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A new genus of fossil coelacanth (Osteichthyes: Coelacanthiformes) from the Middle Devonian of southeastern Australia

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Abstract – A new primitive coelacanth *Gavinia syntrips* gen. et sp. nov., is described from the upper Middle Devonian Mt Howitt site, central Victoria. The genus is based on a partial skull, complete caudal fin and distal section of trunk and median fins, some isolated scales, and indeterminate remains. It is regarded as the most primitive member of the Coelacanthiformes because it has a very long dentary bone, approximately 36% of the lower jaw length, a relatively elongate cheek region, and coarsely ornamented scales. It retains the basic coelacanthiform synapomorphies of having a tandem double lower jaw joint; broad-headed, short hyomandibular; large, deep operculum; and a rostral organ denoted by the large pore system in the snout bones. Isolated coelacanth remains from the Pambula River site, New South Wales, are also referred to *Gavinia* sp. indet. A provisional phylogenetic analysis places *Gavinia* as the plesiomorphic sister taxon to all other Coelacanthiformes (Actinistia), and this suggests a possible origin for the clade in eastern Gondwana.

INTRODUCTION

The Mt Howitt fauna, from central Victoria (Figure 1), contains a diverse assemblage of fishes preserved in finely-laminated black lacustrine shales of the Avon River Group. The depositional environment has been interpreted as part of an intramontane basinal setting in which lakes were periodically formed by damming of the high energy drainage system by acid lava flows and ignimbritic eruptions (Long 1982). The fish fauna is well-preserved, represented by mostly complete individuals in all stages of growth, indicating that mass kill was most likely a randomly generated, but geologically regular event.

The fauna is dominated by several species of placoderms. Long (1983a) and Long and Werdelin (1986) described three species of the antiarch *Bothriolepis* from the Mt Howitt sites (*B. gippslandiensis, B. cullodenensis, B. fergusoni*) and a fourth species (*B. bindareei*) from a nearby road cutting. Long (1984) described two species of the phyllolepid arthrodire *Austrophyllolepis* (*A. ritchiei* and *A. youngi*). I consider now that there may only be one species of phyllolepid present, as deformation of the strata can account for the distortion of plate measurements that separate the two originally named species. However, despite this, there are still three distinct species of *Bothriolepis* present in the Mt Howitt faunas: the low-crested *B. gippslandiensis*, the high-crested *B. cullodenensis* and the non-crested *B. fergusoni*. Only one species of *Groenlandaspis* appears to be present, and this material is currently under study by Dr Alex Ritchie.

The Mt Howitt fauna also contains several primitive teleostomes, namely the acanthodians *Culmacanthus stewarti* Long, 1983b and *Howittacanthus kentoni* Long, 1986, and the palaeoniscoid *Howqualepis rostridens* Long, 1988. Sarcopterygians are represented by the fleurantiid lungfishes *Howidipterus donnae* Long, 1992 and *Barwickia downunda* Long, 1992 (Long 1993), and the osteolepiforms *Marsdenichthys longioccipitus* Long, 1985 and *Beelarongia patrichae* Long, 1987, plus the new coelacanthiform described herein. *Marsdenichthys* was first referred to the Tristichopteridae (= Eusthenopteridae) by Long (1985) but since then new material has been found that has been studied by the author and Dr Oleg Lebedev, from the Palaeontological Institute of Moscow. We now regard it as possibly a primitive member of the family Rhizodopsidae, due to its intricate scale ornamentation. *Beelarongia* has been referred to the new family Canowindridae by Young *et al.* (1992). In addition, a glyptolepid porolepiform may also be present in the fauna, based on isolated scales and a partial body showing a long, lobed pectoral fin and broad cleithrum. However, as the scales of this form are easily distinguished from those of *Gavinia* gen. nov., the isolated tail described herein is clearly attributed to *Gavinia* gen. nov. rather than the glyptolepid. The sarcopterygian fauna present at Mt Howitt is entirely endemic at the generic level.

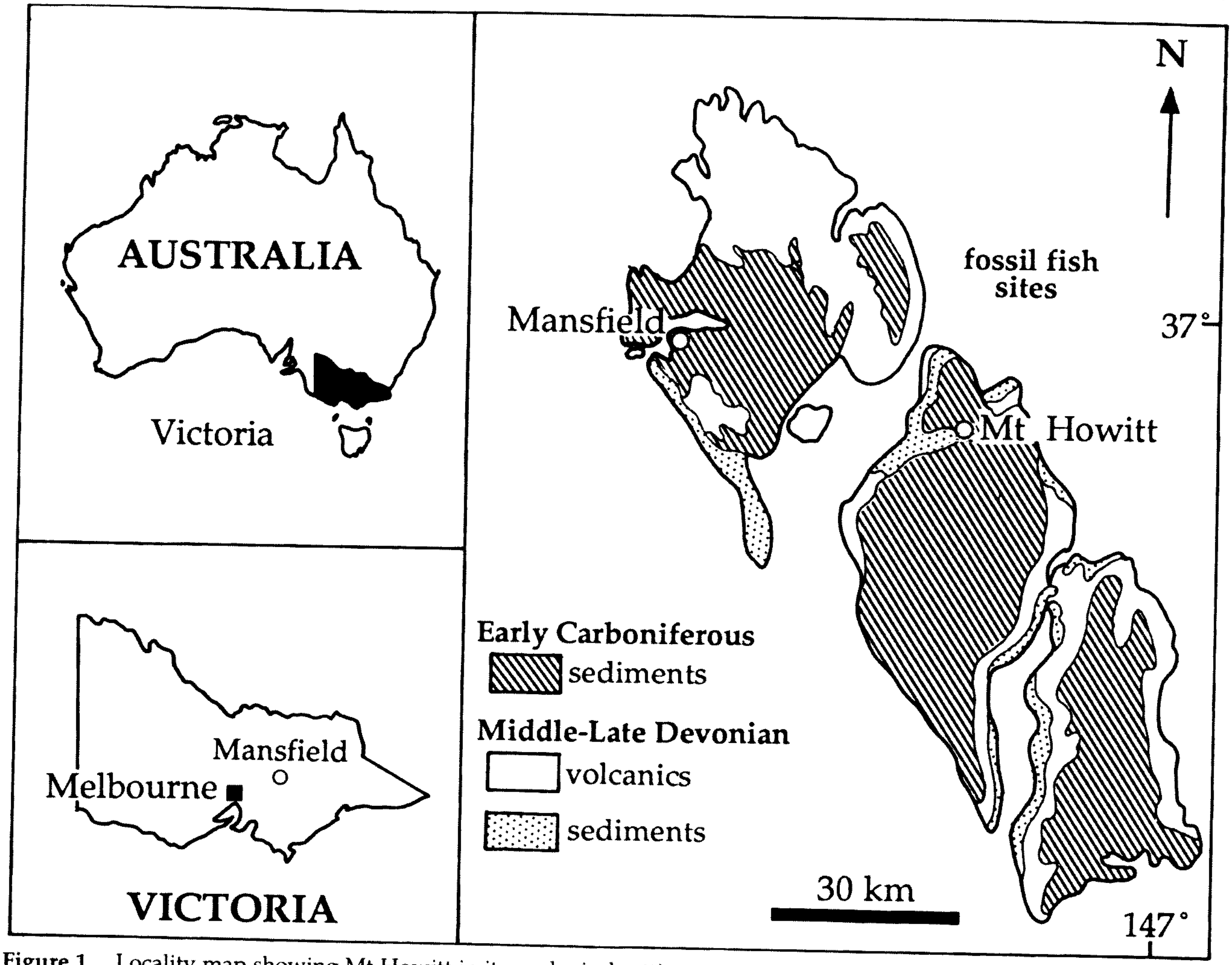


Figure 1 Locality map showing Mt Howitt in its geological setting.

In addition to the articulated coelacanth remains of *Gavinia* gen. nov. from Mt Howitt, an isolated bone and scale of a similar coelacanth is described from the Pambula River site, of probable early-middle Givetian age, estimated to be slightly older than the Mt Howitt site by correlation with the Aztec Siltstone fauna of Antarctica (Young 1983, 1993; Turner 1997).

Coelacanths are known from few other Devonian deposits, all of which fall within the latest Givetian to Famennian age range. Cloutier (1991) reviewed Palaeozoic coelacanth occurrences and recognized a number of synapomorphies that define the group. Figure 2 shows all the major occurrences of Devonian coelacanths in order of age (except for some of the indeterminate forms noted by Cloutier). The coelacanth most often cited in the recent literature as being the oldest member of the group is *Euporosteus eifeliensis* Jaeckel, 1927, from the Crinoidmergel of Germany, now considered to be late Givetian in age (Schultze 1993; Schultze and Cloutier 1996). This specimen is represented by a single ethmosphenoid, which gives no clear indication of its degree of plesiomorphy within the group, as the vitally important features of early coelacanths are related to their cranial proportions, such as the relative size of lower jaw bones to total jaw length, skull table bones and proportions, and cheek length, as will be shown in the discussion below. A newly discovered coelacanth from the Late Givetian Gauja Formation of Latvia is currently under study by Dr Per Ahlberg, and Dr Ervins Lukševičs and colleagues. Known from well-preserved three-dimensional material, it is said to be of similar primitive organization to *Miguashaia*, but further comparisons with the new material described herein must wait until the Latvian genus is fully described (P.E. Ahlberg pers. comm. 1998).

Thus, the earliest coelacanths which offer useful information on the nature of the primitive members of the group are *Miguashaia bureaui* Schultze, 1973 from the Frasnian Escuminac Formation of Canada, *Diplocercides* spp. Stensiö, 1937 and *Nesides? heiligenstockiensis* Jessen, 1966, from the Upper Frasnian of Germany and the Middle Frasnian of Iran (Janvier and Martin 1979). The new form described from Mt Howitt is either a contemporary of, or older than, the previously oldest known

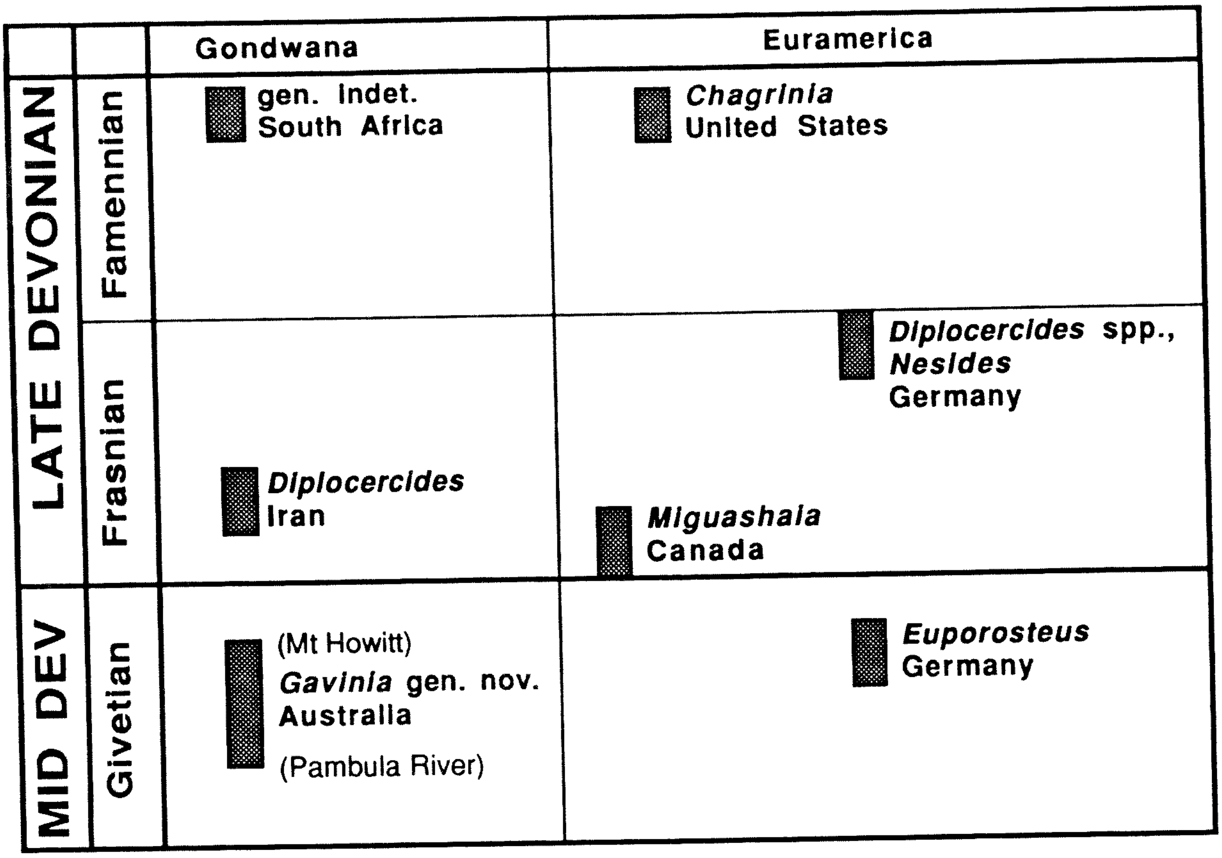


Figure 2 Distribution of Devonian coelacanths in time and space. Sources: Stensiö (1937), Jessen (1966), Janvier and Martin (1979), Cloutier (1991), Anderson *et al.* (1994) and Gess and Hiller (1995).

coelacanthiform, *Euporosteus eifeliensis*, yet despite its relative incompleteness, it can be argued that it is more primitive than any of the other Late Devonian taxa.

THE AGE OF THE MT HOWITT FAUNA

The age of the Mt Howitt fauna is placed as late Givetian by Young (1993), on the basis of its stratigraphic position low in the order of fish-bearing sites in the central Victorian sequence, and from its correlation with the Taggerty site on the basis of both containing *B. gippslandiensis* and *Austrophyllolepis* sp. The Taggerty site has a radiometric date on a rhyolite above the fish-bearing horizon of 367 ± 2 Myr, giving a minimum age of early Frasnian (Williams *et al.* 1982). The Mt Howitt site can also be closely correlated with the Freestone Creek faunas of east Gippsland, on the basis of *Bothriolepis cullodenensis*, *Culmacanthus stewarti*, and *Austrophyllolepis* sp. Furthermore, the recent studies on late Devonian fish sites in New South Wales (Young this volume) also corroborate an older age for the Mt Howitt site by reassessement of some of the *Remigolepis*-bearing sites in New South Wales as being older than previously thought. The correlation between the top of the Aztec Siltstone fauna of Antarctica and the Mt Howitt fauna is seen by the close phylogenetic relationship between the *Bothriolepis* species (Young 1988; Johanson and Young this volume), the presence of the endemic acanthodian genus *Culmacanthus* (Long 1983b; Young 1989), and the possible presence of *Austrophyllolepis* and *Howidipterus* in both faunas.

Overall these data suggest that the Mt Howitt fauna is, at youngest, late Givetian, making it approximately contemporaneous with the German site containing *Euporosteus*; or, maybe older, perhaps lower or middle Givetian. This would imply a slightly older age for the base of the Aztec Silstone than first proposed by Young (1988), and correlations between the base of this unit and the Hatchery Creek Conglomerate in New South Wales (Eifelian age: Young and Gorter 1981; Young 1993; Turner 1997) would not seem unreasonable, given the presence in both faunas of similar thelodonts (*Turinia antarctica* Turner and Young, 1994, *Turinia* sp. cf. *T. hutkensis*), primitive osteolepiforms (*Beelarongia patrichae* and *'Gyroptychius' australis* Young and Gorter, 1981), primitive asterolepidoid and bothriolepidoid antiarchs (*Sherbonaspis hillsi* Young and Gorter, 1981 and *Monarolepis verrucosa* Young, 1988) in the Hatchery Creek fauna, *Pambulaspis* Young, 1983 in the Aztec Siltstone and Pambula River faunas and similar grade phlyctaenioids (e.g. *Denisonosteus* Young and Gorter, 1981 from Hatchery Creek, plus undescribed forms in the Aztec Siltstone fauna).

Turner (1997) also supported an older age assessement for the base of the Aztec Silstone, suggesting that it could have a maximum age of early Eifelian, but a minimum age no older than the *costatus* Conodont Zone (basal Givetian). Thus the latest evidence from correlations with faunas from Antarctica, and the older age assessment of younger faunas in central New South Wales support a slightly older position for the Mt Howitt fauna as probably early to middle Givetian age. This hypothesis is supported by the phylogenetic nature of the fauna in containing primitive members of the many groups present, as outlined above.

MATERIALS AND METHODS

The material is studied by removal of weathered bone from the specimen by weak HCL solution, then making latex casts of the natural mould to reveal details of the bones surfaces, so no details of internal structures of the bones or teeth are available.

During the course of this study, several specimens of fossil coelacanths were examined. These include material of *Miguashaia bureaui* held in the Natural History Museum, London; specimens of *Nesides? heiligenstockiensis* in the collections of the Swedish Museum of Natural History, Stockholm, specimens of *Nesides* sp. from Iran in the Museum of Natural History, Paris, and specimens of an undescribed Late Devonian coelacanth held in the collections of the Albany Museum, Grahamstown, South Africa.

Institutional abbreviations used in this paper are: AGSO, Australian Geological Survey Organisation, Canberra; and NMV, Museum Victoria, Melbourne.

SYSTEMATIC PALAEONTOLOGY

Class Osteichthyes Huxley, 1880

Subclass Sarcopterygii Romer, 1955

Order Coelacanthiformes Cope, 1871

Family Miguashaiidae Schultze, 1993

Gavinia gen. nov.

Type species

Gavinia syntrips sp. nov.

Diagnosis

Actinistian fish having a large, deep premaxilla; lateral rostral of equal length to the premaxilla; large dentary approximately 36–50% total mandible length; enlarged anterior coronoid developed as a symphysial tooth whorl; second coronoid much larger than anterior one; elongate cheek region composed mostly of large squamosal bone having two pit-line canal grooves; deep large operculum which has an anterodorsal margin that is strongly concave for contact with the squamosal bone; anal fin supported by a broadly expanded fin basal; caudal fin heterocercal with weakly-developed epicercal lobe; anterior trunk scales coarsely ornamented with thicker, slightly wavy linear ridges in the anterior third of the exposed scale area, and continuing down the central axis of the scale; about 40–50% of scale area overlapped. Anterior bones of the skull and lower jaw ornamented with coarse, closely-spaced tubercles; rest of dermal bones ornamented with wavy vermiform ridges.

Etymology

The genus name is for Dr Gavin Young, Canberra, in recognition of his excellent work on fossil fishes.

Remarks

The lower jaw has a dentary which is proportionately much longer than that of any other Devonian coelacanth, and a reconstructed cheek which is also longer, relative to total head length, than that of any other Devonian-Carboniferous coelacanth genus, more approaching the primitive sarcopterygian condition, as for example in *Onychodus*. Furthermore, the lateral rostral bone is of similar size to the premaxilla, which is unusual in that it is generally much larger in all post-Devonian coelacanths (e.g. Forey 1981; Lund and Lund 1985). Such features were regarded by Cloutier (1996) and Cloutier and Ahlberg (1996) as primitive for coelacanths, based on comparisons with other basal osteichthyans: e.g. the actinopterygians *Cheirolepis* (Pearson and Westoll 1979) and *Howqualepis* (Long 1988); the primitive lungfish *Dipnorhynchus* spp. (Campbell and Barwick 1987); and basal rhipidistians like *Gogonasus* (Long *et al.* 1997) and *Porolepis* (Jarvik 1972). The anterior trunk scales alone are distinctive amongst the earliest actinistians in having centrally-swollen wavy ridges surrounded by finer, parallel ridges, differing from those in *Miguashaia* which have more overlap area on the equivalent scales (60–65%), and distinctly shorter, more robust tubercles and ridges in the central region (Cloutier 1996, figure 17A).

The genus is placed within the family Miguashaiidae Schultze, 1993 because it shares the condition of having short, interlocking lepidotrichia, a feature not seen in any other coelacanths apart from *Miguashaia*.

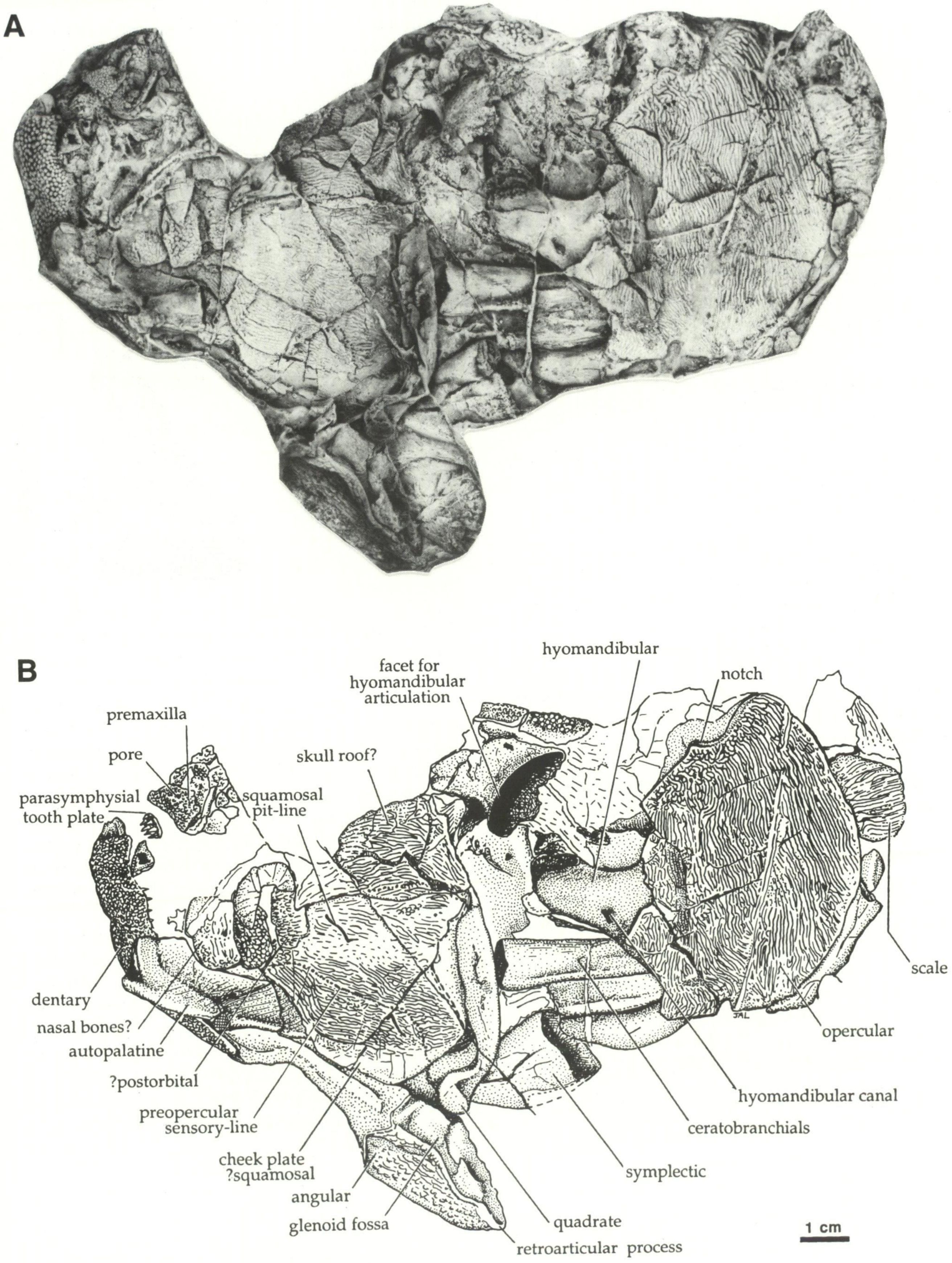


Figure 3 *Gavinia syntrips* gen. et sp. nov. holotype NMV P160710. A, crushed head in left lateral view, latex cast of natural mould whitened with ammonium chloride. B, sketch interpretation of same specimen.

Gavinia syntrips sp. nov.

Figures 3–10

a coelacanth ... Mt Howitt .. : Long 1991: 390.

Actinistian (from Mt Howitt): Young *et al.* 1993: 249.

Material Examined

Holotype

NMV P160710, a crushed head showing the cheek, lower jaws, part of the snout, quadrate, operculum, hyomandibular, parts of the hyoid arch, and some anterior trunk scales (Figures 3–6).

Other Material

NMV P160709, large tail in part and counterpart (Figures 8–10).

Type Locality and Horizon

Lower mudstone unit of the Avon River Group, outcropping on the fork of the Howqua River at the base of Mt Howitt, central eastern Victoria. Probably middle Givetian in age, as discussed above. The large tail came from the snig track (locality 'J').

Diagnosis

As for genus.

Etymology

After "Syntrips", the smasher, in Greek mythology, one who broke pots in the kitchen, alluding to the smashed condition of the skull; noun in apposition.

Description

The head (Figures 3, 4A, 5–7) is large, approximately 15–17 cm in length, and is preserved with the thin dermal bones being crushed down, overprinted on top of the neurocranium and visceral skeleton. The cheek region is difficult to interpret, although most of the skull bones are recognizable, including a portion of the otico-occipital region of the braincase and major elements of the visceral skeleton, such as the hyomandibular, ceratohyal and symplectic. The palatoquadrate is represented by the quadrate and autopalatine, from which its overall shape can be provisionally reconstructed.

Skull Roof

Most of the skull roof is not preserved, apart from some edges of dermal bones at the top (dorsal) margin of the specimen (labelled as "skull roof?" in Figure 3B). These might be the lateral edges of the supratemporal or tabular bones, as evidenced by the presence of a sensory-line canal represented by a linear series of small pores along the edges of the bones. The position of this small part of the roof near the posterior region of the cheek suggests that the postparietal shield was not separated from the cheek unit by a gap as in *Miguashaia* (Cloutier 1996, figure 5; Figure 12), but was like the majority of coelacanths in this respect.

Another small part of the skull roof is preserved dorsal to the facet for the hyomandibular. Two sections of bone ornamented with coarse tubercles probably represent the junction between the intertemporal and supratemporal bones. If this interpretation is correct then *Gavinia* gen. nov. shares an intertemporal as a primitive feature with *Miguashaia* and some of the Bear Gulch coelacanths (Lund and Lund 1985).

Cheek

A large area of ornamented bone can be seen immediately above the palatoquadrate and dorsal to the upper margin of the lower jaw. This large sheet of dermal bone lies above the palatoquadrate, the latter being clearly denoted by the double condyles of the quadrate abutting the lower jaw, and the protruding autopalatine division at the front. Thus the relationship of the dermal cheek bones to the size of the palatoquadrate is clearly established. As the end of the preopercular sensory-line canal finishes a long distance away from the beginning of the mandibular sensory-line canal on the lower jaw, it would appear that the intervening dermal bone, the preopercular, has been displaced ventrally, and is missing from the specimen.

The centre of the dermal cheek bone has a sinuous sensory-line canal, here interpeted as the preopercular sensory-line canal (Figure 3), and with two clear pit-line canals present, one dorsal to the main sensory line, the squamosal pit-line, and another one ventral to the canal near the contact margin for the (missing) preopercular. Despite the crushed nature of the specimen, with several linear and curved breakages present, no bone margins can be seen and the continuity of the vermiform ornamentation across these breaks supports my interpretation that they are not bone margins, but represent one large bone, here interpreted as being the squamosal (but quite possibly incorporating the quadratojugal). The squamosal has little of its margins well-preserved, apart from a short section of the anterodorsal sloping margin, presumably contacting the jugal bone, and part of the rounded posteroventral corner for contacting the preopercular.

The anterior extremity of the cheek is not clear and the squamosal appears to be covered by two smaller rectangular bones having a coarse tubercular ornamentation, a feature also seen on the anterior snout bones and the dentary, indicating that these elements are from the front part of the head, possibly the postorbital and one of the supraorbital bones.

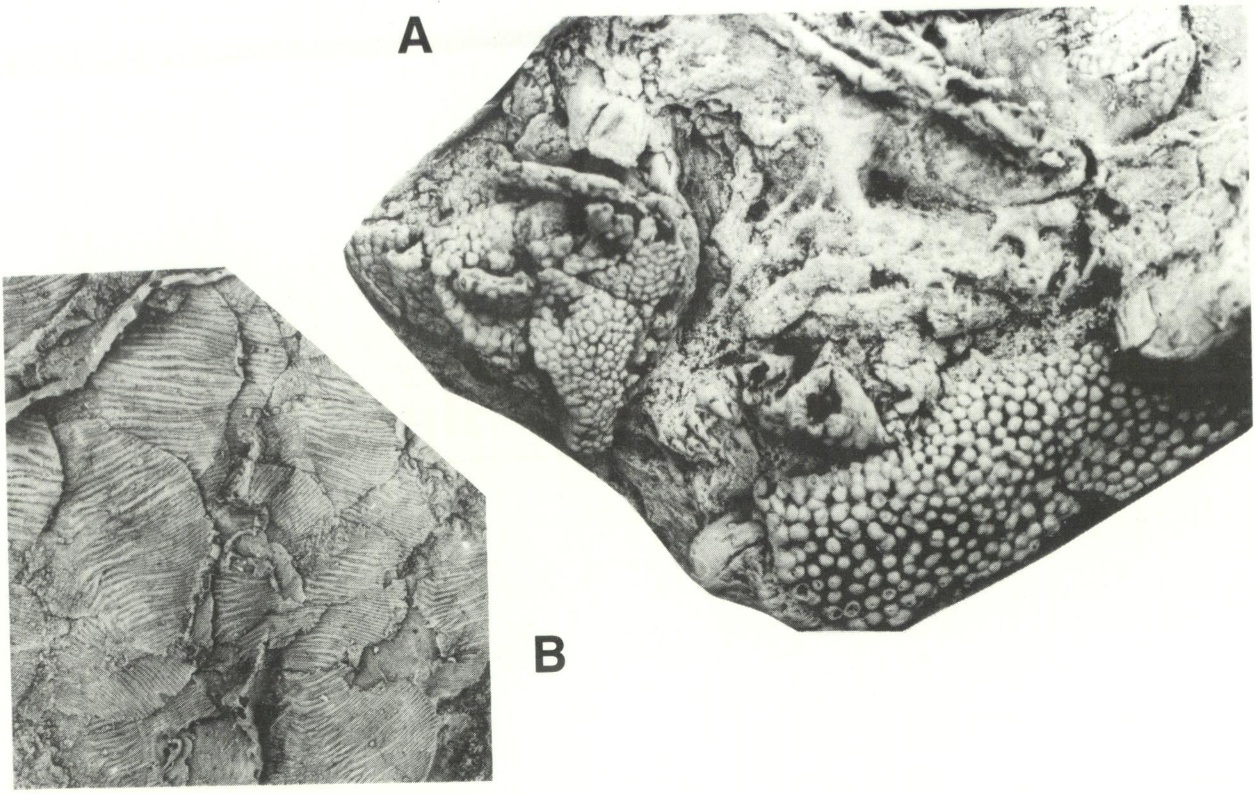


Figure 4 *Gavinia syntrips* gen. et sp. nov. A, detail of left dentary, premaxilla and anterior coronoid (parasymphysial tooth whorl); cf. Figure 3. B, scales posterior to opercular. Both are from the holotype NMV P160710, and are latex casts of natural moulds whitened with ammonium chloride.

The postorbital, if correctly identified, is a deep, short bone as in *Miguashaia*. It carries the infraorbital sensory-line canal down from the dermosphenotic ('supraorbital' of Cloutier 1996).

Snout

The only discernable bones in the snout (Figures 3, 4A, 5) are the two large premaxillae, seen from both sides in external views, and the immediately adjacent bones. Posterior to the right premaxilla is the lateral rostral (Figure 5). Its ventral margin is straight, continuing the biting margin of the premaxilla, although no teeth are seen on the single specimen. It lacks a strong ventral process as is found in many of the Bear Gulch coelacanths (Lund and Lund 1985) and some other genera, and is of approximately the same size as the premaxilla.

The left premaxilla (Figure 4A) is seen in position just dorsal to the anterior tip of the lower jaw. It is higher than long, and has coarse tubercular ornamentation with a large pit present, presumably for the rostral organ. The teeth are small and curved. I estimate about 6–8 teeth would have been present. The right premaxilla (Figure 5) is seen on a separate piece of rock that has most likely come from the holotype specimen, but is no longer joined to the main skull. It is of similar shape and size to the left premaxilla.

Many smaller bones abut both premaxillae. Some of these show large foramina present for the rostral organ, possibly indicating the presence of the preorbital bone. Others are presumably some of the numerous supraorbital or nasal bones (Figures 4A, 5) which formed the snout area, as is also seen in other primitive coelacanths such as *Euporosteus* (Stensiö 1937) or *Hadronector* (Lund and Lund 1985).

Neurocranium

Only small parts of the left side of the otico-occiptal division are seen on the main specimen (Figure 3). The articulation area for the hyomandibular is clearly shown on the latex cast as a large crescent-shaped area of presumably non-ossified periosteal bone. It is deeply concave for reception of the broad, curved head of the hyomandibular. The deep groove in the crushed bone of the neurocranium, immediately medial to the hyomandibular facet, is here interpreted as representing the tectosynotic fossa of Bjerring (1977). As far as can be seen, the parts of the neurocranium preserved appear not unlike that of *Nesides schmidti* Stensiö, 1937 as reconstructed from wax serial grindings by Bjerring (1977, figures 23, 24).

Hyoid arch

The hyomandibular and parts of the lower hyoid arch are seen well-preserved in position in front of

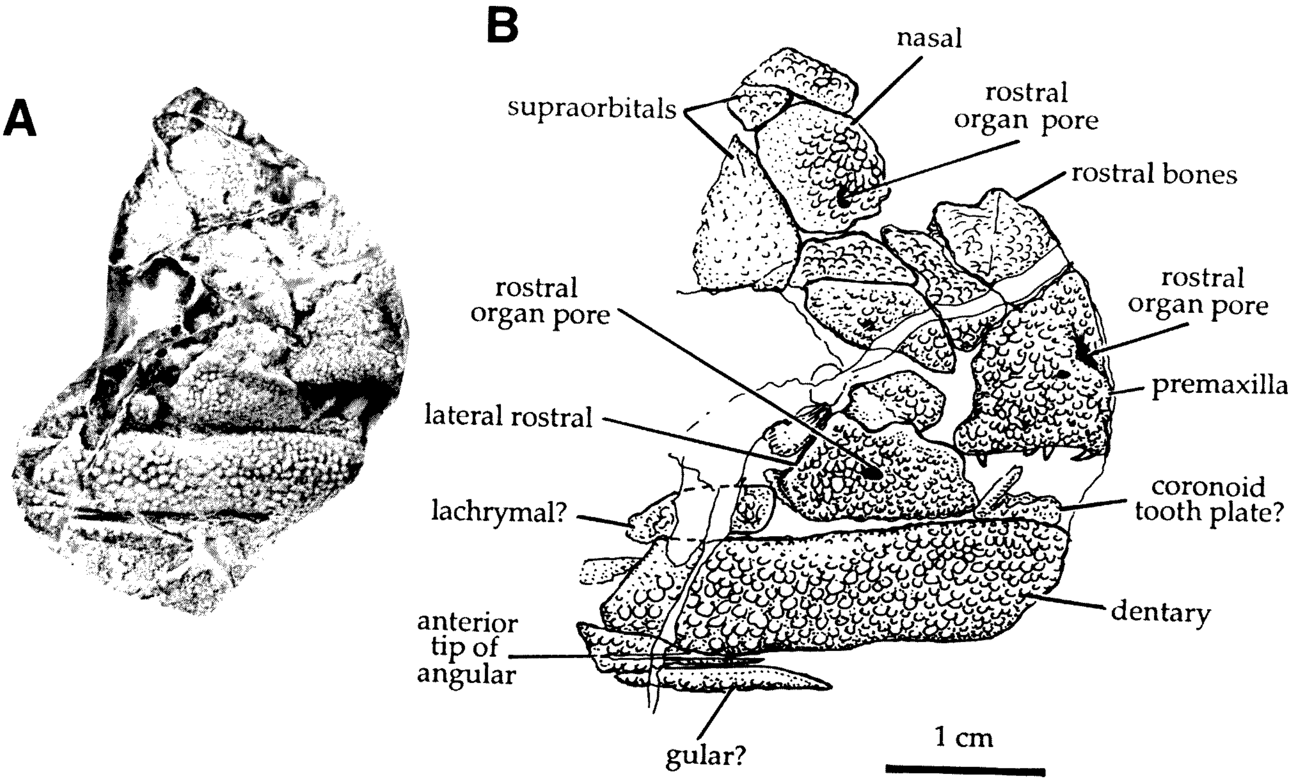


Figure 5 *Gavinia syntrips* gen. et sp. nov. Right side of snout and anterior region of lower jaw, holotype NMV P160710. A, latex cast whitened with ammonium chloride; B, sketch interpretation of same.

the opercular and adjacent to the neurocranium (Figure 3).

The hyomandibular is a large, broad-headed bone, distinctly like that of *Nesides schmidti* in having an expanded head with wide, crescent-shaped articulatory area, short main section, and broad ventral end. It is more elongated than that of *Nesides*, and in this respect would appear to be more primitive for the group, as in other basal sarcopterygians the hyomandibular is more

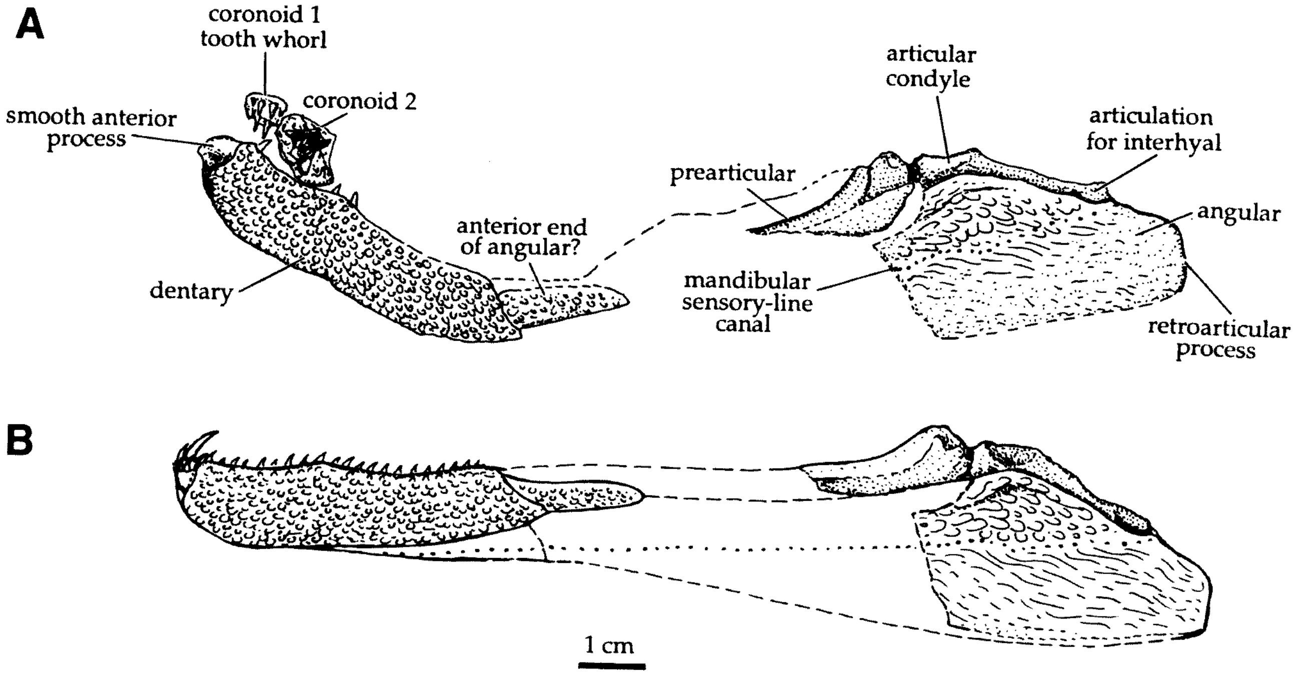


Figure 6 A, sketch of left lower jaw of the holotype of *Gavinia syntrips* gen. et sp. nov. B, attempted reconstruction of the lower jaw. It is not known whether the small sliver of dermal bone posterior to the dentary is a broken posterior part of the dentary, or an anterior section of the angular.

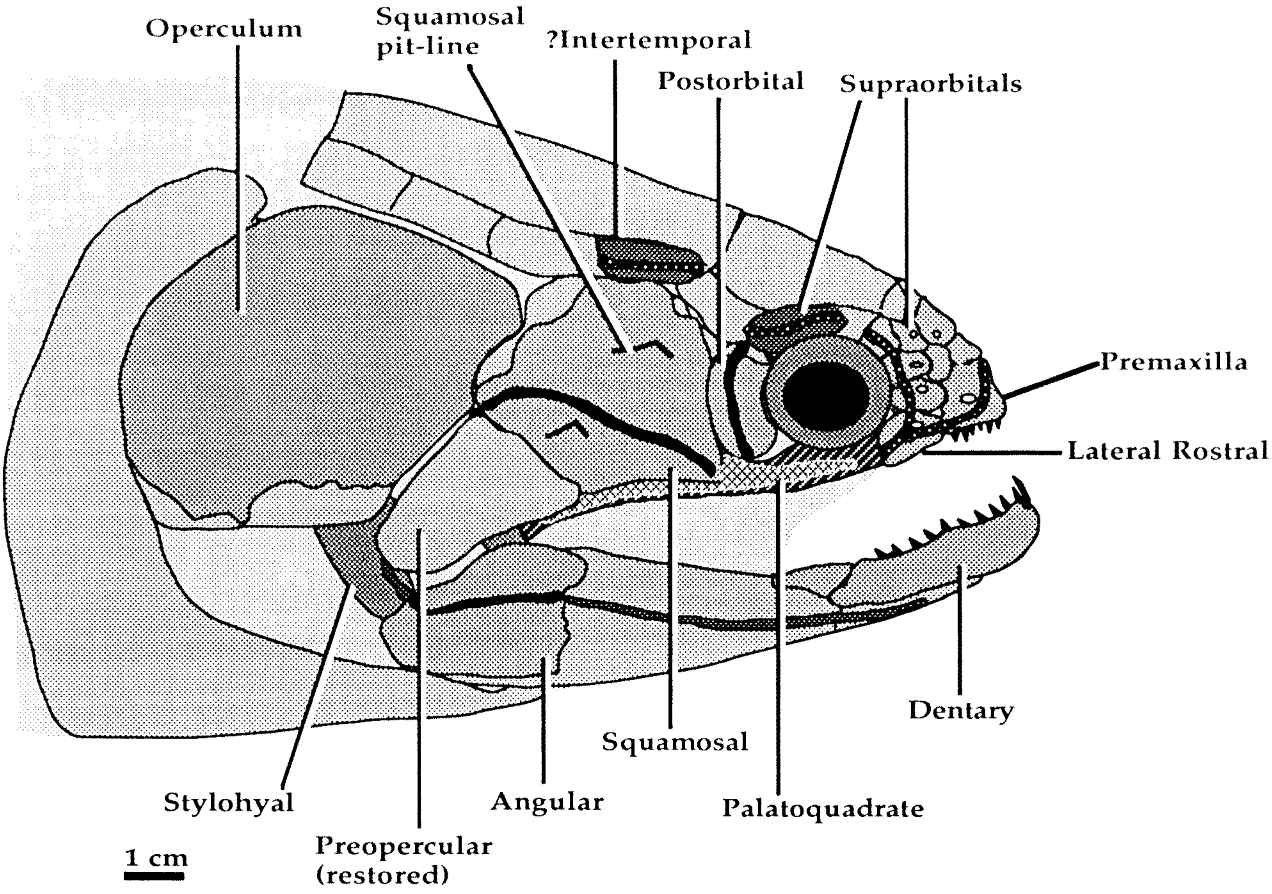


Figure 7 Attempted reconstruction of the skull of *Gavinia syntrips* gen. et sp. nov. Restored dermal bones in lighter stipple; sensory-line canals, palatal and visceral skeleton bones shown in darker, coarse patterns.

elongate (e.g. *Onychodus*, WAM 92.8.2; *Gogonasus*, Long *et al.* 1997). The hyomandibular canal for the n. ramus hyomandibularis is clearly seen in the middle of the bone.

There are several other robust, large elements of the visceral skeleton preserved immediately adjacent to the hyomandibular. One of these is particularly broad and flat and is identified as possibly being the stylohyal that connects the ventral end of the hyomandibular with the interhyal, bracing the lower jaw on the retroarticular process. The other stout, visceral arch elements are most likely ceratobranchials of the visceral arches.

Lower jaw

The anterior and posterior regions of the intact left lower jaw are preserved on the holotype specimen (Figure 3), with the anterior region of the right lower jaw on the associated fragments, assumed to also belong with the holotype (Figure 5). These corroborate the size and shape of the dentary as being a large bone, approximately 36–50% of the jaw length, depending upon whether the small dermal bone at the posterior of the dentary is actually a piece broken off the end of the dentary, or whether it is part of the anterior division of the angular (as it is labelled in Figures 5B, 6A). The posterior region of the lower jaw on the holotype shows the close association of the quadrate and its condyles, as well as the long retroarticular region with articulation surface for the symplectic. The posterior margin is prserved as a blunt, square-cut end of the jaw, as occurs in *Nesides* and *Diplocercides*.

The angular shows that the mandibular sensory-line canal runs in the middle of the bone, closer to the dorsal margin where it exits posterior to the articulation area for the symplectic. This also occurs to a lesser degree in the lower jaw of *Nesides? heiligenstockiensis* (Jessen 1966) and the isolated Middle Frasnian jaw from Iran assigned to *Diplocercides* sp. by Janvier and Martin (1979).

The dentary is a straight, deep bone with a slightly concave scalloped dorsal margin, thick tubercular ornamentation along its outer surface, and a short protruding anterior section of meckelian bone for a small symphysial tooth plate, probably the modified anterior coronoid. Underneath the dentary on the right side is a small sliver of bone, here interpreted as either part of the front of the

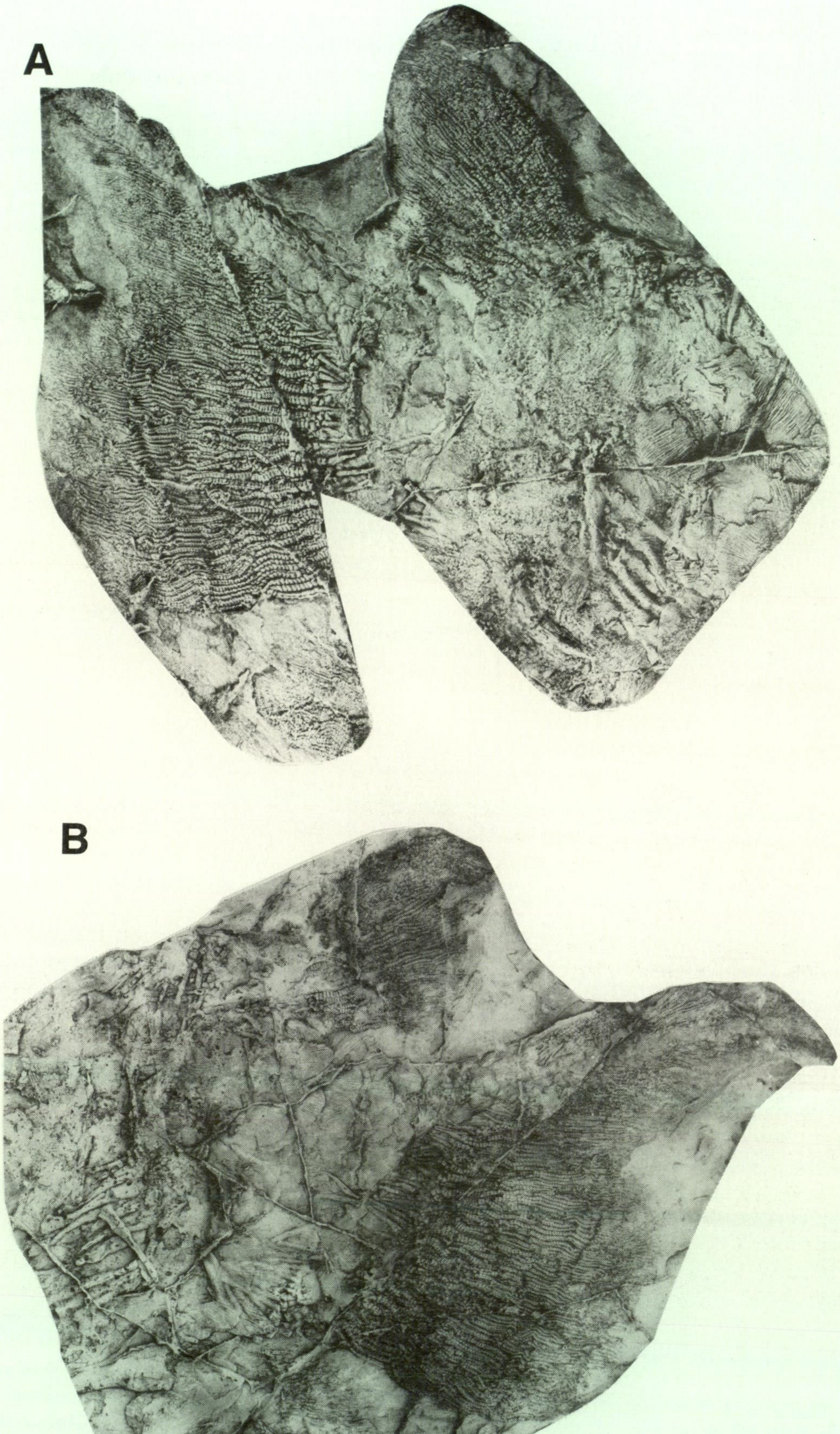


Figure 8 *Gavinia syntrips* gen. et sp. nov. The tail, anal and posterior dorsal fins as preserved from A, the right side, and B, the left side. NMV P106709. Latex casts whitened with ammonium chloride.

splenial, or the anterior prominence of the angular.

The prearticular is poorly preserved, apart from the smooth dorsal margin of it which protrudes above the dermal bone of the angular (Figure 6). There is no distinct dorsal extension of the prearticular above the angular as occurs in *Miguashaia* (Cloutier 1996, figure 5) or all of the Bear Gulch taxa (Lund and Lund 1985).

The anterior two coronoids are preserved in close proximity to the front of both dentaries (Figures 4A, 5, 6). The anterior-most coronoid bears a row of enlarged teeth forming a small parasymphysial tooth whorl (Figure 3A shows this clearly), and this bone presumably sat atop the smooth platform of bone extending from the front of the dentary (Figures 3B, 4A). Both second coronoids are poorly preserved. From the left specimen it appears to have relatively large teeth, and is slightly larger than the small anterior coronoid tooth whorl.

The reconstruction of the lower jaw shown in Figure 6B is based on the actual specimen, with the missing sections restored after other primitive coelacanths.

Operculum

The operculum is a very large bone, and most of it is well preserved except for the posteroventral part of the ventral margin (Figure 3). It is distinct in having a scalloped anterior margin with a well-defined notch in the dorsal region which contacted the cheek. It has gently rounded dorsal and posterior margins. Overall its shape can be restored along the lines of that seen in *Diplocercides*, and in this regard differs considerably from that of *Miguashaia*. It has three small pits present near the contact with the cheek, as also occurs on the operculum of the Mt Howitt dipnoans *Howidipterus* and *Barwickia*, suggested by Long (1992) as being for sensory pit clusters.

Body and axial skeleton

The body is known from a large specimen showing the tail and posterior region of the trunk, preserved in both part and counterpart (Figures 8–10). The scales on the trunk here precisely match those of the section behind the head (Figure 4B), so the two specimens are referred to the same species.

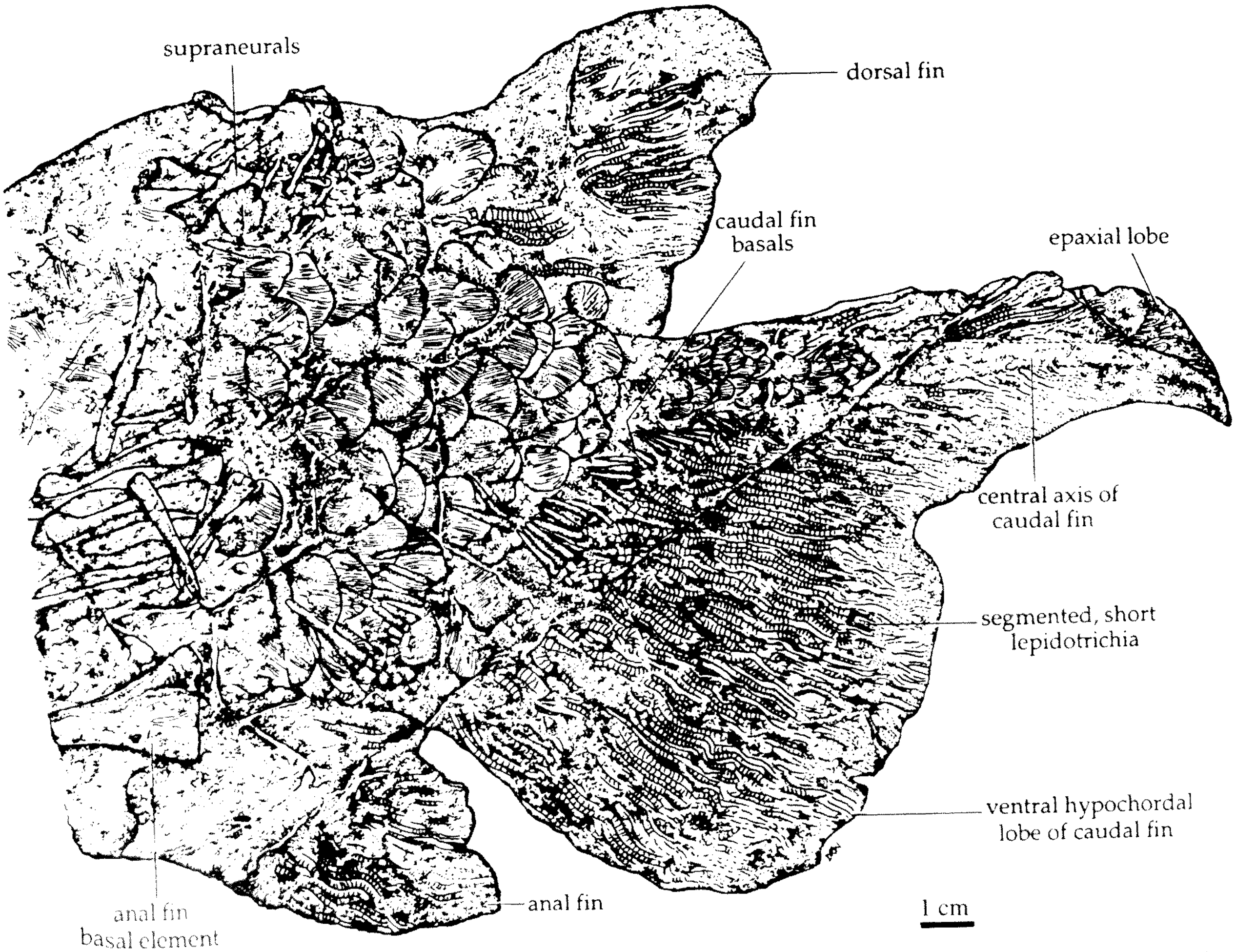


Figure 9 *Gavinia syntrips* gen. et sp. nov. The tail, anal and posterior dorsal fins as shown from the left side, sketched from the latex cast, NMV P106709.

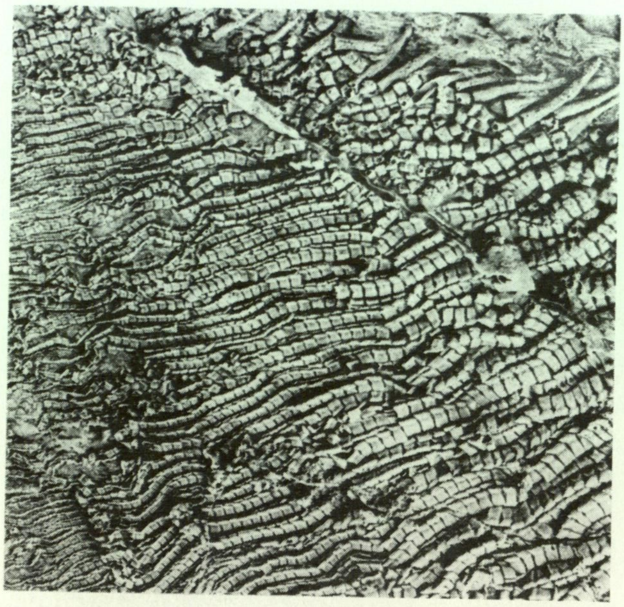


Figure 10 *Gavinia syntrips* gen. et sp. nov. Detail of the right side of the tail, main section of ventral hypochordal lobe, showing fin base and short, disjointed lepidotrichia. X2. NMV P160709. Latex cast whitened with ammonium chloride.

The specimen shows the posterior dorsal fin (Figures 8, 9), which is of similar shape and size as the anal fin, lacking the stiff fin-rays seen in the first dorsal fin of most coelacanths. The posterior dorsal fin is slightly more posteriorly positioned than the anal fin, but of similar size, and is estimated to contain close to the same number of lepidotrichia. The posterior dorsal fin basal is not seen. The anal fin is positioned very close to the ventral hypochordal lobe of the caudal fin. The anal fin is supported by a robust distally-expanded fin basal, but the secondary radials are not seen.

The heterocercal caudal fin is well preserved showing rows of large fin basal elements which closely match those seen in *Miguashaia* (Cloutier 1996, figure 16A), as do the short, irregularly-shaped, interlocking lepidotrichial segments (Figure 10). The main axis of the tail is straight, appearing to have been reasonably stiff in life. It has a small epichordal tuft developed at the end. There are about 36–40 rows of lepidotrichia in the main lobe of the ventral hypochordal region. Each row of lepidotrichia meets one caudal fin radial. These rows branch distally, a feature otherwise only described in *Miguashaia*.

Scales

The scales are best seen near the posterior end of the skull on the holotype (Figure 4B) and on the trunk near the tail region (Figure 8). They are finely striated with slightly wavy ridges in the central region, becoming narrower and more parallel-sided towards the edges. There are few bifurcations of these ridges, of which there may be up to 25 on the largest scales. The preornamental field on each scale comprises a zone of short, pointed tubercles, closely crowded, which increase slightly in size towards the beginning of the linear ornamentation.

ISOLATED BONE AND SCALE FROM PAMBULA RIVER

Part of the lower jaw (angular) and a scale are here described from the Pambula River site, near

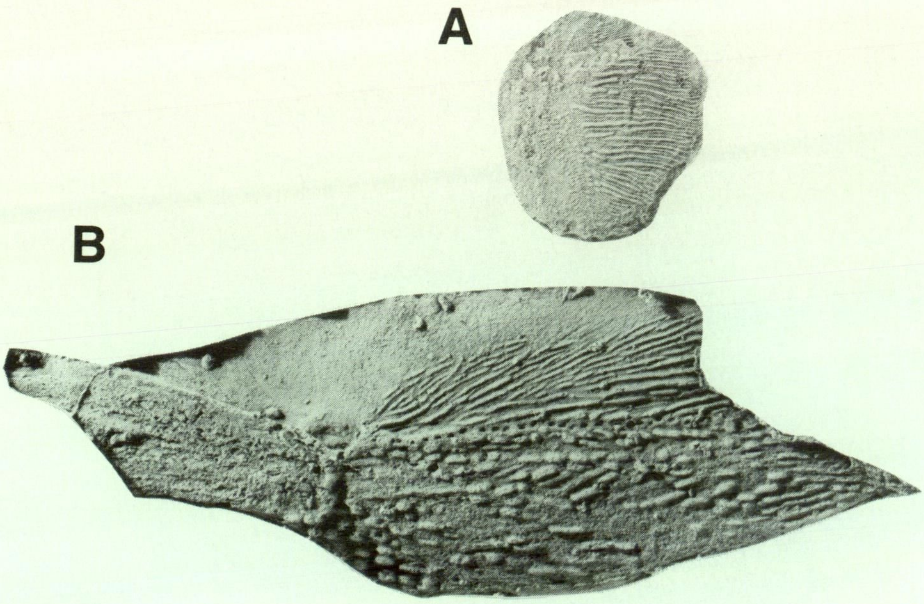
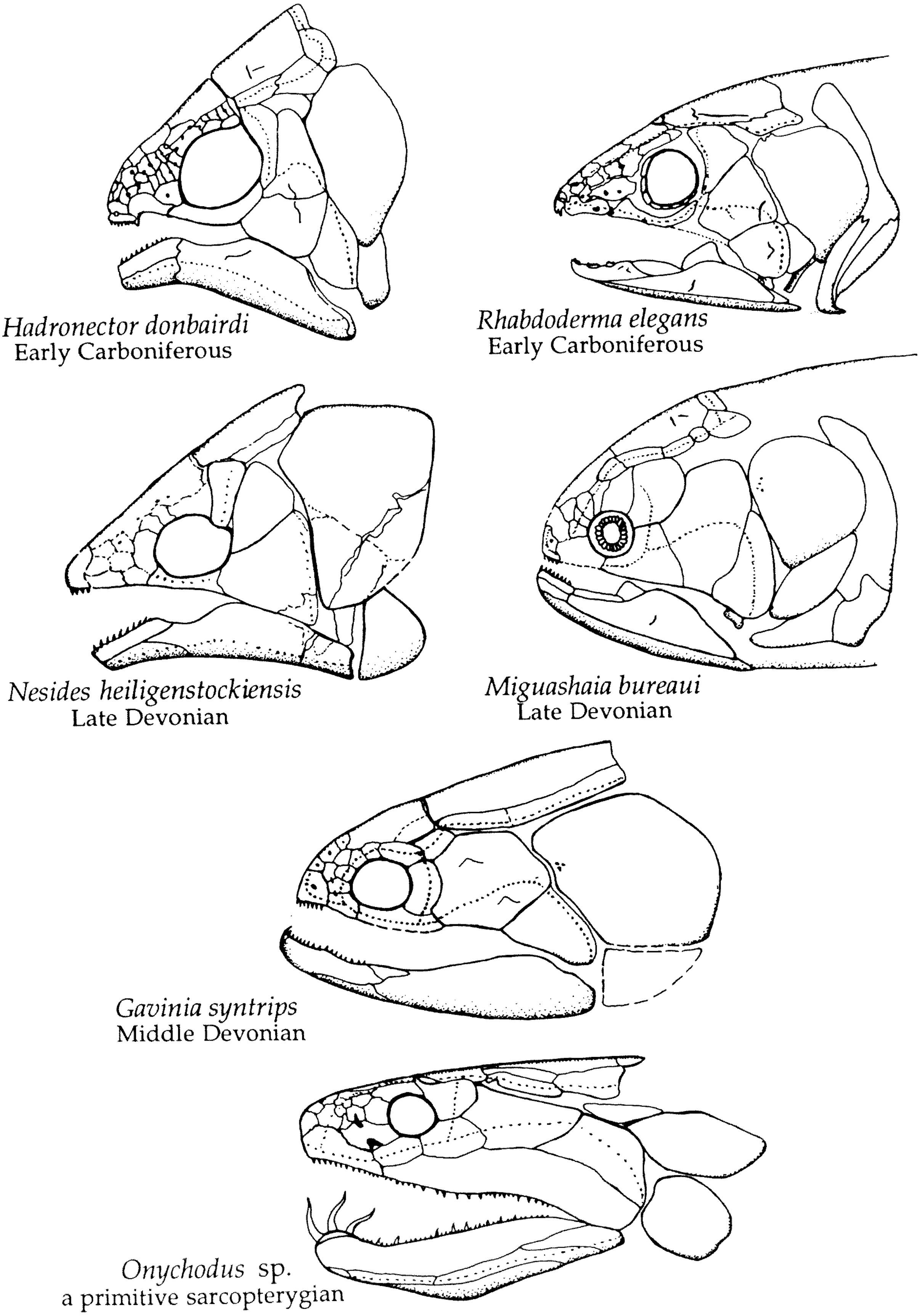


Figure 11 *Gavinia* gen. nov. species indeterminate, from the Pambula River site, New South Wales (Givetian). A, isolated scale. B, part of the right angular, V1564 (AGSO collections). Latex casts whitened with ammonium chloride.



Hadronector donbairdi
Early Carboniferous

Rhabdoderma elegans
Early Carboniferous

Nesides heiligenstockiensis
Late Devonian

Miguashaia bureaui
Late Devonian

Gavinia syntrips
Middle Devonian

Onychodus sp.
a primitive sarcopterygian

Figure 12 The heads in lateral view of primitive coelacanths and an onychodontiform sarcopterygian. *Gavinia* gen. nov. original; *Hadronector* after Lund and Lund (1985); *Miguashaia* after Cloutier (1996); *Nesides heiligenstockiensis* is a new reconstruction, modified after Cloutier (1991); *Onychodus* sp. from Gogo, drawn from WAM 92.8.2; *Rhabdoderma* after Forey (1981).

Eden, New South Wales (late Givetian-early Frasnian age: Young 1993). The scale (Figure 11A) closely resembles that of *Gavinia syntrips* in its overall shape, and nature of external ornamentation, and is here referred to that species. However, the lower jaw fragment (Figure 11B) is more difficult to interpret as it is relatively incomplete. It appears to be the posterior region of the angular from the right side, as it has the clear row of sensory-line canal pores for the mandibular canal and the beginning of an angular pit-line canal groove. There is also a smooth unornamented area that possibly represents an overlap area for the lateral gular plate. The ornamentation of this bone is very close to the Mt Howitt specimen in comprising vermiform linear ridges with tubercles. Not enough of the Mt Howitt specimen is preserved to allow direct comparisons, so the jaw material from Pambula River is only provisionally referred to *Gavinia* sp., based largely on the similar morphology of the scales.

DISCUSSION

Phylogenetic position of *Gavinia* gen. nov.

The Coelacanthiformes have been defined as a monophyletic group by Forey (1981), Cloutier (1991, 1996) and Cloutier and Ahlberg (1996), as they possess at least 11 synapomorphies. Of these, the only ones that are seen in *Gavinia* gen. nov. are (1) tandem double lower jaw joint, in which the long retroarticular process of the lower jaw is braced posteriorly behind the quadrate by the long symplectic; (2) pore system in the snout (implying the presence of a rostral organ), and (3) short dentary, relative to the total lower jaw length. Of the remaining synapomorphies listed by Cloutier (1996), the loss of the maxilla and absence of a surangular are consistent with the known morphology of *Gavinia*.

Gavinia gen. nov. shows typically coelacanthiform features in its lower jaw structure; complex hyoid arch with short, broad hyomandibular; large, deep operculum; and tail with short, interlocking lepidotrichia. Similar linear, vermiform ornamentation on scales and dermal bones is seen in many primitive coelacanths, but also occurs on the dermal bones of many early actinopterygians (e.g. *Howqualepis*, Long 1988).

In having a relatively long dentary for a coelacanth, *Gavinia* is seen to resemble the primitive condition seen in other sarcopterygians (onychodontiforms, porolepiforms, osteolepiforms). There appear to be two lines of evolution for the lower jaw in basal coelacanths (Figure 12). The first group contains those like *Miguashaia, Rhabdoderma, Lochmocercus* and *Polyosteorhynchus* (Lund and Lund 1985), in which the angular is rounded posteriorly and the ventral margin of the lower jaw is relatively straight to convex; and the second group consists of those like *Diplocercides, Nesides, Hadronector, Caridosuctor* and *Allenypterus* in which the lower jaw may be concave along its ventral margin or strongly arches with the dentary inflected strongly away from the angle of the posterodorsal margin of the angular (the latter feature being most pronounced in *Hadronector*). If these observations are any indication of early coelacanthiform phylogenetic trends (reflecting perhaps distinct feeding adaptations), then it would suggest that *Gavinia* is more akin to the former group.

The shape of the operculum in *Gavinia* suggests that it is closer to *Diplocercides* than to *Miguashaia*, the latter having a relatively smaller operculum, high up on the cheek, and not coming close to the ventral margin of the cheek area. In *Diplocercides* and *Nesides*, the operculum is very large and triangular in form, extending below the ventral margin of the cheek. Although the ventral edge of the operculum is tentatively restored in *Gavinia*, it still shows that this is a very large bone and may easily have extended to the ventral margin of the cheek.

Figure 13A shows the latest hypothesis of sarcopterygian interrelationships, based on the data matrix analysis using 140 characters (158 apomorphic character states) by Cloutier and Ahlberg (1996). It can be seen from this scheme that onychodontids (as known from their relatively incomplete data set) are regarded as more derived than Coelacanthiformes. Cloutier and Ahlberg (1996) based this on nine characters but only one was not subsequently transformed: the presence of a surangular in the lower jaw. From this larger scheme their basal coelacanthiform cladogram placed *Miguashaia* as the primitive sister taxon to all other coelacanthiforms, with *Allenypterus* being the next most primitive form, and *Diplocercides* spp. representing the first node of the base of the more advanced coelacanthiform groups.

Cloutier (1996) united all coelacanthiforms (apart from *Miguashaia*) on the basis of the following characters: loss of the intertemporal and heterocercal type of tail; presence of a subopercular that is longer than deep; a supplementary caudal fin; and having the distal ends of lepidotrichia branched. *Gavinia* gen. nov. is seen to be as primitive as *Miguashaia* in that it appears to have an intertemporal present, and has a heterocercal tail. However, in having a caudal fin with branching lepidotrichia and a weakly developed epichordal lobe (on the dorsal hypochordal division of the caudal fin), it appears to be more derived than *Miguashaia*, according to Cloutier's (1996) analysis.

Gavinia gen. nov. shows other features here deemed to be more primitive than *Miguashaia* in (a) the presence of a relatively longer dentary, (b) lack

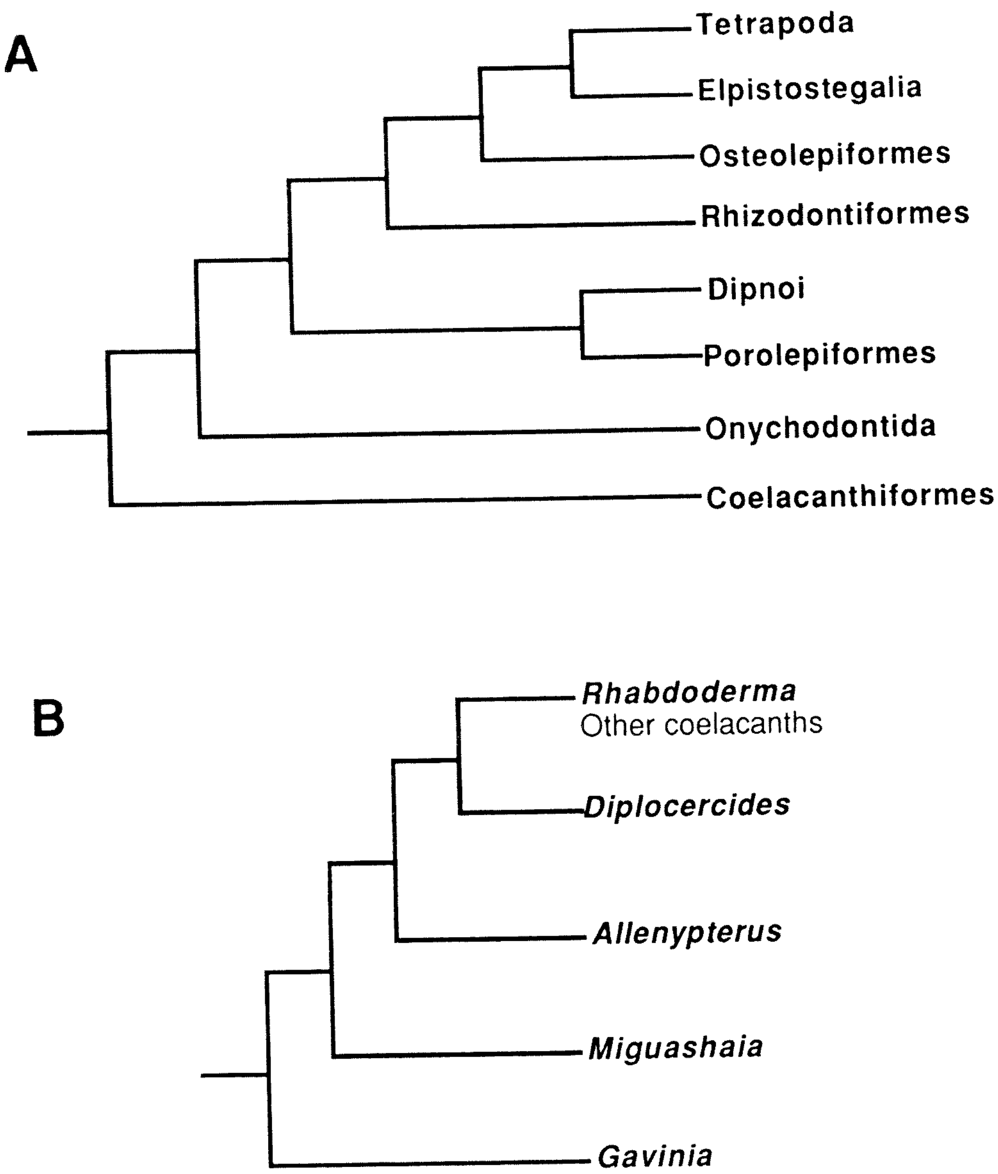


Figure 13 A, hypothesis of sarcopterygian interrelationships, after Cloutier and Ahlberg (1996). B, simplified cladogram of early coelacanth interrelationships, modified from Cloutier and Ahlberg (1996) to show the suggested phylogenetic position of *Gavinia* gen. nov., as discussed in the text.

of a high-profiled angular, (c) having an anterior coronoid developed as a small parasymphysial tooth plate (although this could alternatively be regarded as an autapomorphy of the genus), and (d) possessing an apparently longer cheek region. Although unknown in *Miguashaia*, the large lateral rostral of *Gavinia* gen. nov. (being of equal size to the premaxilla) is a character not found in any other primitive coelacanth. The premaxilla of *Gavinia* gen. nov. appears to be significantly larger than the premaxilla, relative to overall head size, in the Early Carboniferous forms from Bear Gulch (Lund and Lund 1985) and in *Rhabdoderma elegans* (Forey 1981).

At this stage, without more material to elucidate the anatomy of this tantalizing form, *Gavinia* gen. nov. can be placed equivocally as either the basal plesiomorphic member of the Coelacanthiformes or as a sister taxon to *Miguashaia*, based on shared absences of the more derived coelacanthiform synapomorphies listed above. The closer similarity between the proportional shape of the head of *Gavinia* gen. nov., when compared with the most primitive of the remaining sarcopterygian groups, the onychodontids (based on the Gogo *Onychodus*, Figure 12), shows that the long cheek, low, elongate lower jaw, large dentary, and relatively larger premaxilla, would suggest that *Gavinia* gen. nov. is less derived than *Miguashaia* in terms of general sarcopterygian skull structure. I therefore suggest that it be placed as the plesiomorphic sister taxon to all other coelacanthiforms (Figure 13B).

The fragments from Pambula River attributed to *Gavinia* gen. nov. sp. indet., dated at possibly earliest Givetian, constitute the oldest coelacanth remains currently known. The older age assessment of the Mt Howitt site as being probably early to middle Givetian, as discussed in the beginning of this paper, and the plesiomorphic nature of *Gavinia* gen. nov., compared to other Devonian coelacanths, prompts the suggestion that eastern Gondwana may have been the location for the origin of the coelacanths. The presence of other primitive coelacanths along the northern margin of Gondwana (Frasnian of Iran, Janvier and Martin 1979; Morocco, Lelièvre and Janvier 1988) adds further weight to this hypothesis. The rapid dispersal of the group to Euramerica by the late Givetian is also in accord with the faunal interchange event for this time between East Gondwana and Euramerica proposed by Young (1981). This working hypothesis, however, can only be tested further by the predicted discovery of coelacanthiform remains in older deposits of Early-Middle Devonian age in Gondwanan regions.

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REFERENCES

Anderson, M.E., Hiller, N. and Gess, R.W. (1994). The first *Bothriolepis*-associated Devonian fish fauna from Africa. *South African Journal of Science* **90**: 397–403.

Bjerring, H.C. (1977). A contribution to the structural analysis of the head of craniate animals. *Zoologica Scripta* **6**: 127–183.

Campbell, K.S.W. and Barwick, R.E. (1987). Palaeozoic lungfishes — a review. *Journal of Morphology* Supplement **1**: 93–131.

Cloutier, R. (1991). Interrelationships of Palaeozoic actinistians: patterns and trends. *In* Chang, M.M., Liu, Y.H. and Zhang, G.R. (eds), *Early vertebrates and related problems of evolutionary biology*: 379–428, Science Press, Beijing, China.

Cloutier, R. (1996). The primitive actinistian *Miguashaia bureaui* Schultze (Sarcopterygii). *In* Schultze, H.-P. and Cloutier, R. (eds), *Devonian fishes and plants of Miguasha, Quebec, Canada*: 227–247, Verlag, Dr Friedrich Pfiel, Munich, Germany.

Cloutier, R. and Ahlberg, P.E. (1996). Morphology, characters, and the interrelationships of basal sarcopterygians. *In* Stiassny, M.L.J., Parenti, L.R. and Johnson, G.D. (eds), *Interrelationships of fishes*: 445–479, Academic Press, London, U.K.

Cope, E.D. (1871). On two extinct forms of the physostomi of the neotropical region. *Proceedings of the American Philosophical Society, Philadelphia* **12**(86): 53–55.

Forey, P.L. (1981). The coelacanth *Rhabdoderma* in the Carboniferous of the British Isles. *Palaeontology* **24**: 203–29.

Gess, R.W. and Hiller, N. (1995). A preliminary catalogue of fossil algal, plant, arthropod, and fish remains from a Late Devonian block shale near Grahamstown, South Africa. *Annals of the Cape Provincial Museums (Natural History)* **19**: 225–304.

Huxley, T.H. (1880). On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* **1880**: 649–662.

Jaeckel, O. (1927). Der Kopf der Wirbeltiere. *Ergebnisse der Anatomie und Entwicklungsgeschichte* **27**: 811–927.

Janvier, P. and Martin, M. (1979). Les vertébrés dévoniens de l'Iran central. II — Coelacanthiformes, Struniiformes, Osteolepiformes. *Géobios* No. 12: 497–511.

Jarvik, E. (1972). Middle and Upper Devonian Porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* n. sp. *Meddelser om Grønland* **187**(2): 1–295.

Jessen, H. (1966). Die Crossopterygier des Oberen Plattenkalkes (Devon) der Bergisch-Gladbach-Paffrather Mulde (Rheinisches Schiefergebirge) unter Berücksichtigung von amerikanischem und europäischem *Onychodus*-material. *Arkiv Zoologi* **18**: 305–89.

Johanson, Z. and Young, G.C. (this volume). New *Bothriolepis* (Placodermi; Antiarchi) from the Braidwood region, New South Wales, Australia (Frasnian). *Records of the Western Australian Museum* Supplement No. 57: 55–76.

Lelièvre, H. and Janvier, P. (1988). Un Actinistien (Sarcopterygii, Vertebrata) dans le Dévonien supérieur du Maroc. *Comptes-Rendus de l'Academie des Sciences*, Paris **307**: 1425–1430.

Long, J.A. (1982). Late Devonian fish taphonomy in Victoria: a cautionary note to biostratigraphers. *In* Rich, P.V. and Thompson, E.M. (eds), *The fossil vertebrate record of Australasia*: 120–127, Monash University Offset Printing Unit, Clayton, Victoria.

Long, J.A. (1983a). A new diplacanthoid acanthodian from the Late Devonian of Victoria. *Memoirs of the Association of Australasian Palaeontologists* **1**: 51– 65.

Long, J.A. (1983b). New bothriolepid fishes from the Late Devonian of Victoria, Australia. *Palaeontology* **26**: 295–320.

Long, J.A. (1984). New phyllolepids from Victoria and the relationships of the group. *Proceedings of the Linnean Society of New South Wales* **107**: 263–304.

Long, J.A. (1985). The structure and relationships of a new osteolepiform fish from the Late Devonian of Victoria, Australia. *Alcheringa* **9**: 1–22.

Long, J.A. (1986). A new Late Devonian acanthodian fish from Mt Howitt, Victoria, Australia, with remarks on acanthodian biogeography. *Proceedings of the Royal Society of Victoria* **98**: 1–17.

Long, J.A. (1987). An unusual osteolepiform fish from the Late Devonian of Victoria, Australia. *Palaeontology* **30**: 839–852.

Long, J.A. (1988). New palaeoniscoid fishes from the Late Devonian and Early Carboniferous of Victoria. *Memoirs of the Association of Australasian Palaeontologists* **7**: 1–64.

Long, J.A. (1991). The long history of fossil fish. *In* Vickers-Rich, P., Monaghan, J.M., Baird, R.F. and Rich, T.H. (eds), *Vertebrate palaeontology of Australasia*: 336–428, Pioneer Design Studios, Lilydale, Victoria.

Long, J.A. (1992). Cranial anatomy of two new Late Devonian lungfishes, from Mt. Howitt, Victoria. *Records of the Australian Museum* **44**: 299–318.

Long, J.A. (1993). Cranial ribs in Devonian lungfishes and the origin of dipnoan air breathing. *Memoirs of the Association of Australasian Palaeontologists* **15**: 199–210.

Long, J.A., Campbell, K.S.W. and Barwick, R.E. (1997). Osteology and functional morphology of the osteolepiform fish *Gogonasus andrewsae* Long, 1985, from the Upper Devonian Gogo Formation, Western Australia. *Records of the Western Australian Museum* Supplement No. 53: 1–89.

Long, J.A. and Werdelin, L. (1986). A new species of *Bothriolepis* from Tatong, Victoria, with descriptions of other species from the State. *Alcheringa* **10**: 355–400.

Lund, R. and Lund, W. (1985). The coelacanths from the Bear Gulch Limestone (Namurian) of Montana and the evolution of the Coelacanthiformes. *Bulletin of the Carnegie Museum of Natural History* **25**: 1–74.

Pearson, D.M. and Westoll, T.S. (1979). The Devonian actinopterygian *Cheirolepis* Agassiz. *Transactions of the Royal Society of Edinburgh* **70**: 337–99.

Romer (1955). Fish origins — fresh or salt water? *In: Papers in marine biology and oceanography*: 262–280. Pergamon Press, London, U.K.

Schultze, H.-P. (1973). Crossopterygier mit heterozerker Schwanzflosse aus dem Oberdevon Kanadas, nebst einer Beschreibung von Onychodontida-Resten aus dem Mitteldevon Spaniens und aus dem Karbon der USA. *Palaeontographica* **A143**: 188–208.

Schultze, H.-P. (1993). Sarcopterygii. *In* Benton, M. (ed.), *The Fossil Record* **2**: 657–673, Chapman and Hall, London, U.K.

Schultze, H.-P. and Cloutier, R. (1996). Comparison of the Escuminac Formation ichthyofauna with other late Givetian/early Frasnian ichthyofaunas. *In* Schultze, H.-P. and Cloutier, R. (eds), *Devonian fishes and plants of Miguasha, Quebec,* Canada: 348–368, Verlag, Dr Friedrich Pfiel, Munich, Germany.

Stensiö, E. (1937). On the Devonian coelacanthids of Germany with special reference to the dermal skeleton. *Kungliga svenska VetenskapAkadamiens Handlingar* **16**(4): 1–56.

Turner, S. (1997). Sequence of Devonian thelodont scale assemblages in East Gondwana. *Geological Society of America Special Paper* **321**: 295–315.

Turner, S. and Young, G.C. (1994). Thelodont scales from the Middle-Late Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Antarctic Science* **4**: 89–105.

Williams, I.S., Tetley, N.W., Compston, W. and McDougall, I. (1982). A comparison of K-Ar and Rb-Sr ages of rapidly cooled igneous rocks: two points in the Palaeozoic time scale re-evaluated. *Journal of the Geological Society of London* **139**: 557–568.

Young, G.C. (1981). Biogeography of Devonian vertebrates. *Alcheringa* **5**: 225–243.

Young, G.C. (1983). A new antiarchan fish (Placodermi) from the Late Devonian of southeastern Australia. *Bureau of Mineral Resources Journal of Australian Geology and Geophysics* **8**: 71–81.

Young, G.C. (1988). Antiarchs (placoderm fishes) from the Devonian Aztec Siltstone, southern Victoria Land, Antarctica. *Palaeontographica* **A202**: 1–125.

Young, G.C. (1989). New occurrences of culmacanthid acanthodians (Pisces, Devonian) from Antarctica and southeastern Australia. *Proceedings of the Linnean Society of New South Wales* **111**: 11–24.

Young, G.C. (1993). Middle Palaeozoic macrovertebrate biostratigraphy of Eastern Gondwana. *In* Long, J.A. (ed.), *Palaeozoic vertebrate biostratigraphy and biogeography*: 208–251, Belhaven Press, London, U.K.

Young, G.C. (this volume). Preliminary report on the biostratigraphy of new placoderm discoveries in the Hervey Group (Upper Devonian) of central New South Wales. *Records of the Western Australian Museum* Supplement No. 57: 139–150.

Young G.C. and Gorter, J.D. (1981). A new fish fauna of Middle Devonian age from the Taemas/Wee Jasper region of New South Wales. *Bulletin of the Bureau of Mineral Resources* **209**: 83–147.

Young, G.C., Long, J.A. and Ritchie, A. (1992). Crossopterygian fishes from the Devonian of Antarctica: systematics, relationships and biogeographic significance. *Records of the Australian Museum* Supplement No. 14: 1–77.

Young, G.C., Long J.A. and Turner, S. (1993). Appendix 1: faunal lists of eastern Gondwana Devonian macrovertebrate assemblages. *In* Long, J.A. (ed.), *Palaeozoic vertebrate biostratigraphy and biogeography*: 246–251, Belhaven Press, London, U.K.

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