remains of the carcass then sank from the epilimnion (oxygenated waters) through the hypolimnion (anoxic deep waters) to the bottom of the lake, which was free of scavengers due to the anoxic conditions (Figure 9).

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