

## A New Osteolepidid Fish from the Upper Devonian Gogo Formation, Western Australia

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### Abstract

A new osteolepidid crossopterygian, *Gogonasmus andrewsi* gen. et sp. nov., is described from a single fronto-ethmoidal shield and associated ethmosphenoid, from the Late Devonian (Frasnian) Gogo Formation, Western Australia. *Gogonasmus* is distinguished from other osteolepids by the shape and proportions of the fronto-ethmoidal shield, absence of palatal fenestrae, well developed basipterygoid processes and moderately broad parasphenoid. The family Osteolepididae is found to be paraphyletic, with *Gogonasmus* being regarded as a plesiomorphic osteolepidid at a similar level of organisation to *Thursius*.

### Introduction

Much has been published on the well-preserved Late Devonian fish fauna from the Gogo Formation, Western Australia, although to date all the papers describing fish have been on placoderms (Miles 1971; Miles and Dennis 1979; Dennis and Miles 1979-1983; Young 1984), palaeoniscoids (Gardiner 1973, 1984; Gardiner and Bartram 1977) or dipnoans (Miles 1977; Campbell and Barwick 1982a, 1982b, 1983, 1984a). This paper describes the only osteolepiform from the fauna (Gardiner and Miles 1975), a small snout with associated braincase, ANU 21885, housed in the Geology Department, Australian National University. The specimen, collected by the Australian National University on the 1967 Gogo Expedition, was prepared by Dr S.M. Andrews (Royal Scottish Museum) and later returned to the ANU. *Onychodus* is the only other crossopterygian in the fauna.

In its proportions and palatal structure the new specimen provides some additional new points of the anatomy of osteolepiforms. Few Devonian crossopterygians are known from Australia, and so the specimen is significant in having resemblances to typical Northern Hemisphere species. The only other osteolepiforms described from Australia are *Canowindra grossi* (Thomson, 1973; Long, 1985b), the osteolepidid *Gyroptychius* cf. *G. australis* (Young and Gorter, 1981) and a primitive eusthenopterid, *Marsdenichthys longioccipitus* (Long, 1985a). *Canowindra* and *Marsdenichthys*, both of Late Devonian age, are endemic genera but *Gyroptychius* is well known from Northern Hemisphere Middle Devonian faunas (Jarvik 1948; Jessen 1968; Vorobjeva 1977). Other undescribed Australian osteolepidids have been found recently from Mt Howitt and the South

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Blue Range, Victoria, and from the Narrien Range, Queensland (*Megalichthys* sp., Long and Turner, 1984; Long, in press).

The fronto-ethmoidal shield and ethmosphenoid of osteolepiforms is well known largely through the works of Jarvik (1942, 1954, 1966). Within osteolepidids the anatomy of the ethmosphenoid has been described in *Osteolepis* (Thomson, 1965), *Thursius*, *Megistolepis* (Vorobjeva, 1977), *Megalichthys* (Jarvik, 1966), *Ectosteorhachis* (Thomson, 1964) and *Chrysolepis* (Lebedev, 1983). This work describes the anatomy of the new specimen with particular reference to the structure of these taxa.

### Systematics

Subclass Osteichthyes

Order Osteolepiformes Jarvik, 1942

#### Remarks

Despite recent suggestions that the Osteolepiformes may be a paraphyletic collection of primitive fishes (Janvier 1980; Gardiner 1980; Rosen *et al.* 1981) Long (1985a) has argued that the group is monophyletic, although he admits that some of the characters used to demonstrate monophyly are not widely known throughout the group. Osteolepiformes are the only group of primitive osteichthyans which possess cosmine and a single pair of external nares plus a choana. Rosen *et al.* (1981) have presented an alternative explanation for the choanae of osteolepiforms, arguing that a true choana is present only in dipnoans and tetrapods. This has been refuted by Campbell and Barwick (1984a), and here the choana in osteolepiforms is accepted. The new specimen is referable to the order because it is cosmine-covered, possesses one pair of nares plus choanae, and has a dermal bone pattern identical with that of osteolepiforms.

Family Osteolepididae Cope, 1889

#### Remarks

This family is difficult to define as it is characterised essentially by generalised features of osteolepiforms and other osteichthyans, which suggests that the Osteolepididae could be paraphyletic. This is discussed further at the end of this paper. In lacking characters found in the higher groups of Osteolepiformes, such as eusthenopterids or panderichthyids, the new specimen must be referred to the Osteolepididae.

*Gogonasus* gen. nov.

#### Type Species

*Gogonasus andrewsi* sp. nov.

### Diagnosis

A cosmine-covered osteolepidid having a fronto-ethmoidal shield possessing the following suite of characters: breadth/length index of around 80; ethmosphenoid twice as long as deep; rostral margin is almost a complete hemisphere across the anterolateral corners; external nares are subrectangular, each with a strongly developed dermintermedius process; ethmoid and sphenoid divisions of the neurocranium are separated by an irregular suture running through the optic foramen; basipterygoid processes are strongly developed and suprapterygoid processes weakly developed; palatal lamina lacks apical fossae.

### Remarks

As shown below the proportions of the dermal shield together with the deep ethmosphenoid shape and featureless palate distinguish the genus from other osteolepidids. Although some of the diagnostic features listed could be symplesiomorphies for osteolepidids, the genus is characterised by the suite of listed characters, one of which is unique, and others of restricted distribution in the known osteolepidiforms. The genus is named after the Gogo Fm from which the specimen comes, and the Latin 'nasus' meaning nose.

### *Gogonasmus andrewsi* sp. nov.

Figures 1-6, 7-E

Osteolepid — Gardiner and Miles, 1975: 75 indeterminate genus (Osteolepidae) — Long and Turner, 1984: 241.

### Holotype

ANU 21885, only specimen. Locality 93b (Miles 1971, Figure 1; Paddy's Springs), Gogo Formation (Frasnian), near Fitzroy Crossing, Western Australia.

### Diagnosis

As for genus.

### Etymology

In honour of Dr S.M. Andrews (Royal Scottish Museum) who has contributed much to our knowledge of crossopterygian fishes.

### Description

The specimen is almost complete but lacks the central anterior dermal bones between the nares, the dermosphenotics and supraorbitals, and the anterior end of the parasphenoid (Figures 1-6).

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Abbreviations Used in Figures

II	optic nerve (or its foramen)
III	oculomotor nerve foramen
IV	trochlear nerve foramen
a.aut	attachment area for autopalatine
a.iob	attachment area for obliquus inferior muscle
ant.r	anterior rectus muscle
ao	orbital artery
a.sob	attachment area for superior obliquus muscle
a.T	anterior tectal
a.Vom	attachment area for vomer
bac	attachment area for subcranial muscle
bac.m	subcranial (basicranial) muscle
bpt	basipterygoid process
cr.cav	cranial cavity
d.lev	attachment area for arcus palatini muscle
f.end	fenestra endochoanalis
Fr	frontal
fr.pl	frontal pit-line groove
ifc	infraorbital canal
in.c	internal carotid foramen
in.r	internal rectus muscle
i.ob	inferior obliquus muscle
MPR	median postrostral
Na	nasal
nar	external naris
nas.c	nasal capsules
not	notochordal concavity
oa.SOT	attachment area for supraorbito-tectal
or.s	orbital vein sinus
pal.de	palatal depression
pal.lm	palatal lamina
pa.PM	palatal division of premaxilla
perf	small foramina for perforans profundus nerves
pin	pineal foramen
pit.v	pituitary vein foramen
plc	posterolateral corner of dermal shield
PM	premaxilla
pos.r	posterior rectus muscle
pr?	small process of unknown function
pr.con	processus connectens
pr.der	processus dermintermedius
pro	main branch of profundus nerve (or foramen)
PSp	parasphenoid
RL	lateral rostral bone
s.ob	superior obliquus muscle
soc	supraorbital sensory-line
so.cr	crista suspendens
sop	superior ophthalmic nerve foramen
spt	suprapterygoid process
s.rec	superior rectus muscle

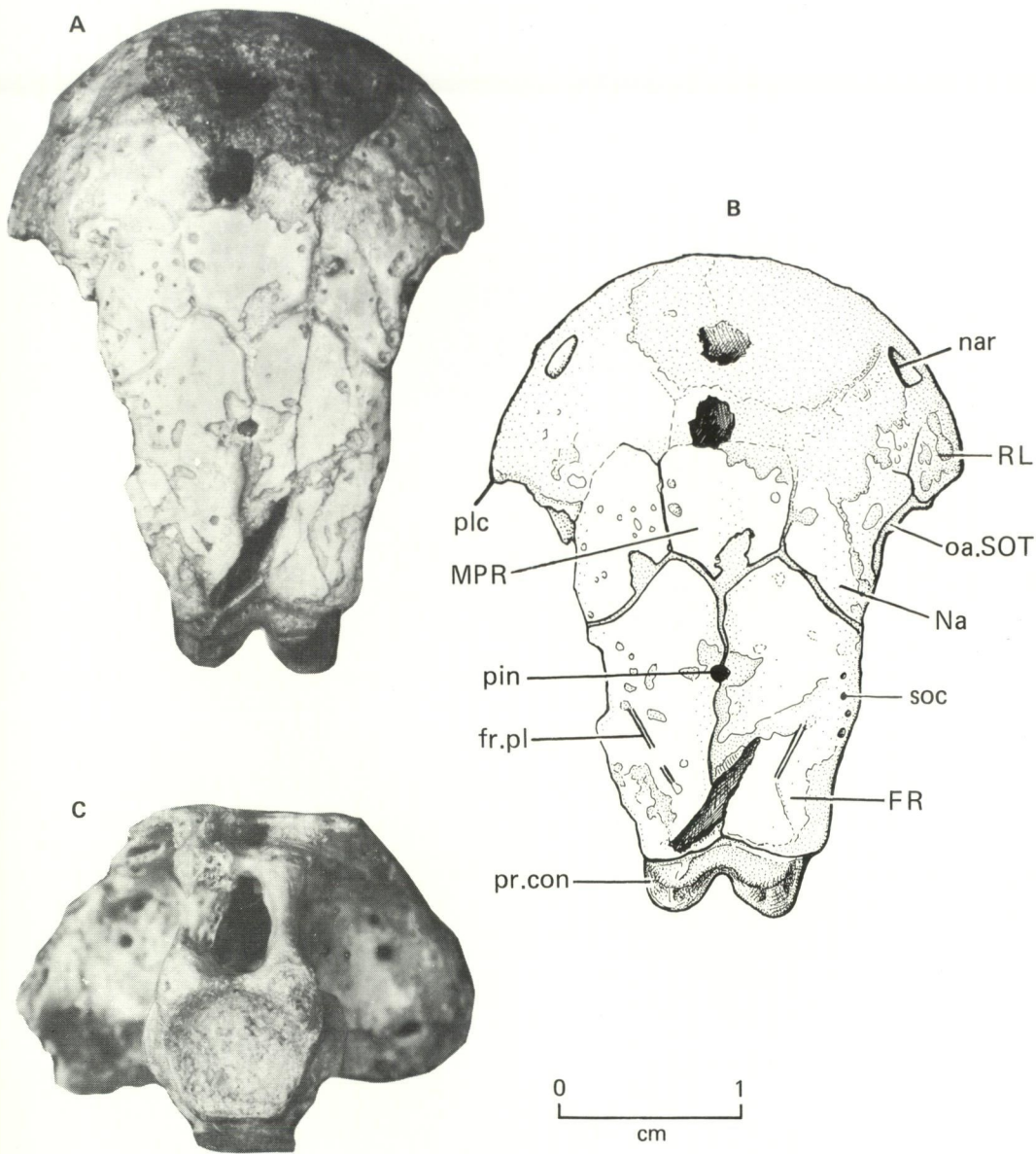
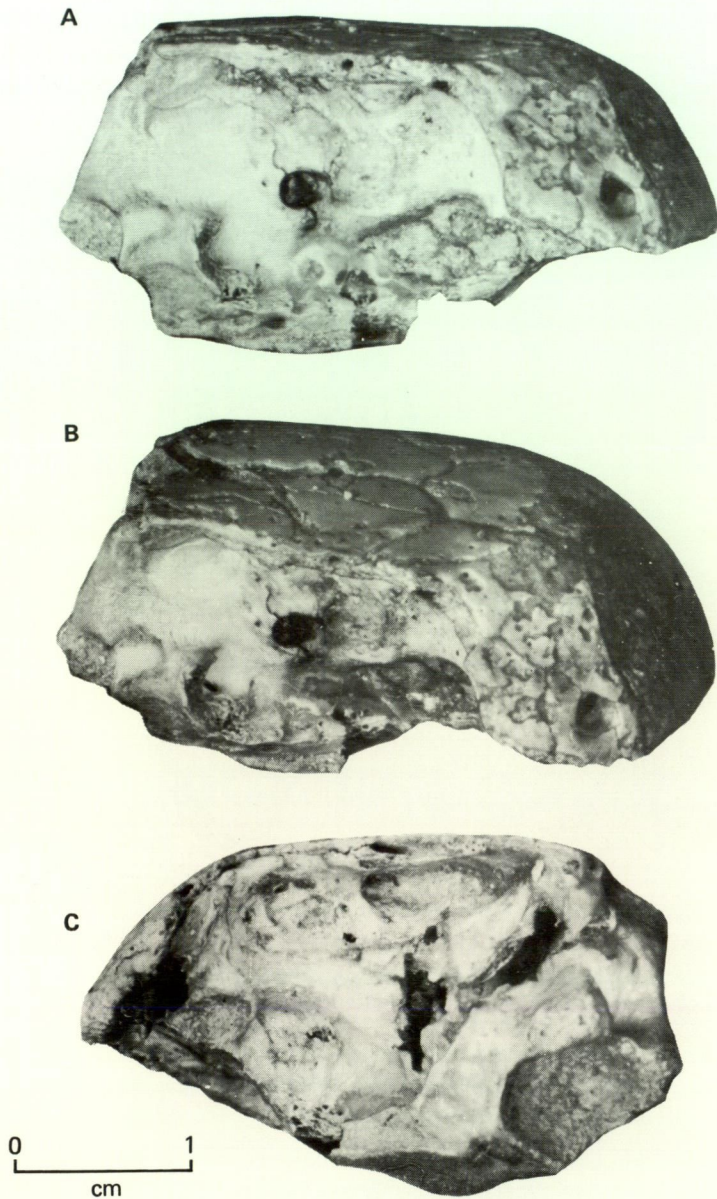


Figure 1 *Gogonasmus andrewsi* gen. et sp. nov., Late Devonian Gogo Fm., Western Australia. Holotype. ANU 21885. A, B, fronto-ethmoidal shield in dorsal view; C, posterior view of ethmosphenoid showing postnasal wall.



**Figure 2** *Gogonasmus andrewsi* gen. et sp. nov., Late Devonian Gogo Fm., Western Australia. Holotype, ANU 21885. Ethmosphenoid. A, left lateral view; B, oblique dorso-lateral view; C, oblique posterolateral view showing postnasal wall.

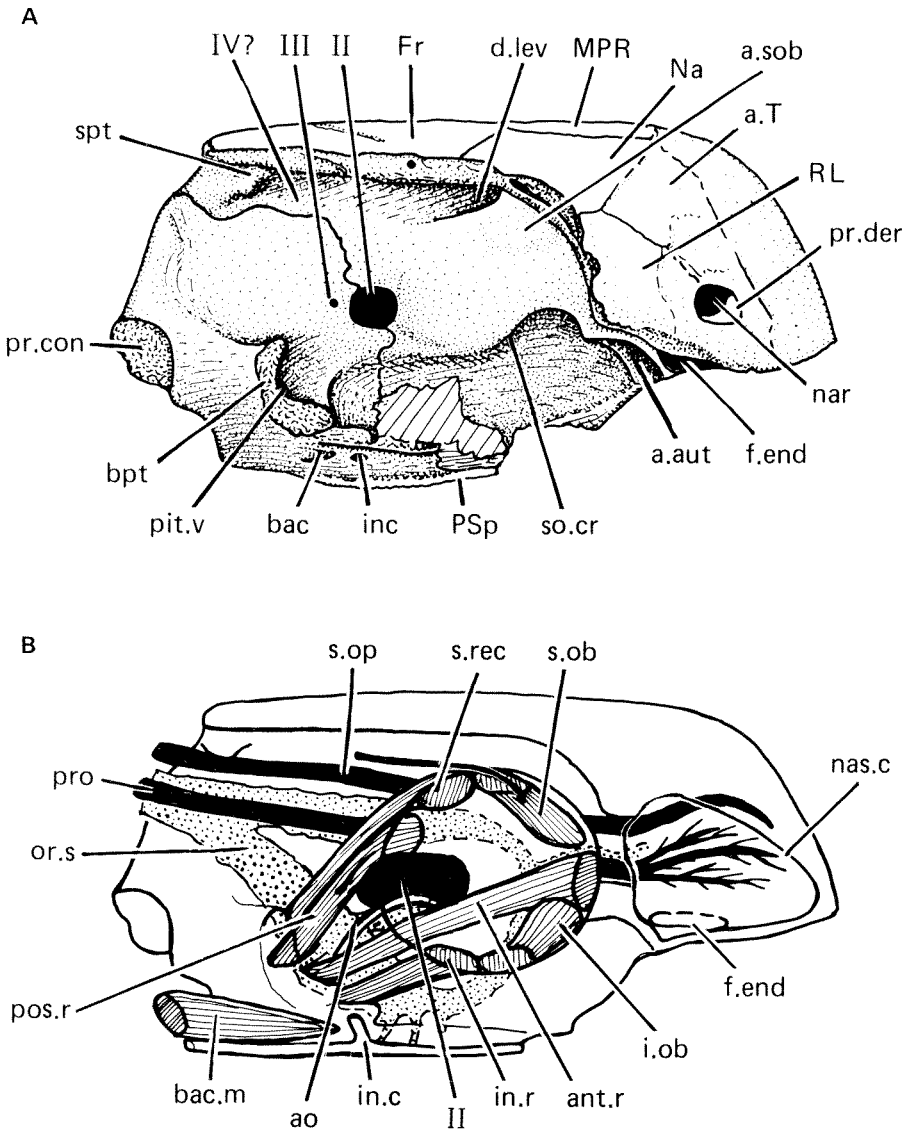


Figure 3 *Gogonasmus andrewsi* gen. et sp. nov., Late Devonian Gogo Fm., Western Australia. A, sketch interpretation of holotype, ANU 21885, in lateral view; B, attempted restoration of some aspects of the soft anatomy, as discussed in the text. Nerves black, veins stippled, arteries white, muscles striped.

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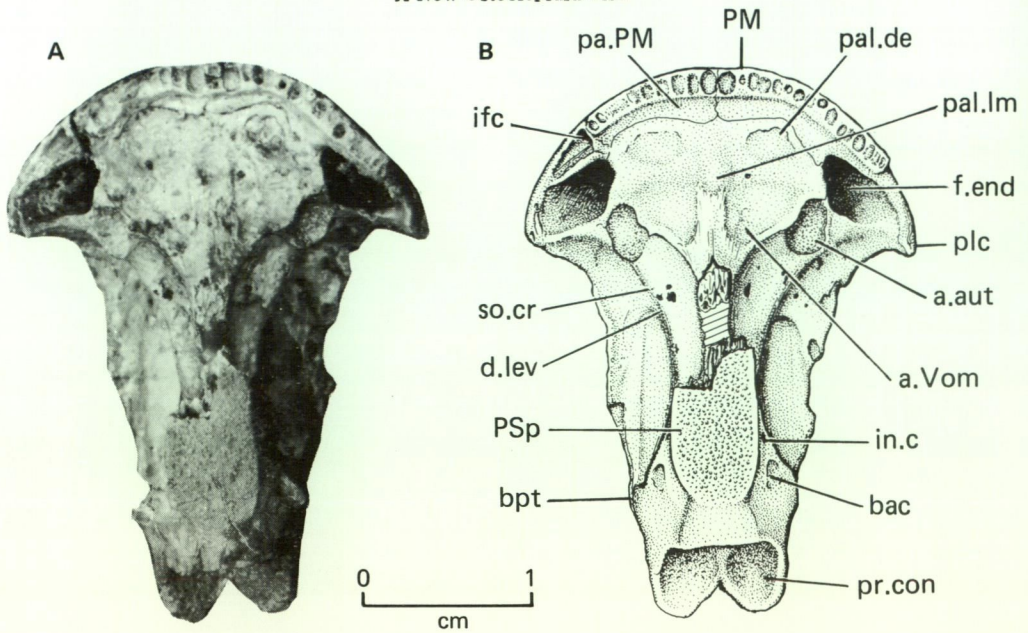


Figure 4 *Gogonasmus andrewsi* gen. et sp. nov., Late Devonian Gogo Fm., Western Australia. Holotype ANU 21885. A, B, ethmosphenoid and parasphenoid in ventral view.

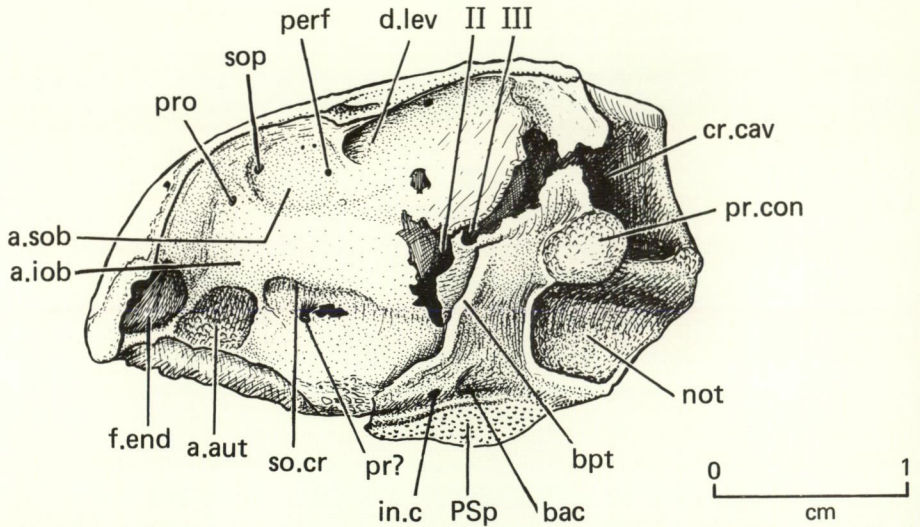


Figure 5 *Gogonasmus andrewsi* gen. et sp. nov., Late Devonian Gogo Fm., Western Australia. Holotype ANU 21885 in posterior oblique view showing postnasal wall (see Figure 2-C for photograph).



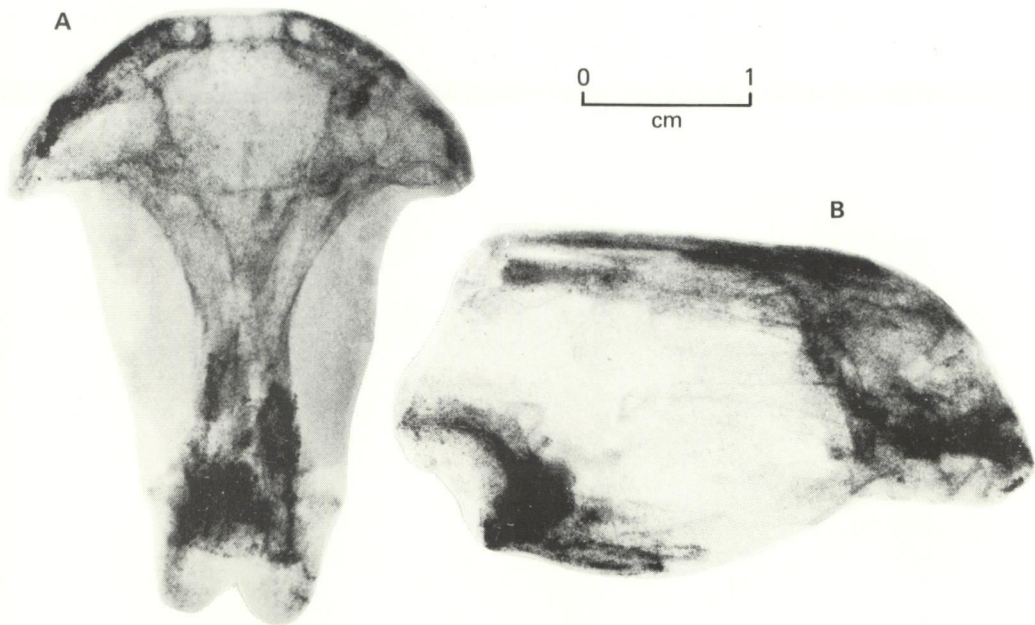


Figure 6 *Gogonasmus andrewsi* gen. et sp. nov., Late Devonian Gogo Fm., Western Australia. Holotype ANU 21885. Positive prints of radiographs of the specimen in A, dorsal view; B, lateral view.

The pattern of dermal bones (Figures 1, 2) is similar to *Osteolepis* (Jarvik, 1948), except that the anterior nasal series is not defined due to the extensive cosmine cover. There appears to be large lateral rostral and anterior tectal bones enclosing the external nares. Few laterosensory canal pores are visible, and these have a scattered distribution on the nasals.

In having a breadth/length index of 81, and a breadth/depth index of around 40 the ethmosphenoid of *Gogonasmus* can be separated from other osteolepidids for which this region is known (*Gyroptychius* spp., *Thursius* spp., *Osteolepis* spp., *Megistolepis*; Figure 7). It is distinguished from *Latvius* spp. by its narrower fronto-ethmoidal shield and fewer sensory-line canal pores, and from advanced osteolepidids such as *Megalichthys* and *Ectosteorhachis* by the shapes of the external nostrils and premaxillae and the absence of palatal fenestrae or apical fossae (Thomson 1964; Jarvik 1966). The ethmosphenoid is divided into anterior ethmoid and posterior sphenoid (or postethmoid) divisions by a suture which runs from the posterior margin of the specimen horizontally and then ventrally through the optic nerve foramen (Figures 2, 3). Ventral to this opening the suture disappears into the damaged area of the specimen and cannot be traced, but it presumably follows the contact between the parasphenoid and

sphenoid. The external nostrils are almost square in outline, being slightly longer along the ventral border, from which the well developed processus dermintermedius inwardly extends. There is no tectal process present. The nasal capsules are widely separated by an internasal vacuity, visible through the damaged anterior of the snout. In dorsal view (from radiographs; Figure 6) the nasal capsules are about twice as broad as their rostrocaudal length. The ventral opening from the nasal capsule to the palate (fenestra choanalis endonarhina) is just over half the area of the nasal capsule, and is situated posterior to the external nostrils.

The palatal lamina is simple, being an almost flat triangular sheet from the parasphenoid to the lateral corners of the premaxillae. There are shallow paired depressions just posterior of the premaxillae, and paired broader depressions upon which the vomers sat posterior to these. The parasphenoid is developed essentially as in *Thursius estonicus*, although the buccohypophysial foramen is not visible on the specimen.

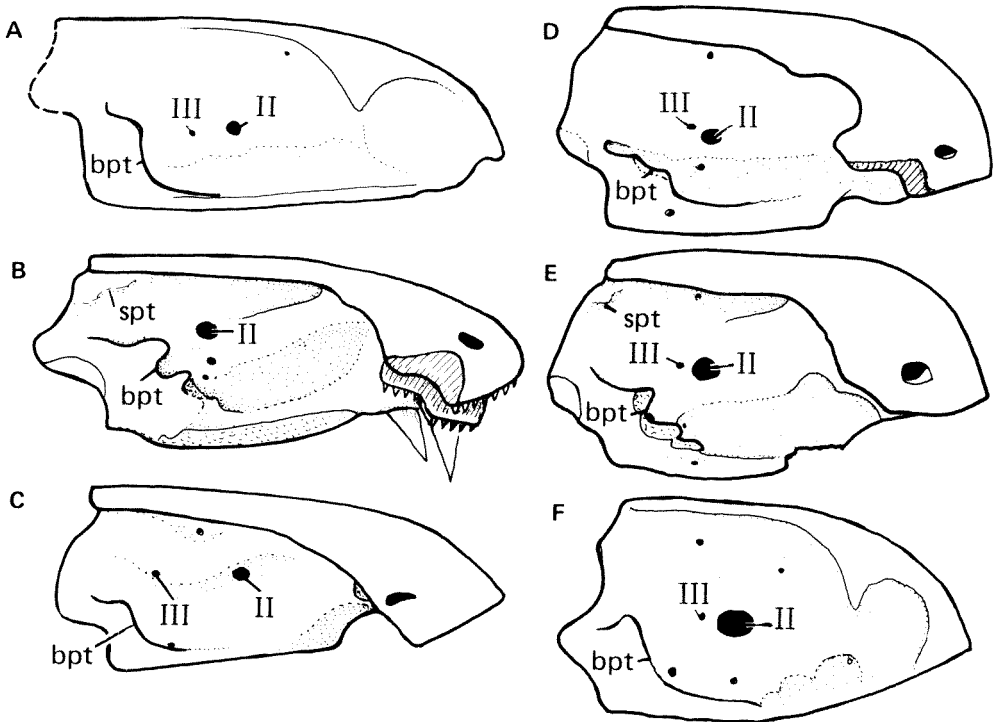


Figure 7 Comparative anatomy of osteolepidids (and *Rhizodopsis*) in which the ethmosphenoid is known. A, *Osteolepis* (from Thomson, 1965); B, *Megistolepis* (from Vorobjeva, 1977); C, *Chrysolepis* (from Lebedev, 1983); D, *Thursius* (from Vorobjeva, 1977); E, *Gogonasus*, gen. nov.; F, *Rhizodopsis* (from Jarvik, 1966).

The lateral faces of the ethmosphenoid show the normal osteichthyan arrangement of foramina for the optic (II) and oculomotor (III) nerves, which exit the braincase just dorsal of the basiptyergoid process. Although the foramen for the trochlear nerve (IV) cannot be seen as it is covered by glue its position can be estimated as dorsal to the optic nerve foramen. The pituitary vein foramen lies in the pit for the insertion of the posterior eye muscles, medial to the basiptyergoid process. Foramina for the ophthalmica magna and internal carotid arteries are situated just posteroventral to the optic nerve foramen as in *Eusthenopteron* (Jarvik, 1954). Of note is the strongly developed basiptyergoid process which has an almost U-shaped profile with the anterior, dorsally facing division extending forward into a narrow shelf running along the dorsal edge of the parasphenoid. The basiptyergoid process is not comparably developed in *Eusthenopteron*, *Osteolepis* or *Rhizodopsis* (Figure 7) where it is more evenly curved, almost an L-shaped platform (Jarvik 1954, 1966; Thomson 1965). Similar development of a strongly curved basiptyergoid process is seen otherwise only in *Megistolepis* and to a lesser extent *Thursius* (Figure 7; Vorobjeva, 1977). The supraptyergoid process is weakly developed in *Gogonasmus* as a small bump near the posterodorsal corner of the ethmosphenoid (Figures 2-A, 3-A). It is covered by periosteal bone, unlike the basiptyergoid process which has a rough area for attachment of a cartilage cap. Among other osteolepidids the supraptyergoid process is absent in *Chrysolepis* (Ledede, 1983) and appears absent in *Thursius estonicus* (Vorobjeva, 1977; Figure 25), but is developed in *Megistolepis*. The supraptyergoid process in *Gogonasmus* differs markedly from that in *Eusthenopteron*, where it is well developed and lacking periosteal bone, indicating a ligamentous connection with the ascending process of the palatoquadrate.

The autopalatine connective area on *Gogonasmus* is well developed. There is a strong crista suspensens (so.cr) present which curves anteroventrally to meet the autopalatine attachment area. In the anterior expanded region of the autopalatine fossa, ventral to the crista suspensens, is a small process on the left side of the specimen (Figure 5, pr?), possibly for ligamentous attachment to the palatoquadrate. The muscle attachment area for the superior obliquus (a.sob) is weakly defined as a shallow ovoid depression on the dorsal side of the post-natal wall near the profundus nerve foramen (pro, Figure 5) as in *Latimeria* (Millot, Anthony and Robineau, 1978, Figure 27). The inferior obliquus must have inserted just ventral to this area (a.iob, Figure 5), although its attachment surface is not well defined. It is probable that all the posterior eye muscles inserted in the pits medial to the basiptyergoid process (Figure 3-b). Dorsal to the optic nerve foramen there is a well developed dorsal depression for insertion of muscles between the neurocranium and dermal skull roof (d.lev), presumably for the levator arcus palatini as in *Latimeria*. Some aspects of the soft anatomy of the snout of *Gogonasmus* are restored in Figure 3-B, by comparison with *Latimeria* (Millot, Anthony and Robineau 1978) and *Eusthenopteron* (Jarvik, 1980). The processus connectens (pr.con) at the rear of the ethmosphenoid projects strongly as in *Megistolepis* and *Thursius*.

Radiographs of the specimen (Figure 6) show that the tracts for the olfactory nerves meet halfway along the length of the specimen, immediately anterior to the optic nerve foramen. The ventral course of the fossa hypophyseos and the dorsal extension of the pineal tube is developed almost exactly as in *Eusthenopteron*, and require no further comment.

#### Discussion of the endocranial suture of *Gogonasmus*

The division of the ethmosphenoid into separate ethmoid and sphenoid divisions has not previously been reported in osteolepiform fishes. Placoderms are the only group of early gnathostomes which show the nasal capsules ossified inside a separate anterior division of the braincase, the rhinocapsular (Stensiö 1963). Although this separation of the rhinocapsular from the postethmoid is most distinct in early euarthrodires (actinolepidoids, some phylctenaspidooids; Denison, 1978), some palaeacanthaspidooids (e.g. *Romundina*, Ørvig, 1975) and ptyctodontids (Miles and Young, 1977), it is not seen in petalichthyids or antiarchs. Within the various osteichthyan groups the braincase may be divided principally into occipital, otico-occipital and ethmosphenoid divisions. In actinopterygians all three divisions may be present with fissures filled by cartilage in life (Gardiner 1973, 1984). In osteolepiforms, rhizodontiforms (*sensu* Andrews, 1973), porolepiforms and actinistians there are usually only two portions of the braincase: ethmosphenoid and otico-occipital. The condition seen in *Gogonasmus* can therefore be interpreted as either a gnathostome symplesiomorphy shared with placoderms which has been lost in early actinopterygians, or as a juvenile feature of the ethmosphenoid in osteolepiforms, or as an autapomorphy of the genus.

Little is known of the ontogenetic development of osteolepiforms, although recently Schultze (1984) provided data on the growth of the dermal skeleton of the head of *Eusthenopteron*. Schaeffer (1968) suggested that the rhipidistian braincase ossified from the trabecular and parachordal embryonic components. *Gogonasmus* represents a condition which is probably immature, because sutures between neurocranial components of most vertebrates are often fused or lost in maturity (De Beer 1937). The occurrence in *Gogonasmus* of a suture dividing ethmoid and sphenoid portions of the braincase would not seem likely to be an adult autapomorphy in view of the conservatism shown by the patterns of osteolepiform neurocrania (Figure 7), or even those of other primitive osteichthyans, although certain specialised actinistians may retain sutures between growth centres of the neurocranium throughout life (*Laugia*; Forey, 1981, page 208). The intracranial joint might have been secondarily lost, or was not developed in the first case, in the osteolepiform-like *Youngolepis*, from the Early Devonian of China (Chang Mee-man 1982). However, as there is no known record of subdivision of the ethmosphenoid into separate ossifications in other osteolepiforms, porolepiforms or actinistians the condition in *Gogonasmus* is most easily explained as an immature condition. The significance of this persisting suture between

growth centres may be more fully understood when more is known of the braincase in primitive osteolepiforms, onychodontids and actinopterygians.

### Relationships of *Gogonasus*

Before discussing the phylogenetic position of the new form it is necessary to discuss the relationships of the major groups within the Osteolepididae. Vorobjeva (1977) recognised seven subfamilies within the Osteolepididae: Osteolepidinae, Gyroptychinae, Megistolepidinae, Glyptopominae, Vilulichthyinae, Megalichthyinae and Thysanolepidinae. The supposed relationships of these groups are translated into a cladogram by me in Figure 8-A, but synapomorphies uniting these groups are not known. Broadly Vorobjeva unites osteolepidinids, gyroptychinids and megistolepidinids as a plesiomorphic group relative to the rest, in which glyptopominids are the plesiomorphic sister group to the three higher subfamilies. The relationships of the monotypic taxa Thysanolepidinae or Vilulichthyinae are not considered here as they are too poorly known. Characters defining the Osteolepididae (e.g. cosmine present, pineal foramen present, extra-temporal bone in the skull roof, generally long parietal shield) are not unique to the group, and there does not appear to be any one synapomorphy defining the family. Specialised characters are found only within higher osteolepidids, and therefore I conclude that the family, as currently defined, could be paraphyletic. Because osteolepidids possess characters used by Long (1985a) to demonstrate monophyly of the Osteolepiformes they must be retained within that order. The Osteolepididae is, however, here regarded as the plesiomorphic sister group to higher Osteolepiformes (eusthenopterids, rhizodopsidids, panderichthyids).

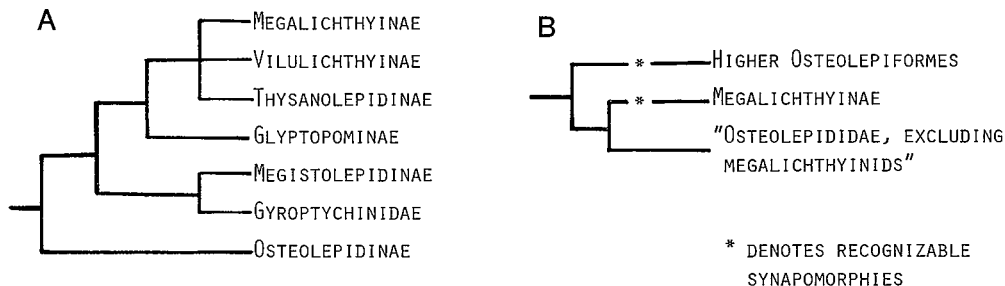


Figure 8 A, Vorobjeva's scheme of osteolepidid relationships converted into a cladogram (after Vorobjeva 1977, fig. 27). B, scheme proposed herein whereby Osteolepidids exclusive of megalichthyinids are shown to be paraphyletic. Synapomorphies discussed in text.

Within the Osteolepididae there are few taxa which vary enough from the generalised forms like *Osteolepis* or *Thursius* to warrant the erection of subfamilies. Advanced forms like *Megalichthys* and *Ectosteorhachis* are perhaps

the only exception to this as they are characterised by at least two synapomorphies: the development of the external nares as slit-like openings, partially enclosed by a small posterior tectal bone; and the presence of an interpremaxillary process with teeth on the premaxillae (Schultze 1974). Further specialisations of this group could be in the structure of the cosmine (Thomson 1975), the extremely deep maxilla (Jarvik 1966), and possibly the complex dermal articulation between the parietal and frontal shields, and the extensive branch of the main lateral-line canal into the parietals (Bjerring 1972). Of the remaining Osteolepididae gyroptychinids (*Gyroptychius* spp. only, Vorobjeva, 1977, page 138) are distinguished from other genera by having a rounded snout with external nares not visible from dorsal view, and glyptopominids (*Glyptopomus* spp., *Latvius* spp., *Megapomus* spp., Vorobjeva, 1977, page 147) presumably by their small orbits, deep cranial form, and numerous laterosensory pores. The characters defining these two groups are of dubious phylogenetic value. The nares of gyroptychinids are only marginally more ventral than those of other osteolepidids, and in their gross anatomy resemble the nares of any other osteolepiform (Jarvik 1942, 1966). Small orbits occur repeatedly within osteolepiforms at various levels of organisation (*Glyptopomus*; *Eusthenodon*; Jarvik, 1950; 1952) and the shape of the head is also variable from one group to another (deep in *Eusthenopteron*, relatively broad in *Eusthenodon*). The arrangement of the laterosensory pores in certain osteolepidids may be a synapomorphy once more is known of their structure within the whole group. I suggest that because of the lack of recognisable synapomorphies most of the Osteolepididae as previously defined, should be regarded as a plesiomorphic sister group to the recognisable monophyletic group such as the megalichthyids (Figure 8-B).

Little can be said of the phylogenetic position of *Gogonasmus*. The simple external nostrils, simple premaxillae and absence of apical fossae on the palatal lamina exclude *Gogonasmus* from close relationship to advanced osteolepiforms such as megalichthyids. The well developed basipterygoid processes and deep shape of the neurocranium most closely approach the condition in *Thursius estonicus* and *Megistolepis*, although the latter genus is distinctly specialised in the profile of the snout and paired apical fossae. In the absence of other information *Gogonasmus* cannot be placed as a sister taxon to any other osteolepidid, but I suggest that it be regarded as a plesiomorphic taxon at an equivalent grade of organisation as *Thursius*. As the relationships of *Gyroptychius*, *Thursius*, *Osteolepis*, and *Latvius* are not clear the higher osteolepidids which do show distinct specialisations must remain as the sister group to a plesiomorphic group containing all these taxa of uncertain affinity. *Gogonasmus* should be regarded as within this group.

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