Revision of osteolepiform sarcopterygians (lobe-finned fishes) from the Middle Devonian Hatchery Creek fish assemblage, Wee Jasper, Australia.

James R Hunt.

15th September 2008
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Abstract

Young and Gorter (1981) described nine fish species from the upper part of the Hatchery Creek Conglomerate (herein the Corradigbee Formation, Eifelian, Middle Devonian) of Wee Jasper, Australia, and Hunt (2005) identified additional actinolepid placoderms and 'osteolepids'. Young & Gorter tentatively assigned the osteolepiform *Gyroptychius? australis* (characterised by an extremely short and broad fronto-ethmoidal shield) to the Scottish genus *Gyroptychius* (Jarvik, 1948). Chang & Zhu (1993) suggested that *Kenichthys* from China was very similar in the size and proportions of the fronto-ethmoidal shield, along with grooved nares. *Kenichthys* has been placed as the most primitive tetrapodomorph in the phylogeny of Ahlberg & Johanson (1998). This research agrees with some previous authors that the osteolepiform *Gyroptychius? australis* represents a new genus and species. A further two osteolepiforms are identified in the formation differing from *Gyroptychius? australis*. Some of the new material includes many lower jaws, seven fronto-ethmoidal shields, four parietal shields, four cheek units, four jugals and four suboperculars. Three different morphologies will be illustrated for this material. The new data shows the cheek was short and broad in NG 2. The lower jaw shows primitive features (foramina along the ventral surface) as in the basal sarcopterygians *Youngolepis* and *Psarolepis* from China. One of the major differences noted is the presence of two tooth rows in the premaxilla, with no other known osteolepiform exhibiting this character.
1. Introduction

1.1 Overview

The broad aim of the research was to investigate the lobe-fined bony fish traditionally placed in the family Osteolepididae. The fish remains are located in the upper part of the Hatchery Creek Conglomerate (Eifelian in age). The upper beds have been separated off as a finer sequence of sandstones, mudstones and shales and considered as a new formation - the Corradigbee Formation (Hunt & Young in prep). In describing the osteolepids their functional morphology was considered along with their evolutionary relationship with the other osteolepids from a global scale. A comparative study with other identified Middle Devonian osteolepids from Australia as well as those from a global context was undertaken. In demonstrating this several specific goals were needed to provide a support and framework for the research on the tetrapodomorphs.

The specific goals of this research were to:

- Describe two new osteolepids from the formation.
- Determine a stratigraphic sequence of the tetrapodomorphs in relation to the other fossil fish in the formation.
- Hypothesize possible relationships which these new tetrapodomorphs may have with other described tetrapodomorphs and other forms of osteolepids and 'porolepiforms' of similar age.

The following research presents detailed descriptions of the new material and discussions on that material.

1.2 General Geology

The Corradigbee Formation lies North West of Canberra near the Goodradigbee River (Fig. 1A,B). The Corradigbee Formation was previously identified as the upper
beds of the Hatchery Creek Conglomerate (Owen & Wyborne, 1979; Young & Gorter, 1981; Hood & Durney, 2002; Francis, 2003; Hunt, 2005). It is now considered a separate formation named the Corradigbee Formation (Hunt & Young in prep). The formation was defined as a finer sedimentary sequence of mudstones, siltstones and sandstones about 231.5 m thick overlying the Hatchery Creek Conglomerate. The age of the formation is Eifelian (Middle Devonian) on work by Young & Gorter (1981) from the original fossil fish assemblage, which is now identified as from unit A (Hunt, 2005). The Formation has been divided into fourteen subunits C' to N (Fig. 2A). The surrounding geology includes massive conglomerates to the East (Hatchery Creek Conglomerate) and Devonian intrusives to the West. Outcrops of the Corradigbee Formation are capped by Tertiary Basalts. The basalts are quarried for paving stone.
Figure. 1 A. Generalised geological map of the Corradigbee Formation and Hatchery Creek Conglomerate based on Owen & Wyborn (1979) Brindabella 1:100 000 geological map; detailed field mapping showing the study area of Hunt (2005) along with the identified syncline, the original fossil locality (Windy Top; Young & Gorter 1981) along with the second fossil locality (JF, Francis 2003) and the syncline identified by Hood & Durney (2002). B. Regional locality map adapted from Young & Gorter, (1981. fig. 1).
Figure 2. A. Map showing all the fossil localities within the area. Base map is the Wee Jasper 1:25000 topographic map 8627-4N [second edition]. Dashed lines indicate roads with the solid lines indicating creeks. B. Diagram showing the units of the finer sequence Corradigbee Formation, total thickness (individual subdivision thickness is not represented) and which osteolepid localities fall into the specific horizons.
1.3 Corradigbee Formation - Stratigraphy

The Corradigbee Formation is named after the property which encompasses most of its outcrops. In the previous studies the area has been referred to as the ‘Middle Ridge Shales’ (Edgell, 1949), upper Hatchery Creek Formation (Young & Gorter, 1981; Francis, 2003; Hunt 2005), upper beds of the Hatchery Creek Conglomerate (Owen & Wyborn, 1979). The measured thickness of the Corradigee Formation (232 m) extends from unit C’ to unit N. Each unit is of a differing thickness. The colour of the mudstones and siltstones alternates predominately from grey to red. The units start with a basal sandstone usually around 1 m and can be thicker, up to 3 m. Overlying the basal sandstone are various beds mudstones and siltstones.

The boundary between the Hatchery Creek Conglomerate and the Corradigbee Formation is defined at the base of unit C’ (Cycles D’ - F’ are the uppermost beds of the Hatchery Creek Conglomerate). This boundary is marked by a sediment change from massive conglomerates to fine sandstones and mudstones in the northern area of the field site at locality 068a (647793,6118228) (Fig. 1) and in the southern area of the field site (Fig. 1) is marked by a slight sediment change at locality 063a (0647598,6117285). At locality 063a the sediment changes from a coarse grained sandy-mudstone, very light in colour (which contains root casts, bioturbation to a dark red sequence of mudstones containing fossil fish and plant material (this boundary is located near locality 70; near the new forestry road). From the dating point of view most of the Corradigbee Formation is Eifelian in age (Young & Gorter, 1981) but the presence of an astrolepid with a dorsal spine suggests that the upper bed may continue into the Givetian.
Figure 3. A, Map of the 14 units within the formation. Dotted lines are where the terrane became too steep to determine individual units. B, Stratigraphic column of most of the Corradigbee Formation (Units C'-J). C, Cycle F from the western creek- which is much thicker than F from the Eastern Side of the formation.
1.4 Corradigbee Formation - Lithologies and Sedimentary Structures

**Conglomerate**

Almost no conglomerate is located in the Corradigbee Formation. However one bed of pebbly conglomerate (~2.5 cm thick) red in colour was located at locality 70 (Fig. 2B), and was associated with a fish fauna. Two other beds of grey conglomerate (no thicker than 4 cm) were identified in erosion gullies at localities 98 and 138 (Fig. 2B) both contained fragmented fish material (osteichthyes and placodermi). The conglomerates consisted of rounded small pebbles no larger than 2cm and fragmented fish remains. The conglomerate at locality 70 (Fig. 2B) comprises of small mudclasts, mudballs and rounded pebbles with rounded quartz grains with some of the finer and smaller grains (<0.5mm) being subangular.

**Sandstones**

The sandstone layers at the base of each cycle vary in thickness (1.5 m in cycle G, 3 m in cycle F). Grain size is uniform within one bed but they vary between different beds. Grain size ranged from around <0.2mm from each layer of sandstone. None of the sandstones in the formation were noted to be very coarse grained. Good exposures of the basal sandstones were observed at localities 64, 11, 14, 154 (Fig. 2B). Cross bedding, scour marks, mudclasts or other evidence of a river deposit were not observed except for cross bedding at one locality 108 (Fig. 2B).

**Mudstones**

The mudstones in the formation are predominantly grey-black, but others also occur in orange, red, dark purple and light grey. These colours are identified as primary colours, by the fact that the colour terminated with the bedding plane. The grey and red mudstone layers often contain small carbonate nodules (up to 5cm) which are common at localities 62, 97, 109, 128, 137 and 158 (Fig. 2B), but were noted at many other localities. Weller (1960) states "Calcareous nodules are less abundant in fresh water deposits than marine sediments". In the Corradigbee Formation the nodules are extremely abundant throughout the fresh water mudstones. Weller also suggests that fresh water
Calcareous nodules deposits are largely a result of biologic activity. Perhaps the nodules formed around, or were produced from the decay of plant or animal remains (one sectioned example what a clay/organic core). The nodules are found in three dimensions in the mudstone as are some of the fossil fish remains. Cubic pyrite crystals along with small quartz vein fragments were identified near a fossil locality. Hamilton et al. (1989: 30) state that pyrite occurs in a variety of environments “in sedimentary rocks, particularly in black shales formed under stagnant, anaerobic conditions”. It is possible that these were formed in anaerobic conditions as the presence of laminar bedding in the formation suggests intermittent lake sediments. Isolated occurrences of laminar bedding were seen in some of the grey green mudstones at locality 24 (Fig. 1B). Laminar bedding was also found by Francis (2003) and Young & Gorter (1981). Ripple marks were identified at localities 129-131 (Fig. 2B). Also the bedding surface of a red bed at locality 80, showed evidence of exposure to the atmosphere with the presence of rain drop impressions.

**Interpretation of Depositional Environment**

The Corradigbee Formation, upper part of the Hatchery Creek Conglomerate was previously interpreted as the distal regions of a humid alluvial fan (Hunt, 2005; Francis, 2003). Cyclothsems comprising mudstones, siltstone and sandstone of differing colour were identified by Hunt (2005) and are thought to have developed in a similar way to the sedimentary cycles of the Sandwick Fish Beds on Orkney (Marshall et al. 2007).

The sandstones are uniform in structure and thought to be deposited in flooding events. The formation is interpreted as a non-marine sequence, with numerous root casts found in the mudstones. However laminar bedding within the mudstones indicates areas of ephemeral lakes.
1.5 Localities

The osteolepids localities are quite abundant within the formation (Fig. 2B) and are found throughout all the units except unit C', where only the actinolepid arthrodire (*Edgellaspis* get. et sp. nov.) was found. The osteolepids in the overlying unit B' include specimens collected in 1978 (Fig. 2B). The main localities producing good osteolepid material in ascending stratigraphic order were 134, 138, 120 and 161. However less complete material came from numerous other localities (Appendix 1).

Locality 134 is situated on the slope of the ‘Western’ Creek and is in a soft yellow mudstone, in between two layers of sandstone and belongs to unit F. The sandstone layers are coarse sand. The site is easily detected by numerous *Xanthorrhea* trees growing out on a small rise. The outcrop itself is quite poor with minimal rock exposed at the surface. However, under the surface, (the topsoil is quite shallow, less than 5 cm) rock material can be found in bedding planes. The fossils are quite abundant at this locality. The osteolepid material is found as both articulated scales and disarticulated bones. An unidentified arthrodire also occurs at this locality. The material identified at this locality belongs to an osteolepid similar to *Gyroptychius? australis*. Isolated onychodont teeth have also been identified. The site is steep and is coarser than most other mudstones in the area.

Locality 120 has been bulldozed and ripped up from forestry work. This has revealed large amounts of rock previously unexposed to the surface. The site represents unit I (Fig. 2A) and is one of the uppermost horizons which contains significant osteolepid material (apart from fragments). The overlying horizons contain fish fauna with disarticulated remains noted in the field which has not been collected in detail. From field observations these upper units also contain osteolepids which may be more common than the placoderms. At site (120) large blocks of fossil material were found, containing disarticulated remains of thelodonts, antiachs and osteolepids. A new species of *Sherbonaspis* with a dorsal spine comes from this locality as well (Hunt, 2005). Locality 120 is a red mudstone and also contains small (up to 5 cm) carbonate nodules.
Locality 138 is located in an eroded gully along the western side of the ‘Western’ Creek and represents unit E. The fossils exposed were found in the gully on bedding planes in a fine grey siltstone, which is very hard. Material was also found in the adjacent slope of the gully. Digging into the side of the exposed gully reveals softer sediment which contains large quantities of fossil material. At the top of the hill above this site lies another fossil fish locality (site 139), but it has only yielded one parietal shield and many plant fossils.

Locality 161 is found in a forestry rip in a grey mudstone. The mudstone is quite hard when first unearthed, but left in the atmosphere for a short time weathers quickly. The site contains both osteolepid and placoderm (antiachi) remains. The locality is in unit I slightly higher in the beds than locality 120 (Fig. 2A).
2. Palaeontology

2.1 General Fauna and Flora

The fossil fish come from many localities from horizon C' through to I, and are mostly disarticulated, with good examples observed at localities 91 and 134, which lie in cycles H and F (Figs. 2B). However at localities JF, 120, 81 (Fig. 2B), articulated plates from placoderms and osteolepid scales are found. The remains are found as three dimensional uncrushed specimens, being compacted by the mudstone as would be expected. A new genus of actinolepid arthrodire was found to exist in the lowest fossiliferous subunit of the formation. The lowest osteolepid remains (Gyroptychius? australis) are found above the actinolepids in unit B' (Fig. 1C). This could be due to the individual’s palaeoecology. The actinolepid is thought to be a bottom dweller, due to the large orbits and flat body plan like Actinolepis (Mark-Kurick, 1979) and may have been able to cope with rougher conditions, as it was found in amongst small pebbly conglomerates, which indicating a slightly higher energy environment. Arthropods have now been discovered at locality 91, in cycle H. The arthropods were found with the new form of Sherbonaspis and a species of Monarolepis. Both fish and arthropod remains have been found accreted in such a way as to lie perpendicular to the bedding. Small gastropods (Fig. 4) were found in the grey shale at locality 062a, and compared with Middle Devonian (Eifelian) gastropods from southeastern Alaska (Blodgett et al. 2001). While hardly likely to be the same species (the Alaskan gastropods come from a marine limestone) the closest similarities in shape are with Euryzone sp. (Blodgett et al. 2001 pl. 1. fig. 2). The gastropods are associated with plant material which differs to all other plant material from the Corradigbee Formation, and is provisionally identified as Zosterophyllum (Fig. 4A, B). Similar Middle Devonian plants have been found in Southern China (Hao et al. 2007). Unidentified plant material was also found in the mudstones layers at localities many other (17, 60, 63, 71, 74, 96, 106 121, 122, 150, 159; Fig. 2B). The plants are preserved as flattened stems in the bedding planes as well as three dimensional (pencil like) within the bedding. Lepidodendroid lycopod material was noted in sandstone from unit G, locality 65 (Fig. 2B). Root casts and bioturbation were seen at locality 75 (Fig. 2B) in a dark red mudstone.
2.2 Previous fossil studies

The first fossil assemblage from the Corradigbee Formation was described by Young & Gorter (1981). Since then, two further studies have been carried out on the formation by Francis (2003), Hunt (2005) and Burrow (2002) reassessed the acanthodian scales. Young & Gorter identified nine species of fossil fish. Since that study seven other fish have been identified (Table 1) including actinolepid and coccosteid arthrodires, and onychodonted and 'osteolepid' sarcopterygians. The three 'osteolepid' taxa are described in detail in this study.

The osteolepid *Gyroptychius? australis* from Young & Gorter (1981) was tentatively assigned to the genus *Gyroptychius* as there was limited Australian genera for comparison. The authors note that this was only a tentative placing, based on both generic and specific characters. With collection of new material a re-examination of the osteolepiform was warranted. The osteolepids from the formation fall into a larger grouping the Sarcopterygii.
Figure 4. Fossil Plants and a Gastropod from the Corradigbee Formation. A, B, Possible Zosterophyllum plant remains in a grey shale from locality 062a. C, Unidentified gastropod from locality 062a. D, Unidentified plant material in a grey mudstone. E, Lepidodendroid lycopod plant material from a sandstone in horizon G (locality 65; see Fig. 2B).
Fauna and Flora List of the Corradigbee Formation

Vertebrata
Agnatha
Thelodontida
*Turinia* sp. cf. *T. hutkensis* Blieck & Goujet (Young & Gorter, 1981)

Gnathostomata
Acanthodii
Climatiid gen. et sp. indet. (Young & Gorter, 1981)
?ischnacanthiform gen. et sp. indet. (Young & Gorter, 1981)
*Tareyacanthus* sp. cf. *T. magnificus* Valiukevičius 1994 (Burrow 2002: fig. 20)
*Watsonacanthus*? sp. (Burrow 2002: 103)

Osteichthyes
Sarcopterygii
Onychodontid? cf. *Onychodus jandemarrai* [Under Study]

Tetrapodomorpha
New Genus 1 *australis* (Young & Gorter, 1981) [This work]
New Genus 1 and species B [This work]
New Genus 2 and species [This work]

Placodermi
Arthrodira
*Denisonosteus weegisasperensis* (Young & Gorter, 1981)
*Denisonosteus*? new species (Hunt, 2005)
Actinolepid [Under Study]
Coccosteomorph cf. *Coccosteus* [Under Study]
*Arthrodira incertae sedis* (Young & Gorter, 1981)

Antiarchi
*Sherbonaspis hillsi* (Young & Gorter 1981)
*Sherbonaspis* new species (Hunt, 2005)
*Monarolepis verrucosa* (Young & Gorter 1981) Young, 1988

Placodermi incertae sedis

Inverterbrata
Arthropoda
Myriapoda *incertae sedis* (Hunt, 2005)

Gastropoda
cf. *Euryzon* [This work]

Plants
Flora
*Lepidodendron* (Hunt, 2005)
cf. *Zosterophyllum* [This work]
Unidentified plant remains (Hunt, 2005)

Table 1. Fauna and Flora list for the Corradigbee Formation.
3. Methodology

3.1 Field Work

The field program was initiated for an honours project (Hunt, 2005). Further field work and fossil collecting was conducted in 2006 and 2007. Osteolepid material collected in 2005, but not studied in depth, is also presented in this study. Fossil material studied came from localities from Hunt (2005), along with several recently discovered localities (161, 162, 163 and 56; Fig. 1B). New localities were numbered with a GPS waypoint. Locality numbers with longitude and latitude were recorded as a means of future identification and reference. A 4wd vehicle was required to access the localities. Previously drawn maps from the 2005 study were used to locate study sites for further collection. The maps needed to be updated as the study area had been ripped for a new pine forest plantation. New roads enabled easier access to some localities. Specimens collected were labelled in the field with a site number, and the unit from which the specimen was collected was also recorded.

3.2 Laboratory Work

Specimens were washed, cleaned and trimmed on a rock saw. Specimens were labelled with ANU V numbers and catalogued in the vertebrate registrar and are housed at the Australian National University, Canberra. Rock matrix covering areas of bone where prepared out further using a Vibro-Tool and Jewellery drill. Some important specimens which indicated morphological differences from their external features were sent to China for further preparation of the internal structures at the Institute of Vertebrate Paleontology and Paleoanthrpology, Beijing. Material which was poorly preserved or had minimal bone preserved was placed in hydrochloric acid to remove the bone. Impressions were cleaned in water and rubber latex casts were made. The surface was dampened before lightly painting on a layer of latex. The latex was blown to get the layer as thin as possible to remove any air bubbles. The casts were whitened using ammonium chloride and examined under the microscope. Specimens preserved as bone were either studied directly under the microscope using alcohol to highlight the bone or whitened using the ammonium chloride. Pencil drawings were made using a Heerbrugg Wild M7A
microscope with a camera lucida attachment.
Three specimens were XCT scanned; ANUV505, ANUV525, ANUV3128. Scanning was carried out by Associate Professor T. Senden (Department of Applied Mathematics, RSPhysSE). A visit to the Australian Museum in Sydney was undertaken to view osteolepiformes in their collection, and comparative material was borrowed from Geoscience Australia, Canberra (G? australis CPC19586-19646), Canterbury Museum, Christchurch (Platyethmoidia AF266), and the Australian Museum, Sydney (Platyethmoidia AMF54405).
3.3 Bone Measurements

Bones were measured according to the system developed by Jarvik (1948). While most of these specimens are disarticulated and some incomplete the measurements can only be regarded as approximations giving general comparisons. Table 5 presents the measurements and proportions of all measured specimens in this study.

Figure 5. Diagram representing measurements on the dermal plates (From Jarvik, 1948 fig. 12).


a, median length of parietal shield; b, median length of fronto-ethmoidal shield; br.G, breadth of principal gular; c, distance from centre of pineal foramen to posterior margin of frontal; d-h, breadth of cranial roof at various places; d, at preorbital corner; e, at the deepest point of the orbital notch; f, at the deepest point of the postorbital notch; g, at the spiracular notch and h, at posterolateral corner of parietal shield; dp.io, depth of orbital notch; ht.Ch, height of external cheek plate; ht.La, height of lachrymal at anterior end of its orbital notch; ht.Sq, height of squamosal; ht.l, height of posterior margin of lachrymal; r.La+Mx, lachrymomaxillary notch; i.o, orbital notch; i.po, postorbital notch; i.spir, spiracular notch; k, distance from vertical pit line of infradentary 2 to posterior end of lower jaw; l.Ch, length of external cheek plate; l.G, length of principal gular; l.Sq, length of squamosal; m, distance from vertical pit line of infradentary 2 to anterior of lower jaw; n, distance from pit line of principal gular to anterior end of non-overlapped part of bone; p, distance from pit line of principal gular to posterior end of bone; plc, postero-lateral corner of cranial roof; pl.G, pit line of principal gular; plv.Id.2, vertical pit line of infradentary 2; proc, preorbital corner; ptoc, postorbital corner; r, median length of preorbital division of fronto-ethmoidal shield; s, median length of orbital division of fronto-ethmoidal shield; snce, subnarial corner; t, median length of postorbital division of fronto-ethmoidal shield; v, distance from middle point of orbital notch to anterior end of fronto-ethmoidal shield; w, distance from middle point of orbital notch to posterior end of fronto-ethmoidal shield.
3.4 Terminology

The term “osteolepidids” means belonging to the family Osteolepididae, even though some authors (Ahlberg, 1991; Ahlberg & Johanson, 1998) believe the family may not be monophyletic and use the term Tetrapodomorpha (Ahlberg, 1991). Tetrapodomorpha includes Sarcopterygii which are not Dipnomorpha and that have tetrapod-like characters (ie skull roof pattern). The term “osteolepid” is used in this work to mean a general grouping of cosmine covered individuals. “Osteolepiformes” is used to mean Osteolepids and Tristichopterids (both cosmine and non-cosmine covered).

Fish terminology used in this study follows Jarvik (1948). Although some authors (Ahlberg & Johanson, 1998) use ‘tetrapod’ terminology for the dermal bones of the skull roof. The terminology for the fish terms is shown in Jarvik’s diagram (see Fig. 5). A comparison of fish and tetrapod skull bone names is listed below:

<table>
<thead>
<tr>
<th>Fish</th>
<th>Tetrapods</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frontal</td>
<td>Parietal l</td>
</tr>
<tr>
<td>Parietal</td>
<td>Postparietal</td>
</tr>
<tr>
<td>Dermosphenotic</td>
<td>Intertemporal</td>
</tr>
<tr>
<td>Intertemporal</td>
<td>Supratemporal</td>
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<tr>
<td>Posterior tectal</td>
<td>Prefrontal</td>
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<td>Supraorbital</td>
<td>Postfrontal</td>
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</table>

3.5 Dermal Bones

The dermal bones comprise three layers, a thin outer layer of shiny enamel and dentine (cosmine), a middle trabecular layer and a basal layer of laminar bone. The outer cosmine layer was resorbed and replaced as the bones grew. In some of the studdied material small blisters are seen or cosmine is lacking. These are areas where the cosmine
was being replaced or resorbed before the death of the fish. The osteolepid bones in this study are mainly of a smooth appearance (cosmine covered). Cosmine bones are common to many of the early Sarcopterygii.

Figure 6. Individual bones from the skull region identifying their name and position (from Jarvik (1980 fig. 115). A. Skull roof on left side; B. left cheek, lower jaw and submandibular bones on right.
<table>
<thead>
<tr>
<th>Abbreviations in text and figures</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>?aci fo</td>
<td>foramen, probably for internal carotid artery</td>
</tr>
<tr>
<td>ads</td>
<td>parasympophysial plate</td>
</tr>
<tr>
<td>ad fo</td>
<td>adductor fossa</td>
</tr>
<tr>
<td>art</td>
<td>articulation</td>
</tr>
<tr>
<td>At sut</td>
<td>anterior tectal suture</td>
</tr>
<tr>
<td>Bh fo</td>
<td>buccophyophysial foramen</td>
</tr>
<tr>
<td>bli</td>
<td>blister</td>
</tr>
<tr>
<td>bp pr</td>
<td>basipterygoid process</td>
</tr>
<tr>
<td>c. a. ci</td>
<td>canal for a. carotis interna</td>
</tr>
<tr>
<td>c. a. occ</td>
<td>canal for occipital artery</td>
</tr>
<tr>
<td>c. cav</td>
<td>cranial cavity</td>
</tr>
<tr>
<td>cf</td>
<td>contact face</td>
</tr>
<tr>
<td>co fo</td>
<td>coronoid fossa</td>
</tr>
<tr>
<td>co1</td>
<td>coronoid 1</td>
</tr>
<tr>
<td>co2</td>
<td>coronoid 2</td>
</tr>
<tr>
<td>tusk co1</td>
<td>first coronoid tusk</td>
</tr>
<tr>
<td>tusk co2</td>
<td>second coronoid tusk</td>
</tr>
<tr>
<td>tusk co3</td>
<td>third coronoid tusk</td>
</tr>
<tr>
<td>cr sus</td>
<td>crista suspendens</td>
</tr>
<tr>
<td>CII</td>
<td>cranial nerve II</td>
</tr>
<tr>
<td>CIII</td>
<td>cranial nerve III</td>
</tr>
<tr>
<td>den</td>
<td>denticles</td>
</tr>
<tr>
<td>den co1</td>
<td>denticles on co1</td>
</tr>
<tr>
<td>depr</td>
<td>depression</td>
</tr>
<tr>
<td>Dsph</td>
<td>dermosphenotic</td>
</tr>
<tr>
<td>Dsph sut</td>
<td>dermosphenotic suture</td>
</tr>
<tr>
<td>?eys</td>
<td>possible eye stalk</td>
</tr>
<tr>
<td>Fr</td>
<td>frontal</td>
</tr>
<tr>
<td>Fe.end</td>
<td>fenestra endochoanalis</td>
</tr>
<tr>
<td>fe. exa</td>
<td>fenestra exonarina</td>
</tr>
<tr>
<td>f. pin</td>
<td>pineal foramen</td>
</tr>
<tr>
<td>fo</td>
<td>foramen</td>
</tr>
<tr>
<td>G. m</td>
<td>median Gular</td>
</tr>
<tr>
<td>gl fos</td>
<td>glenoid fossa</td>
</tr>
<tr>
<td>gr sp</td>
<td>group of sensory pores</td>
</tr>
<tr>
<td>int cor fo</td>
<td>intercoronoid fossa</td>
</tr>
<tr>
<td>i. La+Mx</td>
<td>lachrymo-maxillary notch</td>
</tr>
<tr>
<td>i. o</td>
<td>orbital notch</td>
</tr>
<tr>
<td>i. po</td>
<td>postorbital notch</td>
</tr>
<tr>
<td>i. spir</td>
<td>spiracular notch</td>
</tr>
<tr>
<td>ioc</td>
<td>infraorbital sensory canal</td>
</tr>
<tr>
<td>juc</td>
<td>jugal sensory canal</td>
</tr>
<tr>
<td>jug can</td>
<td>jugular canal</td>
</tr>
<tr>
<td>Ju</td>
<td>jugal</td>
</tr>
<tr>
<td>La+Mx</td>
<td>lachrymo-maxillary notch</td>
</tr>
<tr>
<td>La</td>
<td>lachrymal</td>
</tr>
<tr>
<td>Lj</td>
<td>lower jaw</td>
</tr>
<tr>
<td>m sut</td>
<td>midline suture</td>
</tr>
<tr>
<td>Mg</td>
<td>maxilla</td>
</tr>
<tr>
<td>Mx</td>
<td>New Genus 1</td>
</tr>
<tr>
<td>NG 1</td>
<td>New Genus 2</td>
</tr>
<tr>
<td>NG 2</td>
<td>New Genus 3</td>
</tr>
<tr>
<td>NG 3</td>
<td>New Genus 3</td>
</tr>
<tr>
<td>oa.Dsph</td>
<td>overlapping area for Dsph</td>
</tr>
<tr>
<td>oa.Cheek</td>
<td>overlapping area for the cheek</td>
</tr>
<tr>
<td>oa.Gm</td>
<td>overlapping area for the G.m</td>
</tr>
<tr>
<td>oa.Ju</td>
<td>overlapping area for the Ju</td>
</tr>
<tr>
<td>oa.La</td>
<td>overlapping area for the La</td>
</tr>
<tr>
<td>oa.Lj</td>
<td>overlapping area for the</td>
</tr>
</tbody>
</table>
Lj  pnw postnasal wall
oa.Mx overlapping area for the maxilla
poc postotic sensory canal
oa.Op overlapping area for the Op
preopcular preopercular suture
oa.Pop+Lj overlapping area for the Pop + Lj
prearticular processus connectens
oa Po overlapping area for the Po
premaxilla suture
oa.Qj overlapping area for the Qj
parasphenoid
oa.Rbr overlapping area for the Rbr
posterior tectal suture
oa.Sop overlapping area for the Sop
branchiostegal ray
olf ri olfactory ridge
or mar orbital margin
Op operculum
posterior branchiostegal ray
Pa parietal
St supratemporal
Pt fo pineal foramen
scd semi-circular disc
plam palatal lamina
soc supraorbital sensory canal
pl.Fr frontal pit line
So sut supraorbital suture
plh.Id horizontal pit line
Sop subopercular
pl. pop preopercular pit line
sq squamosal
pl. Sq squamosal pit line
sn solum nasi
pl. Qj quadratojugal pit line
vo vomer
pl.po.Pa posterior obliques parietal pematt vomer attachment area
pit line
pl.tr.Pa transverse parietal pit line
plv. Id infradentary pit line
plv. Id2 infradentary pit line 2
plv. Id3 infradentary pit line 3
p mcp mandibular sensory canal
pnp prenasal pit
4. Osteichthyes

4.1 General Introduction to Sarcopterygii

Osteichthyes are the most numerous and diverse vertebrates. The oldest osteichthyans are known from the Silurian period. Two main groups are recognised: ray-finned fishes (Actinopterygii) and lobe-finned fishes (Sarcopterygii). The descendants of these early forms radiated into nearly all aquatic environments (Star & Taggart, 2001). Only four genera (six species) of sarcopterygians (lobe-finned fishes) survive to the present: the actinistian; *Latimeria* (two species *L. chalumnae* & *L. menadoensis*) and three dipnoans (lungfish); *Neoceratodus*, *Protopterus* and *Lepidosiren* (*Protopterus* contains two species *P. aethiopicus*, *P. annectens*).

Sarcopterygians are characterised chiefly by the monobasal articulation of the paired fins with fin musculature extending in a more or less developed basal lobe (Janvier, 1996). However they can also have an unpaired lobe fin as in the case of the modern day actinistian *Latimeria* which has an unpaired (single) dorsal lobe fin near the caudal fin (Thomson, 1991; Holder et al. 1999), *Osteolepis* (Jarvik, 1948) and *Eusthenopteron* (Jarvik, 1980 fig. 71).

Other characters of the Sarcopterygii include; the rear most gill arch articulating with the preceding one; more than four sclerotic plates; an ascending process of the palatoquadrate; enamel in the entire tooth (Janvier, 1996: 195).

Ahlberg and Johanson (1998, fig. 2) followed Ahlberg’s (1991) subdivision into two main groups for the Sarcopterygii: Dipnomorphs (which includes Dipnoi (lungfishes)), and Tetrapodomorphs (which includes all those more closely related to tetrapods).

One of the earliest known sarcopterygians is *Psarolepis* from the Late Silurian of China (Zhu & Schultze, 1997). Other Sarcopterygii which appear early in the fossil record are the dipnomorphs (lungfishes and “porolepiforms”), along with the tetrapodomorphs (“osteolepiformes”, all remaining sarcopterygians). The earliest known Tetrapodomorpha (“osteolepiformes”) is *Kenichthys campbelli* (Chang & Zhu, 1993; Zhu

Other groups (onychodontiforms and actinistians - coelacanths) supposedly more primitive Sarcopterygii appear later in the Early Devonian. Dipnomorphs include the Porolepiformes, which are represented by several genera including Porolepis, Glyptolepis and Holoptychius. In contrast to the “Osteolepiformes”, the pineal usually does not pierce the skull roof and the anterior proportion of the skull is especially short with small orbits and two external narial openings.

The Tetrapodomorpha was erected by Ahlberg (1991) and clumps together all fishes which are not Dipnoi and dipnomorphs - those whom have some tetrapod-like characters, but are still fish. The Tetrapodomorpha encompasses the previously defined groups “Osteolepididae”, Tristichopteridae, Rhizodontida and Tetrapoda. Most of the “Osteolepididae” were predatory fish ranging in size from quite small ~ 30 cm (Thursius) to large. The “Osteolepiformes” have been typified by the Upper Devonian genus Eusthenopteron (Jarvik, 1980), along with other well preserved genera Osteolepis (Thomson, 1968; Jarvik 1948), Ectosteorhachis and Megalichthys (Long & Turner, 1984).
Table 2. Simplified table illustrating Sarcopterygii groupings (names in quotes may not be monophyletic – Alberg & Johanson 1998).

Jarvik (1948) carried out a study on the Middle Devonian osteolepids from Scotland and Latvia. He organised the specimens from the Middle Devonian of Scotland, which had previously been described by Woodward, Sedgwick, Murchison, Agassiz and McCoy. Since Jarvik (1948) new genera of Sarcopterygii have been identified, along with numerous genera of “osteolepidids”. New forms have been discovered from Australia, Antarctica, Canada, and China. Table 3 lists the identified Australian and Antarctic tetrapodomorphs.
<table>
<thead>
<tr>
<th>Genus</th>
<th>Author</th>
<th>Grouping</th>
<th>Locality</th>
<th>Other References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aztecia</td>
<td>Johanson &amp; Ahlberg, 2001</td>
<td>Rhizodontida</td>
<td>Mount Richie Antarctica</td>
<td>Young et al. 1992</td>
</tr>
<tr>
<td>Cabonnichthys</td>
<td>Ahlberg &amp; Johanson, 1997</td>
<td>Trisitchopterida</td>
<td>Canowindra. NSW</td>
<td></td>
</tr>
<tr>
<td>Canowindra</td>
<td>Thomson, 1973</td>
<td>Canowindridae</td>
<td>Canowindra. NSW</td>
<td>Long, 1985b; Young et al. 1992</td>
</tr>
<tr>
<td>Cladarosymblema</td>
<td>Fox et al. 1995</td>
<td>Megalicthyidae</td>
<td>Drummond Basin, QLD</td>
<td>Long &amp; Turner, 1984</td>
</tr>
<tr>
<td>Baromedea</td>
<td>Holland et al. 2007</td>
<td>Rhizodontida</td>
<td>Mansfield, VIC.</td>
<td></td>
</tr>
<tr>
<td>Beelarongia</td>
<td>Long, 1987</td>
<td>Canowindridae</td>
<td>Mount Howitt, VIC</td>
<td></td>
</tr>
<tr>
<td>Gyroptychius?</td>
<td>Young &amp; Gorter, 1981</td>
<td>'Osteolepiform'</td>
<td>Wee Jasper, NSW</td>
<td></td>
</tr>
<tr>
<td>Gyroptychius?</td>
<td>White, 1968</td>
<td>'Osteolepiform'</td>
<td>Mount Crean, Antarctica</td>
<td>Young et al. 1992</td>
</tr>
<tr>
<td>Antarcticus</td>
<td></td>
<td></td>
<td></td>
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<td>Koharalepis</td>
<td>Young et al. 1992</td>
<td>Canowindridae</td>
<td>Mount Crean, Antarctica</td>
<td></td>
</tr>
<tr>
<td>Mahalalepis</td>
<td>Young et al. 1992</td>
<td>Megalicthyidae</td>
<td>Mount Crean, Antarctica</td>
<td></td>
</tr>
<tr>
<td>Mandageria</td>
<td>Johanson &amp; Ahlberg, 1997</td>
<td>Trisitchopterida</td>
<td>Canowindra. NSW</td>
<td></td>
</tr>
<tr>
<td>Marsdenichthys</td>
<td>Long, 1985a</td>
<td>'eusthenopterid'</td>
<td>Mount Howitt, VIC</td>
<td></td>
</tr>
<tr>
<td>Muranjilepis</td>
<td>Young &amp; Schultzze, 2005</td>
<td>'Osteolepiform'</td>
<td>Amadeus Basin, NT</td>
<td></td>
</tr>
<tr>
<td>Notorhizodon</td>
<td>Young et al. 1992</td>
<td>Trisitchopterida</td>
<td>Mount Richie Antarctica</td>
<td>Johanson &amp; Ahlberg 2001</td>
</tr>
<tr>
<td>Platyethmoidia</td>
<td>Young et al. 1992</td>
<td>'Osteolepiform'</td>
<td>Mount Ritchie, Antarctica</td>
<td></td>
</tr>
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<td>Vorobjevaia</td>
<td>Young et al. 1992</td>
<td>'Osteolepiform'</td>
<td>Mount Crean, Antarctica</td>
<td></td>
</tr>
</tbody>
</table>

**Table 3.** Alphabetical listing of Australian and Antarctic tetrapodomorph taxa

The identified forms from Australia have revealed new “osteolepid” designs; in the pattern on the dermal bones along with phylogenetic information. Long (1987) suggested that some Australian species together with the Antarctic species may represent an endemic Gondwanan group of “Osteolepiformes”. Young et al. (1992) erected a Gondwanan family; the Canowindridae containing the genera *Canowindra, Koharalepis*.
and *Beelarongia*, and possibly *Platyethmoidia*. Studies from China (Chang, 1991; Fan, 1992; Chang & Zhu, 1993; Chang & Yu, 1997; Zhu & Shultze, 2001; Zhu et al. 2006) have also turned up unusual “osteolepiforms” which share similar characters to the tetrapodomorphs in this study. The Corradigbee Formation tetrapodomorphs are compared with the standards developed by Jarvik, but also with the similar “osteolepiforms” found close by in the East Gondwana region.

### 4.2 The Corradigbee Formation Osteolepids

Previously to this study, only one “osteolepid” species had been identified from the formation, *Gyroptychius? australis* (Young & Gorter, 1981). New material has been collected which contained numerous “osteolepid” remains. This study focuses on the new tetrapodomorph material from the Corradigbee Formation. Three identified tetrapodomorphs are found in the formation and are similar in morphology. They are found in association with numerous arthrodires and antiarchs, plants, gastropods and arthropods. The material is all covered by smooth cosmine as in the Middle Devonian “osteolepids” from Scotland. Only one type of scale has been identified from the formation, i.e. a rhombic scale similar to *Osteolepis* (Janvier, 1996 fig. 4.88A2) with a median boss for articulation with surrounding scales and a small overlap area on 3 sides for the surrounding scales.

### 4.3 Previous assessments of *Gyroptychius? australis* Young & Gorter (1981)

Several authors (Chang & Zhu, 1993; Long, 1987; Young et al. 1992) have assigned and compared their material to *G? australis*.

Long (1991) suggested that *Gyroptychius? australis* may be referable to a new genus, in that the species is highly unusual in the degree of overhang of the snout and grooved nares. This point by Long is valid and *G? australis* is placed into the New Genus 1.

Young et al. (1992) suggest that *P. antarctica* and *G? australis* are closely related
stating (1992: 25) “the shape of the lower jaw resembles that of *Gyroptychius? australis* Young & Gorter (1981), which also had a short broad fronto-ethmoidal shield as in the holotype of *P. antarctica*, and may be closely related”. Young et al (1992: 26) also state “the jaw is distinguished from that of many osteolepids by the ventral position of the articular region relative to the dorsal margin of the jaw. This is also a feature of *Gyroptychius? australis*. They also suggest similarities between *Koharalepis* and *Gyroptychius? australis* stating the following; (1992: 10-11) “It is about 1.2 times as long as broad, which is thus more elongate than *Gyroptychius? australis* and *Beelarongia*”. “The large postorbital plate is preserved in approximate position, and in dorsal view shows an anterodorsal process to fill this notch, as predicted by Young and Gorter (1981: 118) for *Gyroptychius? australis*, the only other osteolepid to show a similar configuration in this region. In front of the notch is a short anterolaterally directed margin … again as in *Gyroptychius? australis*”. They also recognise that “In *Koharalepis* the orbit evidently was somewhat smaller … than in *Gyroptychius? australis* (Young & Gorter, 1981: fig. 25C)”. *Koharalepis* also resembles *Gyroptychius? australis* in the suboperculars and branchiostegal rays, “In shape this bone resembles that of *Gyroptychius? australis*” (Young et al, 1992: 18). They also noted (1992: 69) that “the possible close relationship of *Platyethmoidia* …to the osteolepid described from the Hatchery Creek Formation … is consistent with the fact that this and the Aztec fauna are the only ones so far known in which turiniid thelodonts and bothriolepid antiarchs are associated”.

However, Young et al (1992: 23) also noted differences between “*Gyroptychius? australis* and *Platyethmoidia* in the “greater breadth of the fronto-ethmoidal shield, the less pronounced orbital notch, and nares partly visible from above, with snout not folded under towards the mouth margin. *Gyroptychius? australis* has a similar postorbital notch to *Koharalepis*… and it is possible that both this form and *Platyethmoidia* are canowindrids”.

Chang & Zhu (1993: 195) consider “The characters it (*Kenichthys*) shares uniquely with *Gyroptychius? australis* indicate their close relationship”. The characters which they have in common are;
1. very short and broad snout, shortest among known osteolepidids.
2. Deep embayment behind postorbital corner,
3. nostril groove-like.

Chang & Zhu (1993: 186) state “the nasal opening preserved at the left side of the holotype is elongated or ‘grooved’ as in the naris of Gyroptychius? australis (Long, 1991)”. Chang & Zhu (1993: 187) also state “A comparable, unusually deep embayment behind the postorbital corner has so far been described, among osteolepidids, only in G.? australis (Young & Gorter, 1981, fig. 25A,C)”. In addition “The principal gular ... is relatively short and broad among osteolepidids, with its length/breadth ratio ...matching that of G.? australis” (Chang & Zhu, 1993: 194).

From the subsequent descriptions of ?Gyroptychius australis, both old and new specimens, it is now not thought to have a close relationship with Kenichthys or the Scottish osteolepids. It has its own unique characters described further on which separate it from previously studied taxa.
5. Systematic Palaeontology

Sarcopterygii Romer, 1955

"Rhipidistia"

Tetrapodomorpha Ahlberg & Johanson, 1998

Family: “Osteolepididae" Cope, 1889

NG 1 australis gen. nov. (Young & Gorter, 1981)

Gyroptychius? australis Young & Gorter, 1981: 116-122, 144-148 pl.7&8
Gyroptychius? australis Young & Schultze, 2005: 23-24

Holotype
ANU V505 (CPC19586 of Young & Gorter, 1981)

Other Material
From the original study (Young & Gorter, 1981):
Four fronto-ethmoidal shields (CPC19586- 89); one parietal shield (CPC19590); one possible left lateral extrascapular (CPC19591); a left preopercular and squamosal (CPC19591); three incomplete canal baring bones (CPC19597-99); nine lower jaws (CPC19592, 19600-607); one isolated tooth (CPC19608); four branchiostegals (CPC19609-12); seven principal gulars (CPC19613-19); two cleithra (CPC19620-21); four clavicles (CPC19622-25); various scales (CPC19626-645); possible epineural or epihaemal spine (CPC19646): See Appendix 2 for CPC specimens corresponding ANU V numbers.

New material:
Four fronto-ethmoidal shields (V3133, V3310, V3338, V3344); one parietal shield (V2268); two lower jaws (V2269, V3229); two principal gulars (V3298, V3132); and one subopercular (V3131); one maxilla (V3345); one unidentified bone (V3343); one section of scales from body (V3228).
Localities & Horizon

The original material from Young & Gorter (1981) comes from Windy Top locality (Fig. 2B) which belongs in unit A. The new material comes from four localities: 81 (V3133, V3298, V3131) which is in unit J; 134 (V3338, V3310) – unit F; 1978 locality (V2268, V2269) – unit B; locality 161 (V3229, V3345) – unit J; locality 120 (V3344, V3343) from unit I.

Diagnosis:

"An osteolepid [tetrapodomorph] in which the fronto-ethmoidal shield is short and broad, with breadth between the orbits equal to its length, and about 1.13 times as long as the parietal shield; lachrymo-maxillary notch deep and angular and of similar length to the orbital notch, which lies in the anterior half of the fronto-ethmoidal shield; preorbital corner almost right angular; the frontal pit line is at a level with the pineal foramen, or just posterior to the pineal foramen" (Young & Gorter, 1981); the lower jaw containing infradentary foramina along the ventral surface, short and deep, about 4.5 times as long as high with pit-lines variably developed; principal gular narrow anteriorly; cleithrum short and broad; clavicle with long ascending process, and interclavicle probably large; parashenoid concave with large denticles on the margin; basipterygoid process transverse and low on the endocranial wall; a single depression on the palatal lamina.

Remarks

Some of the diagnosis above is taken from Young and Gorter (1981: 116). Young & Gorter (1981) provisionally placed the species in Gyroptychius, from the option of six then described genera (Osteolepis, Thursius, Gyroptychius, Latvius, Megalichthys and Ectosteoroachis) but now is considered a new genus. The new genus is distinguished from Gyroptychius in having a greater range of breath/length (d/b) proportion 0.67-1.11, the t/s+t and t/r+s proportions fall outside of the Gyroptychius species in Jarvik (1948), with only Gyroptychius milleri having a similar range. The e/b proportion of Gyroptychius milleri is far less than this new genus which range from 0.78 – 1. 00. The new genus is similar to Kenichthys in the breadth length index with Kenichthys in the proportional range of NG 1, but NG 1 has a greater range from 0.67-1.11. NG 1
differs from *Kenichthys* in the proportion of the breadth between orbits over length; larger in *NG 1*, the depth of the orbital notch, it is much deeper in *NG 1* (2.2-2.7). The proportions of r/s+t are greater in *NG 1* than *Kenichthys*, also the t/r+s is greater. It is also similar to the “porolepiform” *Porolepis* along with *Gogonasus* in having a broad concave parasphenoid, but differs from *Porolepis* greatly by not having the posterior nostril (a feature of “porolepiforms”). *NG 1 australis* differs from *Gogonasus* in the recessed premaxilla, the parasphenoid projecting behind the processus connectens and the single depression on the palatal lamina. The lower jaw shows similarities with *Youngolepis, Psarolepis* and *Gogonasus* with small foramina on the external surface. It is distinguished from the other “osteolepids” in the fauna by the foramina on the lower jaw, which are thought to only occur in *NG 1 australis*. The parietal is square with proportions of f/a ranging from 0.57-0.63 with g/a of 0.92-1.01, this differs immensely to the elongate parietals in the formation. The orientation and grooved nares also distinguishes *NG 1 australis* from the other “osteolepids” in the formation.

**Description**

Measurements for all specimens are given in Appendix 3.

**Fronto-ethmoidal shields**

Four examples of the fronto-ethmoidal shield were described by Young & Gorter (1981). A further four have been identified. The fronto-ethmoidal shield of *NG 1* is distinctive in having deep orbits with an e/b proportions ranging from 0.78 – 1.00. The fronto-ethmoidal shields have a breadth/length index (d/b) ranging from 0.67 – 1.11 this range is also greater than any of the “osteolepids” (*Osteolepis* and *Thursius*) in Jarvik (1948). The range also fluctuates both smaller and larger than *Kenichthys* *(with a range of 0.98-0.99). The proportion of v/w is smaller (0.5-0.8) than the “osteolepids” of Jarvik (1948) [*Osteolepis macrolepidotus 1.45; O. panderi, Th. macrolepidotus 1.55; Th. moythomasi 1.15; Th. philidotus 1.60; G. agassize 1.10; G milleri 1.50]*.

In dorsal view the holotype (ANU V505) has all margins intact. The fronto-ethmoidal shield is slightly more elongate than figured by Young & Gorter (1981 fig. 25). The specimen has been distorted during preservation. One large crack extends through the left postorbital corner down to the right posterior corner of the specimen. There is a
cluster of sensory pores mesial to the orbit as figured by Young & Gorter (1981 fig. 25). In the distorted orientation the nasal openings are not seen from above, but from new reconstructions it is thought that the nasal openings would be visible from above and below if the specimen had not been distorted (Fig. 12 A), similar to the orientation of the nasal openings in *Kenichthys*. The holotype (ANU V505) has been scanned with high definition CT. This shows features of the specimen not previously exposed. With the CT scanning the endocranium can be identified (Fig. 7-9). Figures 7-9 show a series of slices through the specimen exposing its features. In horizontal plane (Fig. 7) the endocranium is sliced and exposes the cranial cavity. In a vertical transverse section (Fig. 8) the specimen is sliced and shows the endocranium and cranial cavity in a different view. Figure 9 is a vertical longitudinal slice of the skull.

In ventral view the premaxilla and nasal openings are seen folded under the skull roof (Fig. 7A). Below the right nasal opening is a small foramen for the infraorbital sensory canal (ioc Fig 7A). The holotype has a broad concave parasphenoid (psp Fig. 7A,B) covered in denticles, with a band of larger denticles along its margins. This broad concaved shaped and band of larger denticles along the margins is similar to *Gogonasus* (Long et al. 1997 fig. 10C) and *Medoevia* (Lebedev, 1995 fig. 2B). *NG 1 australis* differs from *Kenichthys*, *Thursius wudingensis*, *Cladarosymblema* which all have a long sword shaped parasphenoid. Within the parasphenoid, towards the posterior lies the buccohypophysial foramen (bh fo Fig. 7B). Posterior to the parasphenoid (Fig 7A-C) a solid structure is identified as the basipterygoid process and the processus connectens (bp pr, pr con Fig. 7C). At a higher level a separate bone is seen lodged in the right orbit; given the shape (Fig. 7C,D) the bone may be a palatoquadrate. The fenestra endochoanalisis quite apparent (fe end Fig. 7C–F) showing a triangular shape. The postnasal walls are thick extending laterally. At the margin the postnasal wall turns posteriorly joining the dermal bones of the skull roof (Fig. 7D-F). In *Gogonasus* (Long et al. 1997 fig. 10C) and *Medoevia* (Lebedev, 1995 fig. 2B) the postnasal walls also extend out laterally but curve anteriorly. The shape of the fenestra endochoanalisis also differs, being almost as wide as long in *NG 1 australis*, whereas in *Cladarosymblema* (Fox et al. 1995 fig. 22) it is much longer than wide, as it is in *Gogonasus* (Long et al. 1997 fig. 10C) and *Medoevia* (Lebedev, 1995 fig. 2B). The autopalatine articulation (art Fig.7E,F) has an oval shape and is situated behind the postnasal wall.
Small teeth are preserved on the premaxilla (Teeth Fig. 7D) with a recessed premaxilla lamina similar to *Gogonasus* (Long et al. 1997 fig. 10C). The palatal lamina (Plam Fig. 7E) is an unpaired recessed area anterior to the vomer attachment. This is quite different from *Gogonasus* (Long et al. 1997 fig. 10C), *Medoevia* (Lebedev 1995 fig 2B) and *Cladarosymblema* (Fox et al. 1995 fig. 22), of which all have two depressions on the palatal lamina. The vomer attachment site (vom att Fig. 7E) is quite solid, and triangular in shape. There are two small depressions which reach fairly high up into the endocranium (vom att Fig. 7E) with a ridge down the centre. No vomerine tusks are preserved in the specimen. The cranial cavity (c. cav) is first exposed in Fig. 7D, and is well exposed in Fig. 7E as a narrow cavity which tapers anteriorly.

In lateral view the specimen shows a deep orbital notch, the preorbital and the lachro-maxillary notch form an angle equal to or near a right angle. Scanning the left lateral side (Fig. 9A-F) shows the premaxilla turned under the skull roof (Fig. 9A). The scan shows a large square shaped fenestra endochoanalis (fe end Fig. 9A). The endocranial wall is deep posteriorly, and shallow anteriorly. In contrast, *Gogonasus* has a constant depth along the endocranium (Long et al. 1997 fig. 10A). Small teeth are seen above the premaxilla (Teeth Fig. 7D), whereas in *Gogonasus* the teeth in the premaxilla extend out below the premaxilla margin (Long et al. 1997 fig. 10A). A slice through the midline (Fig. 9F) shows; the buccohypopsial foramen (bh fo), the parasphenoid (psp) and the pineal foramen (fo pi) piercing the skull roof.

The transverse section (Fig. 8) shows the distortion of the specimen, with the right side pushed under the skull roof. On both sides of the premaxilla margin the foramen for the infraorbital sensory canal is seen (ioc Fig. 7A) with infraorbital sensory pores lying along presumably the premaxilla margin. Moving from anterior to posterior, the large square fenestra endochoanalis becomes apparent (fe end Fig. 8C) with arched palatal lamina (Plam Fig. 8C). The tip of the parasphenoid (psp) is exposed in Figure 8E with the cranial cavity (c. cav Fig. 8E). The concave parasphenoid is broader posteriorly (Fig. 8F). Figure 8F also exposes a larger cranial cavity. This also shows that the endocranium is slightly displaced to the right.

ANU V3338 is a very well preserved fronto-ethmoidal shield with most of the
internal and external structures exposed by mechanical preparation (Fig. 10). There is only slight distortion. However some of the margins are incomplete giving the specimen a different shape.

In dorsal view the margins are partly incomplete. The anterior premaxilla margin is damaged on the left and right sides. A small overlap area for the lachrymal is seen on the right side in lateral view (oa La Fig. 10D). The preorbital corners are complete, forming nearly a right angle on the right side (lateral view), and slightly more than a right angle on the left. The postorbital corners have been damaged, with model wax placed on the right side during preparation, presumably from the impression left in the rock matrix. The posterior margin is incomplete, except for the section next to the midline suture (Fig. 10A). Although the specimen is covered in cosmine remnant sutures are visible, indicating some of the dermal bone margins. The midline suture extends to the pineal foramen (M suture Figs. 10A, 12C) with a small midline suture at the anterior of the specimen (Fig. 10A). This is where the left and right frontals adjoin. Just forwards of the midpoint of the orbit on both sides, a suture can be seen between the supraorbital, posterior tectal and the frontal (Fig. 10A). Posteriorly on both sides a small suture is identified between the frontal and the dermosphenotic (dsph suture Figs. 10A, 12C) in relatively the same position as in Eusthenopteron (Jarvik, 1948 fig. 116). Other sutures seen in right lateral view define the posterior tectal and the anterior tectal (Fig. 10C). The sutures indicate an elongate posterior tectal which tapers anteriorly, and a small triangular anterior tectal which encompasses the nasal opening. The ventral margins of the anterior tectal are not preserved in the specimen. The premaxilla suture in the specimen is unclear, but is presumed to follow the infraorbital sensory canal as in the holotype (V505). The surface of the dermal bones exposes small groups of sensory pores anterior to the left dermosphenotic suture, and anterior to the right nasal opening (gr sp Fig. 10A). The frontal pit-line (pl Fr) extends level with the pineal foramen (fo pl Fig. 10A) on both sides of the specimen. The supraorbital sensory canal (soc Fig. 10A) extends anteriorly turning into the midline of the skull in front of the orbits in a similar fashion to Porolepis (Jarvik, 1972 fig. 61A), the same pattern with the deep loop of the sensory canal is identified in Muranjilepis, Thursius wudingensis and Kenichthys. The infraorbital sensory canal (ioc) presumably extends along the maxilla margin.
The ventral view shows the large ovate parasphenoid (psp Figs. 10B, 12D). The edge of the parasphenoid is bound by large denticles, with smaller ones on the inner concave surface and towards the buccohypophysial foramen (bu fo Fig. 10B), situated just in the posterior half of the parasphenoid. This is a feature in common with Medoevia (Lebedev, 1995 fig. 2B), Gogonasus (Long et al. 1997 fig. 10C) and Cladarosymblema (Fox et al. 1995 fig. 22). The parasphenoid projects out behind the level of the processus connectens (pr con Fig. 10B), the ventral margin of which attaches to the parasphenoid. This is not seen in Gogonasus (Long et al. 1997 fig. 10C) or Medoevia (Lebedev, 1995 fig. 2B). In these two the parasphenoid terminates before the processus connectens. The depression on the processus connectens is circular in shape (pr con Fig. 10D) with a deep embayment for connection with the parietal shield. A transverse basipterygoid process projects from the endocranium wall towards the posterior end in lateral view (bp pr Fig. 10C,D). The basipterygoid process is attached to the sides of the processus connectens in a sturdy, thickened connection. The posterior position of the bp pr is similar to Medoevia, Styloichthys, and Gogonasus, but is slightly more posterior in NG 1 australis and the other associated “osteolepids” – more like Kenichthys. The parasphenoid projecting behind the processus connectens is unique to NG 1 australis from the Corradigbee Formation.

The endocranium is less deep than in NG 2 (ANU V3339), unless compressed post-mortem. The anterior autopalatine articulation is long and slender in ventral view, with a deep recess for the articulation (art Fig. 10B). The shape is similar to Medoevia (Lebedev, 1995 fig. 2B) and Cladarosymblema (Fox et al. 1995 fig. 22), but it is wider in Gogonasus (Long et al. 1997 fig. 10C). The attachment areas for the vomers are relatively flat with slight depressions (vom att Fig. 10B). There are no anterior depressions to the anterior of the snout as in V3339 (Fig. 10B). The fenestra endochoanalis (fe. end) is opposite and well forwards of the autopalatine articulation. Two medium sized foramina lie anterior to the vomer attachment area and are identified as possibly the prenasal fossa (pnp Fig. 10B). The postnasal walls are quite thick and concave. The nasal capsules open ventrally as in Cladarosymblema (Fox et al. fig. 20A) through the region of the solum nasi (sn). The capsules are held more anteriorly than in Cladarosymblema. The postnasal wall (pnw) is well developed and ridged, possibly providing support and framing for the autopalatine articulation.
The premaxilla shows small dental conical depressions (Fig. 10B), and is marked at each end by the infra-orbital sensory foramen (ioc Fig. 10B). The premaxilla palatal lamina has been broken through during mechanical preparation exposing the infraorbital sensory canal (ioc2 Fig 10B). The palatal lamina shows a single depression (plam) with raised ridges in the area where the vomers attached, and defined by a suture with the ethmosphenoid, and can be identified in the scans of V505 (Fig. 7E). The palatal lamina differs from Gogonasus (Long et al. 1997 fig. 10C) and Cladarosymblema (Fox et al. fig. 20A) which have two depressions. A small extension from the palatal lamina of the ethmosphenoid which extends into the nasal capsule is presumably the nasal lamina. This also differs to Gogonasus (Long et al. 1997 fig. 10C) with the palatal lamina not extending as far over the fenestra endochoanalis.

In left lateral view (Fig. 10D) the endocranium is fairly shallow compared to Gogonasus (Long et al. 1997 fig. 10A), with the parasphenoid level with the premaxilla, and probably represents the original depth of the endocranium as the specimen has not been distorted, however some compaction is likely as the specimens are preserved in a mudstone. In Gogonasus the parasphenoid is slightly deeper. The large denticled margin of the parasphenoid is seen (psp Fig. 10D) along with a deep recess for the notochord (notochordal pit Fig. 10D). A transverse basipterygoid process is firmly attached to the endocranium with thickening of the endocranium walls posteriorly. The basipterygoid process is an L shape in lateral view (Fig. 10D). A large foramen in the centre of the endocranium wall is divided into two smaller sections by a slight ridge. The larger posterior section may have connected the optic nerve II (CII Fig. 10D). The smaller opening could have contained the optic artery. In lateral view the attachment area for the autopalatine articulation can be seen (art Fig. 10D). The crista suspendens (cr sus) is well developed on either side of the endocranium. Below the CII and above the parasphenoid is a small foramen for the carotis interna (c. a. ci).

ANU V3133 (Fig. 11A–C) is another fronto-ethmoidal shield, complete on the left side, with the right side partly weathered. In dorsal view the left frontal pit line is seen (pl Fr Fig. 11A). The supraorbital sensory pores are not as well exposed as in ANU V3338, but visible on the left side (soc). The pineal foramen (fo pi) is situated
slightly anteriorly to the frontal pit-line as in the holotype (ANU V505) and (ANU V3338). Behind both orbits the skull margins are weathered. The left posterior corner finishes at the suture between the dermosphenotic and the frontal (Dsph sut Fig. 11A). A small suture in the middle of the orbital margin is visible on both sides (SO sut Fig. 11A). Posteriorly the specimen is broken along the midline suture (m sut Fig. 11A). The left fenestra exonarina anterior is a prominent feature on the specimen (fe.exa Fig. 11C). The sensory canals show a typical “osteolepiform” pattern as in *Osteolepis* (Jarvik, 1972 fig. 61C). ANU V3133 is slightly more elongate than the holotype and has probably a resulted from preservation.

In right lateral view the specimen shows clearly the preorbital corner (proc Fig. 11B) and the orbital notch at almost a right angle (Fig. 11B) as described by Young & Gorter (1981: 118 fig. 25) for the holotype. V3133 differs in that the notch for the lachrymal and maxilla is less pronounced.

In anterior view two small pores of the infraorbital sensory canal (ioc Fig. 11C) are as described by Young & Gorter (1981). Two small patches of groups of sensory pores (gr sp) are seen interorly to the infraorbital sensory canal. The fenestra exonarina anterior is very similar to the holotype in its grooved shape (fe exa Fig. 11C). The premaxilla suture was not identified on the specimen, apparently due to the covering of cosmine.

ANU V3344 (Fig. 11D) is another fronto-ethmoidal shield preserved as an impression with incomplete margins. A rubber cast shows the nasal grooves close to the preserved margin. A small area of the frontal pitline (pl Fr Fig. 11D) has been preserved in the specimen. ANU V3310 is another partly weathered example with much of the outline preserved in the rock, but the midline suture is weathered off. No other sutures are found on V3310 (Fig. 11E). The specimen is slightly deformed, with much of the left side being pushed antero-mesially, but the right side is still intact. The nasal opening can be seen from above (Fig. 11E) and was probably seen from above before deformation. Originally it was the inability to see the nasal openings from above that was one point which set *G? australis* apart (Young & Gorter, 1981: 116) “the fenestra exonarina is ventrally placed and was probably not visible from above”. In ANU V3310 the supraorbital sensory canal (soc Fig. 11E) extends from the posterior anteriorly towards the nares (Fig. 11E). The nares in ANU V3310 are
groove-like as described by Young & Gorter (1981 fig. 25C), the overhang of the snout is quite pronounced as in the holotype, to which is most similar. In ventral view two pores of the infraorbital sensory canal on either side directly below the nasal openings as the holotype. The premaxilla suture is obscured by the cosmine layer. In left lateral view the specimen shows numerous groups of sensory pores. The preorbital corner (proc) is held at a right angle. A small lachrymal overlap is seen (oa [La Fig. 11E]).
Figure 7. *NG 1 australis* fronto-ethmoidal shield (holotype V505) in ventral view. A-H, Sequence of slices through V505 from ventral surface (A) through to the skull roof (H). The images expose the infraorbital sensory canal (ioc), parasphenoid (psp), fenestra endochoanalis (fe exa), cranial cavity (c cav) the articulation for the palatoquadrate (art) along with various other features.
Figure 8. *NG 1 australis* (holotype V505) in anterior view. A-G, Sequence of slices from anterior through to the posterior exposing the parasphenoid (psp), fenestra endochoanalis (fe exa), cranial cavity (c cav).
Figure 9. *NG 1 australis* V505 in left lateral view. A- F, Sequence of slices through the shield to about midway. The images expose the fenestra endochoanalis (fe exa), parasphenoid (psp), pineal foramen (pi fo) and the buccohypophysial foramen (bh fo).
Figure 10. Fronto-ethmoidal shield of NG 1 australis ANU V3338. A, Dorsal view, showing the frontal pitline (pt Fr), infraorbital sensory canal (ioc), groups of sensory pores (gr sp) and various suture between the dermal bones; for complete terminology of the abbreviations in the figures see pages 14-15. B, Ventral view showing the structures identified which include the palatal lamina (plam), basipterygoid process (bp pr) parasphenoid (psp) and the crista suspendens (cr sus). C, Right lateral view identifying the cranial nerve II (CII), basipterygoid process (bp pr) sutures between the anterior and posterior tectals and the supraorbital. D, Left lateral view exposing the articulation for the palaoquadrate (art), cranial nerve II (CII), and the carotid artery foramen (c a ci).
Figure 11. Fronto-ethmoidal shield of *NG 1 australis*. A - C, ANU V3133 in dorsal, right lateral and anterior views. In A, the frontal pitline (pt Fr) is seen along with the infraorbital sensory canal (ioc), pineal foramen (pi fo) and the supraorbital suture. B, Right lateral view showing the deep orbit, the supraorbital suture and the nasal opening (fe exa). C, Anterior view identifying the small group of sensory pores (gr sp) below the nasal opening (fe exa). D ANU V3344 in dorsal view an incomplete fronto-ethmoidal shield with the frontal pit line preserved (marked by the arrow). E, ANU V3310 in dorsal view
Figure 12. *NG 1 australis* A, B, ANU V505 reconstruction drawings of dorsal surface (A), and of the ventral surface (B) from the CT scans (see Fig. 7). C, D, ANU V3338 reconstructions of the dorsal (C) and Ventral surfaces (D).
Figure 12. *NG 1 australis* E, ANU V505 reconstruction drawings of the anterior of the fronto-ethmoidal shield. F, ANU V3338 reconstruction drawings of the anterior of the fronto-ethmoidal shield. G, ANU V505 lateral reconstruction based on Young & Gorter (1981, fig. 25C). H, ANU V3338 drawing based on Figure 10 C, showing the various identified structures.
Parietal Shield

The original description of the parietal shield was based on a single, fairly complete example (ANU V525). ANU V2268 (Fig. 13A- E) is an almost complete and well preserved new example. The ventral surface has been exposed by mechanical preparation completed by the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing. The specimen is wider than long (L =16.9mm, B =19.1mm) with a shape closely resembling Young & Gorter (1981 fig. 25B). The skull margins are mostly complete except for a small fragment on the left anterior margin, and the left posterior margin. The spiracular notch (i.spir) in the lateral margin is clearly evident on both sides. The postorbital notch (i.po) is clear on the left side, but less pronounced on the right. The posterior corners are broad, with the anterior narrower. The postotic sensory canal (poc Fig. 13A) extends close to the lateral margin extending from the supratemporal to the anterior of the intertemporal. The midline suture is preserved at the posterior margin (m suture Fig. 13A). The supratemporal pit-line (pl.tr.Pa) is clearly seen on both sides. The supratemporal bone is not defined by a suture. The posterior oblique parietal pit-line (pl.po.Pa) joins on the inside end of the transverse parietal pit-line, and extends posteriorly.

The ventral structures of the parietal shield have been prepared out but are incomplete. The roof of the braincase are preserved, and the basicranial fenestra (Fig. 13B). A small groove is seen on the lateral sides (left is incomplete) of the shield presumably for jugular canal (jugular canal Fig. 13B).

The posterior view shows the groove for the jugular canal on the right side as a small foramen (Fig. 13E). The jugular canal is incomplete. Above this, where the occipital attaches to the cranial roof, a small foramen may have contained the occipital artery (c. a. occ Fig. 13E).
Figure 13. *NG 1 australis* Parietal shield ANU V2268. A, Dorsal view identifying the horizontal and transverse pit lines (pl.tr.Pa, pl.po.Pa), the spiracular notch (i.spir), the midline suture (md suture) along with the postotic sensory canal (poc). B, Ventral view showing the roof of the braincase, basicranial fenestra and the jugulae groove (jug gr). C, Right lateral. D Left lateral view. E, Posterior view showing the jugular canal, notochordal canal, the fossa bridge and the occipital artery (c a occ).
Lower Jaw

Three new examples of lower jaws are described below. Many other fragments of lower jaws have been collected and stored in the bulk material. They have not been studied in depth.

Young & Gorter (1981: 119) noted “some variation in the shape of the anterior end of the jaw” with two fairly complete new examples the shape of the posterior end of the lower jaw appears fairly uniform. Along with the number and position of the pit-lines differs between individual specimens. In CPC19592 only the horizontal pit line is seen (Fig. 14A), but in the new speciments the vertical pit line has been preserved as well. The number of sensory openings also varies between individuals. However the lower jaw of NG 1 australis is readily distinguished from the other osteolepid jaws in the formation by a notch on the ventral surface which contains a small foramen (fo Fig. 14), this feature associated with a short prearticular and differences in the coronoids as shown by ANU V2269 (see below).

CPC19592 is the only almost complete example originally described by Young and Gorter (1981), missing only some small fragments on the ventral margin (Fig. 14A). The horizontal pit-line (pl Id Fig. 14A) extends along the majority of the lower jaw and lies behind the small fold in the specimen. Large pores of the mandibular sensory canal (p. mcp) are seen along the ventral surface of the specimen. One feature overlooked in the original description by Young & Gorter (1981). The small foramen along the ventral surface (fo Fig. 14A) which is separate from the mandibular sensory canal (p. mcp). This foramen is similar to those seen in Psarolepis (Zhu & Schultze, 1997), Youngolepis (Chang, 1991 fig.10), and in one specimen of Gogonasus (ANU V49259; Long et al. 1997 fig. 36A). The new specimen of Gogonasus does not contain the infradentary foramen. The infradentary foramen in NG 1 australis are not as large as in Gogonasus, Youngolepis or Psarolepis. Three infradentary foramina occur in Achoania, Psarolepis, Styloichthys, Youngolepis, Powichthys and some porolepiforms (Zhu & Yu 2004: 274). Up to two preserved infradentary foramina have been identified in NG 1 and Gogonasus.

Ahlberg (1991) suggest the infradentary foramen lie on the sutures between the infradentaries (fig. 8A). They are seen placed either above, below or in amongst the mandibular sensory pores. The presence of the infradentary foramina in NG 1 australis may be a similar feature to Powichthys – a more primitive porolepiform
which contains infradentary foramina, compared to *Porolepis* which doesn’t have the foramina. Thus *NG 1 australis* would be more primitive on this character than *Kenichthys*, the most primitive ‘osteolepid’ on other characters.

ANU V3229 (Fig. 14B) is a large right lower jaw (L = 67.8mm, H = 13.4mm) mostly complete except for the damaged posterior margin. ANU V3229 is five times as long as high showing a long broad specimen. Jarvik (1948: 94) recorded a L/B of 5.5 - 6.5 for Scottish species. The L/B is 4.5 in the jaw described by Young & Gorter (1981), and only 4 in *Kenichthys*, the shortest and broadest lower jaw recorded for osteolepidids (Chang & Zhu, 1993: 190). The specimen shows a deeply indented horizontal pit line (*pl. Id*), but no vertical pit line. The mandibular sensory pores (*p. mcp*) are ventrally placed but rise anteriorly along the jaw. The mandibular canal extends through the four infradentary bones of the lower jaw as in *Eusthenopteron foordi* (Jarvik, 1980 fig. 127). Half way along the ventral surface is a small foramen (*fo* Fig. 14B), as in the previous specimen. *Youngolepis* (Chang, 1991 fig. 10) has three foramina, but there is only the one on this specimen. Chang (1991) states that these pits are absent in all “osteolepiformes”, but foramina are found in the “osteolepiform” *Gogonasus* (Long et al. 1997 fig. 36A), as well as these new specimens.

ANU V2269 is a left lower jaw (Fig. 14C, D) prepared out to show the internal and external structures of the jaw. It is complete except for a small broken margin at the anterior of ventral surface. Both horizontal and vertical pit-lines are clearly preserved (*pl. Id* and *pl. Id2*). The horizontal pit-line extends about three quarters the length of the jaw starting from the posterior end. The vertical pit line extends down through the mandibular sensory canal (*p.mcp*) to the margin. The jaw and is short and broad (B/L index 0.65). Two foramina notch the ventral margin, one at the posterior end and another about a third of the way along the ventral margin (*fo* Fig. 14C). The anterior foramen has a position similar to (ANU V3229 & CPC19592). There are no obvious connections between the foramina on the external or internal surfaces. A small groove runs between the prearticular and the infradentaries. The infradentary foramen may have provided a connection between this groove for some soft tissue structure. The *p.mcp* follows the curves of the *plh.Id* in a single line. A third infradentary pit line (*pl Id3*) is present at the anterior end of the jaw similar to
what is recorded by Young & Gorter (1981). Scattered sensory pores (sc sp) are
evident on the upper margin of the jaw, but with no regular pattern. The posterior
margin of the jaw is very similar to a specimen belonging to Gyroptychius milleri
(Jarvik, 1948 fig. 23G). The quadratojugal overlap (oa Qj) is preserved as a small
notch.

The inside of the jaw shows the anterior two coronoids (co1, co2). A
presumed third coronoid is largely covered by rock matrix. The coronoid boundaries
are not clear. Anteriorly to the first coronoid is a small depression (dep cor Fig. 14D),
and a large intercoronoid pit (int cor fo) is seen between the first and second
coronoids, as in most osteolepids. The tusk of the first coronoid is present but the
second coronoid’s tusk is missing (surface damaged). The prearticular covered in
small random denticles, tapers anteriorly (pre Fig. 14D). The prearticular does not
continue to the anterior margin of the jaw, terminating before the parasympophysial
plate (Fig. 14D). The prearticular is broad compared to that of NG 2, and does not
extend as far forwards. The parasympophysial plate (ads) has small denticles covering
the surface like Gogonasus (Long et al. 1997 fig.39A); it is small, narrow and
triangular in shape.

Two small teeth can be seen on the posterior ledge of the prearticular, as in
Gogonasus (Long et al. 1997 fig. 39A). The teeth in the dentary are normal conical
shape (Fig. 14D). A large deep adductor fossa (ad fos) can be seen for the adductor
mandibulae (ad fos Fig. 14D). However the adductor fossa is not as deep as seen in
NG 2. The glenoid fossa (gl fos) has the normal double articulation surface as is well
preserved in Gogonasus (Long et al. 1997 fig. 39A) and is also quite deep. On the
anterior margin of the specimen the mandibular symphysis (m sym) is well preserved
showing an attachment area also much like Gogonasus (Long et al. 1997 fig. 39A)
and other forms.
Figure 14. Lower jaws of NG 1 australis. A, CPC19592 in lateral view showing the horizontal pitline on infradentary (plh ld), and small foramen on the ventral margin (fo). B, ANU V3229, lateral view, also showing the small foramen (fo), and the mandibular sensory canal (p mcp). C, ANU V2269 in external showing two foramina on the ventral surface (fo), and horizontal and vertical pit lines (plh ld, plv ld2). D, ANU V2269 lingual exposing a deep glenoid fossa (gl fos), adductor fossa (ad fos), the prearticular (pre) which doesn't extend the length of the jaw, coronoid 1 (cor 1) and the parasymphysial plate (ads) along with the mandibular symphysis (m sym).
Maxilla
ANU V3345 (Fig. 15A) is a complete maxilla. The maxilla is quite long with a small crack extending down from the dorsal margin. It is similar to NG 2 (ANU V3355 and ANU V3356). The posterior is quite curved as in ANU V3355. The ventral margin is straight. At the anterior of the specimen a small overlap area is seen for the lachrymal (oa La Fig. 15A). Along with a small process (flange) as in Gogonasus (Long et al 1997 fig. 21).

Gular
ANU V3298 is a large principal gular from the right side (Fig. 15B,C), with a L/B of 3. It is more elongate than the single gular described by Young & Gorter (1981). Well developed overlaps for the branchiostegal rays and the other principal gular are identified, the labelled ridge (Fig 15 B, C) being a step in the external cosmine indicating a loose overlap with the other gular. This feature is not developed in the Scottish osteolepids (Jarvik, 1948). The gular pit line (pl.G) is small (Fig. 15C). There is a small anterior notch for the median gular, with an overlap surface (od.G.m).

ANU V3132 is another almost complete right principal gular (Fig. 15D). It was also found lying close to a principal gular (ANU V3132) and is also probably from the one individual. The straight median margin extends 25.9mm in length, the anterior end is sharp and pointed, and the posterior is rounded in shape. The gular has a breadth of 9.7mm as measured according to the accepted standard shown by Jarvik (1985 fig. 2). A small pit line (pl.G) on the surface about one third of the way down. There is a small overlap area (oa.G.m) at the anterior end of the specimen. There is no evidence of pores. The shape is comparable to the specimen of Young & Gorter (1981 pl. 9, fig. 11) and also resembles Jarvik’s (1948 fig. 24B) example of Osteolepis macrolepidotus.

ANU V3131 is a subopercular closely associated (~1.5 cm away) with the fronto-ethmoidal shield (ANUV3133) and is presumed to belong to the same individual. It is an elongate oval shaped subopercular. There is a small overlap area which runs along the upper margin for the operculum. The exterior surface of the bone is smooth with fine cosmine. The anterior margin is straighter than illustrated by Young & Gorter (1981 fig 26A) and the dorsal margin is also straighter – not rising posteriorly as in...
Young & Gorter (1981 fig. 26A).

**Unidentifed**

ANU V3343 (Fig. 15E) is a smooth bone, probably from the internal skeleton. It is possibly a haemal spine? Or from the fin region; a ?radial.
Figure 15. A, ANU V3345 maxilla showing the lachrymal overlap area (oa LA) and the flange. B, C, ANU V3298 principal gular showing a prominent ridge, overlap for the branchiostegal rays (oa Rbr) and the overlap for the median gular (oa G m). D, ANU V3132 principal gular identifying the gular pitline (pl G). E, ANU V3343 unidentified bone probably from the internal skeleton.
**Comparisons of NG 1 australis**

This species was a relatively small individual (based on the collected remains) probably attaining a size of ± 400 mm. The fronto-ethmoidal shield is distinctive in having deep orbits with an e/b proportions ranging from 0.78 – 1.00. This is larger than all the Middle Devonian “osteolepids” of Jarvik (1948), but is similar to *Latvius niger* (Jessen, 1973). The orbit proportion (e/b) is also greater than *Gyroptychius groenlandicus* from East Greenland. The fronto-ethmoidal shields have a breath/length index (d/b) ranging from 0.67 – 1.11 this range is also greater than any of the “osteolepids” (*Osteolepis* and *Thursius*) in Jarvik (1948). The range also fluctuates both smaller and larger than *Kenichthys* (*with a range of 0.98-0.99*). The orbital depth is deeper than *Kenichthys*. The proportion of v/w is smaller (0.5-0.8) than the “osteolepids” of Jarvik (1948) [*Osteolepis macrolepidotus* 1.45; *O. panderi*, *Th. macrolepidotus* 1.55; *Th. moythomasi* 1.15; *Th. philidotus* 1.60; *G. agassize* 1.10; *G milleri* 1.50]. The proportion is similar to *Kenichthys* (0.52-0.54).

*NG 1 australis* differs from *Kenichthys*, *Thursius wudingensis*, *Cladarosymblema* which all have a long sword shaped parasphenoid. Its broad concave parasphenoid with larger marginal denticles is most similar to *Gogonasus*, *Medoevia*, *Porolepis* and *Youngolepis*. The parasphenoid in *NG 1 australis* is broad similar to *Gogonasus* and the “porolepiforms” *Porolepis* and *Youngolepis*. However *Kenichthys* and *NG 1* seem to be similar with only one depression on the palatal lamina (see Zhu & Ahlberg, 2004 fig. 2C).

The cheek of *NG 1 australis* remains unknown with only an incomplete squamosal and preopercular identified from Young & Gorter (1981).

The external surface of the lower jaw differs from the other “osteolepids” in the formation, in having at least one or two small infradentary foramina along the ventral surface. This is similar to *Youngolepis*, *Gogonasus*, *Psarolepis*. The inside of the lower jaw has a prearticular which does not extend the length of the jaw and is short and broad (B/L index 0.65). The prearticular is covered in small denticles with small teeth on the dorsal margin. The adductor fossa is not as deep as *NG 2*. Three coronoids are identified in *NG 1 australis*, three coronoids are also found in
Kenichthys the most primitive tetrapodomorph along with Gogonasus and Medoevia.

Kenichthys and NG 1 australis

Chang & Zhu (1993: 195) considered Gyroptychius? australis to be closely related to Kenichthys campbelli, based on four characters:

- Elongate (grooved) nares (Chang & Zhu 1993: 186),
- A deep embayment behind the postorbital corner (Chang & Zhu, 1993: 187),
- A principal gular with its length/breadth ratio matching that of G.? australis (Chang & Zhu, 1993: 194),
- A very short and broad snout.

Although the two genera share these four resemblances, this study has found that NG 1 australis is quite different from Kenichthys in a range of features, as follows:

1. The parasphenoid is sword shaped in Kenichthys, but in NG 1 australis the short, broad parasphenoid is like Gogonasus and Porolepis in shape, and the buccohypophysial foramen is situated closer to the posterior end. These may be primitive features.
2. Nasal openings Zhu & Ahlberg (2004) suggest that Kenichthys has a posterior nostril forming a choana, bound by the lachrymal, premaxilla, maxilla and lateral rostral (see Zhu & Ahlberg, 2004 fig. 1D). NG 1 australis doesn’t have a posterior nasal opening. It only has the anterior nasal opening - groove like. From the preserved material the suture pattern of the lateral rostral, tectals, and premaxilla is unclear in NG 1.
3. The lower jaw contains foramina on the infradentaries which are not in Kenichthys. These may be evidence of a relationship with basal sarcopterygians like Psarolepis and “Porolepiformes”. This would indicate a more primitive condition than Kenichthys.

Thursius wudingensis was described by Fan (1995) and shows similarities in the fronto-ethmoidal shield in the pattern of the supraorbital sensory canal (soc), both have a large loop anterior to the orbit. Orbital notch of 2.2 -3.6 is slightly larger than NG 1 australis. The internal structures of Thursius wudingensis have not been described. Without further information on Thursius wudingensis a detailed comparison between the two is not possible.
Canowindridae and NG 1 australis

Young et al. (1992) suggested that Gyroptychius? australis may have a relationship with the Antarctic osteolepiforms Platyethmoidia antarctica and Koharalepis jarviki which were referred to the family Canowindridae. Young et al’s (1992) suggestion of being a canowindrid is unable to be confirmed at this time. As defined by Young et al. (1992) the family Canowindridae is characterised by:

- Broad extratemporals
- Fused parietal, intertemporal and supertemporal
- Lateral extrascapular extending to the midline
- Median extrascapular broad posterior and narrow anterior
- The main postorbital bone excluded from the orbital margin by one or more small bones in a postorbital position

The preserved material of NG 1 does not include any information on the extratemporals, extrascapular series or the postorbital bones, and so their suggestion cannot be checked. NG 1 does have fused parietal, intertemporal and supratemporal.

Platyethmoidia antarctica and Gyroptychius? australis

Young et al. (1992: 25) suggest the shape of Platyethmoidia’s lower jaw resembles that of NG 1 australis Young & Gorter (1981), “which also had a short broad fronto-ethmoidal shield as in the holotype of Platyethmoidia antarctica n.sp., and may be closely related”. The lower jaw of Platyethmoidia antarctica is similar in shape to NG 1 australis, but it does not have the foramina on the infradentaries as in NG 1 australis (Fig. 14). The jaw resembles NG 2 from locality 138 (described further on), which also does not have the foramina on the infradentaries (Fig. 18). Young et al (1992) “the jaw is distinguished from that of many osteolepids by the ventral position of the articular region relative to the dorsal margin of the jaw. This is also a feature of Gyroptychius? australis”. However, Jarvik (1948) considered that the shape of the lower jaw to be similar for all species, and that proportions are of only small significance.
Platyethmoidia antarctica differs from NG 1 australis in 4 ways:
1. Greater breadth of the fronto-ethmoidal shield
2. Less pronounced orbital notch
3. External nostrils partly visible from above
4. Snout not folded up towards the mouth.

However, although different from Gyroptychius? australis, it does show some significant similarities with the other ‘osteolepids’ from the Corradigbee Formation described further on.

Muranjilepis
Young & Schultze (2005) “The parietoethmoidal shield ... is more elongate, and the postparietal shield is shorter and broader than Gyroptychius? australis”.

A feature Muranjilepis has in common with NG 1 australis is the pattern of the supraorbital sensory canal (soc: see Fig. 12). This deep looped pattern seen in Muranjilepis (Young & Schultze, 2005 fig. 6B), Thursius wudingensis (Fan, 1992 fig. 2A,B) and Kenichthys (Chang & Zhu, 1993 fig. 3D), is also present in NG 1 australis.

Muranjilepis differs from NG 1 australis in four ways. The grooved nasal openings of NG 1 australis are absent. The long postorbital division is not seen in Muranjilepis, the deep embayment behind the postorbital corner is also lacking, and the snout is more elongate.

NG 1 australis and Porolepiformes

The foramina in the lower jaw of NG 1 could be a primitive character retained in one lineage of osteolepidids. Kenichthys the earliest known ‘osteolepid’ does not have any foramina on the lower jaw. Foramina are present in Holoptychius, and some porolepiformes and it is assumed that these foramina are a primitive character. If these foramina are a primitive character they must have been lost in Kenichthys. The foramina in NG 1 are similar to those seen in Psarolepis (Zhu & Schultze, 1997), Youngolepis (Chang, 1991 fig.10), and in one specimen of Gogonasus (ANUV49259; Long et al. 1997 fig. 36A). The new specimen of Gogonasus does not contain the
infradentary foramen. The infradentary foramen in *NG 1 australis* are not as large as in *Gogonasus, Youngolepis* or *Psarolepis*. Three infradentary foramina occur in *Achoania, Psarolepis, Styloichthys, Youngolepis, Povichthys* and some porolepiforms (Zhu & Yu 2004: 274). Up to two preserved infradentary foramina have been identified in *NG 1* and *Gogonasus*.

Ahlberg (1991) suggest the infradentary foramen lie on the sutures between the infradentaries. They are seen placed either above, below or in amongst the mandibular sensory pores. The presence of the infradentary foramina in *NG 1 australis* may be a similar feature to *Povichthys* – a more advanced porolepiform which contains infradentary foramina, than the primitive porolepiform porolepis which doesn’t have the foramina. The same is the case with *NG 1 australis* presumable a more advance ‘osteolepid’ than the most primitive ‘osteolepid’ *Kenichthys*. It is difficult to use this character as it is not certain in Porolepiformes either. But the fact that they are only found in Australian ‘osteolepiforms’ may be of some significance.

*NG 1 australis* shows unique characters only shared with the other osteolepids found in the same formation. These ‘osteolepids’ may belong to one family. *NG 1 australis* is very different from *Kenichthys* as first thought. *NG 1 australis* has no significant characters with the Scottish osteolepids having more in common with *Gogonasus, Medoevia* and *Youngolepis*. 
NG 2 gen. et sp. nov.

Diagnosis
A cosmine covered “osteolepid” with a round basipterygoid process fixed laterally on the endocranium; the fronto-ethmoidal shield has a d/b of 0.93 and an e/b of 0.85; orbital proportions of r/s+t and t/r+s proportions of 0.37; 1.05; postnasal wall convex; preorbital corner at right angles; frontal pit line level with the pineal foramen. The lower jaw about has a k/m of 3.9; a single depression on the palatal lamina; two rows of teeth in the premaxilla; prearticular extends to the jaw symphysis;

Holotype ANU V3338 a fronto-ethmoidal shield.

Other Material
Two fronto-ethmoidal shields (ANU V3338, ANU V3346); Three lower jaws (ANU V3128, ANU V3313, ANU V3352); Four cheek units (ANU V3307, ANU V3308, ANU V3309, ANU V3348); One lateral extrascapular (ANU V3347); Four jugals (ANU V3301, ANU V3294-96); one quadratojugal (ANUV3305); One cleithrum (ANU V3349); Two suboperculars (ANU V3350 ANU V3351); Two operculars (ANU V3353, ANU V3354); Two maxillae (ANU V3355, ANU V3356); One lachrymal (ANU V3357); Two postorbitals (ANU V3293, ANU V3359); Two unidentified bones are provisionally included.
Locality and Horizon

All material described below comes from locality 134 located along the eastern side of the ‘Western Creek’ (Fig. 2B). This is in horizon F which is five horizons above the original study site (WT see Fig. 2B). The material is found in a yellow-grey mudstone that is quite soft compared to most other layers in the formation. The bones do not occur always on the bedding plane some are found perpendicular to the bedding plain.

Remarks

The material is believed to belong to the one species as it comes from the same locality and horizon.

The new genus has a similar breath/length (d/b) proportion to NG 1. The orbital proportions of t/s+t and t/r+s proportions (0.37; 1.05) fall outside the range of NG 1. The proportions also fall outside the range of the “osteolepids” (*Osteolepis, Thursius, Gyroptychius*) in Jarvik (1948, table 1), with only the subsequently described *Kenichthys* having a similar range. The breadth of the skull between the orbits over the length (e/b) proportion of 0.80 is similar to NG 1 but greater than *Kenichthys*. The new genus is similar to NG 1 in d/b, e/b, v/w and most of the proportions, but differs in the internal structures of the endocranium. The basipterygoid process has a completely different structure. It is formed by a small round process situated laterally on the endocranial wall. The basipterygoid process shows slight similarities with the “porolepiform” *Holoptychius*. The depth of the endocranium is much shallower than *NG 1 australis*, the position of the cranial nerves differs, with two larger foramen separated by a small wall. This is possibly an eye stalk. The curvature of the anterior of the fronto-ethmoidal shield differs, and is much broader similar to *Latvius porosus* (Greiner, 1977). The articulations for the palaoquadrate are held slightly more latterly than in *NG 1 australis*. The postnasal walls show some variation between the two. *NG 2* is also similar to the “porolepiform” *Porolepis* in the pattern of the sensory canals. The lower jaw shows similarities with *Platythmoidia* (Young et al. 1992) in the shape and proportions. The lower jaw is distinguished from *NG 1 australis* in the fauna by the absence of the foramina on the infradentaries of the lower jaw. The nasal
openings are seen from above which is similar to *Osteolepis* (Jarvik, 1948). One specimen (ANU V3346) shows possibly a 'sub-narial' gap as in *Latvius porosus* (Greiner, 1977).

**Description**

**Fronto-ethmoidal shield**

Two fronto-ethmoidal shields have been identified. The external surface of the holotype (ANU V3339) is preserved relatively complete, with some bone margins broken. The internal structures have undergone some degree of weathering (Fig. 16B-D), but show the basic structures of the endocranium which is generally similar to *Osteolepis* (Thomson, 1965 fig. 1) or *Eusthenopteron* (Jarvik, 1980 fig. 86).

In dorsal view the margins of the shield are incomplete (Fig. 16A, 17B). The orbit and premaxilla margins are well preserved on the left side. The right margin is incomplete and the posterior margin can be restored from the left corner. The bones of the skull roof are highly fused with only a few sutures able to be identified (Fig. 16A). A frontal pit line (*pl. Fr*) Fig. 16A) is seen on either side of the midline as in *NG 1 australis* (Young & Gorter, 1981 fig. 25), *Koharalepis, Platyethmoidia* (Young et al. 1992 figs. 13,17) and *Thursius* (Jarvik, 1948 fig. 61). An apparent small median foramen towards the anterior of the *pl. Fr* is identified as the pineal foramen (*pi fo*). The supraorbital sensory canal (*soc*) extends closely to the lateral margins of the skull, turning inward towards the anterior. In this sense they are somewhat similar to *Porolepis* (Jarvik, 1979 fig. 61). The postorbital notch (*i po* Fig. 16A) is at right angles like *Mahalalepis* (Young et al. 1992 fig. 15) although it is a little deeper. Small patches of sensory pores (*gr sp*) are seen on the dermal bones of the skull. From the anterior view the premaxilla is fused onto the other elements of the skull as in *Kenichthys* (Chang & Zhu, 1993), with the infraorbital sensory canal presumably following the premaxilla suture. There is only one external nasal opening, which an “osteolepiform” feature. The skull has a breadth length index (d/b) of 0.85. This is very similar and within *NG 1 australis’* b/d index range. The orbit depth of the fronto-ethmoidal shield is slightly shallower, being 1.6.
In ventral view the internal structures have been exposed by mechanical preparation. However the preservation of the structures is not great. The parasphenoid (psp) is missing leaving a large buccohypophysal foramen (bh fo Fig. 16B). Anterolateral to the buccohypophysal foramen on either side is a arcuate shaped structure (scd) solidly attached to the endocranial wall. This may have attached to the dorsal surface of the parasphenoid and/or was an articulatory ridge for the palatoquadrate. Anterior to the buccohypophysal foramen is a small foramen on either side of the ridge (?aci fo Fig. 16B). At this stage it is unsure what these may be but could be arteries of some sort going to the cranial cavity possibly for the internal carotid arteries similar to Medoevia (Lebedev, 1995 fig. 2B). Unlike Medoevia (Lebedev, 1995 fig. 2B), there is no anterior parasphenoid pit.

Posteriorly the processus connectens (pr con) is situated very low and is similar to Medoevia (Lebedev, 1995 fig. 2B) and Gogonasus (Long et al. 1997 fig. 10C). The processus connectens in Styloichthys is situated much more dorsally. In ANUV3339 there is only the one surface for the articulation and it is round in shape. In this aspect the specimen described here is like Medoevia (Lebedev, 1995 fig. 2D). On either side of the processus connectens is a small foramen surrounded by bulbous bone margins presumably filled with cartilage (bp pr Fig. 16B), which is identified as the basipterygoid process. This process is different from NG 1 australis, which has a transverse attachment. ANU V3339 shows slight similarities with Holoptychius (Jarvik, 1980 fig. 149B) but it is different from Styloichthys, Psarolepis, Kenichthys, Youngolepis, Gogonasus, Eusthenopteron, Osteolepis and Medoevia. Anterior to the right fenestra endochoanalis (fe end) and in the premaxilla, a small foramen is visible for the infraorbital sensory canal (ioc Fig.16B, 17A). The anterior autopalatine articulation (art) is preserved in the right side (art Fig. 16B). The walls of the endocranium here are poorly preserved leaving broken margins. The postnasal wall (pnw) is thin and vertical, slightly convex, whereas in NG 1 australis the postnasal wall is concave. The fenestra endochoanalis (fe end) are prominent large, deep and held in a similar fashion to Youngolepis (Chang, 1982 fig. 10), and Gogonasus (Long et al. 1997 fig. 10C). The fenestra endochoanalis seem to be set further back and more sloped as the skull seems to be more pointed. In the right fenestra endochoanalis is a small foramen, it is positioned on the internal side wall where presumably the olfactory track opens, as seen in Cladarosymblema (specimen QMF21083).
Anteriomesial to the fenestra endochoanalis are two depressions on the palatal lamina (plam Fig. 17A) similar to *Gogonasus* (Long et al. 1997 fig 10C). Two rows of conical teeth are seen in the premaxilla, a small row anteriorly and a row with larger teeth posteriorly (Fig. 16B). The vomers are in place in the specimen showing they were solidly attached (vo, Fig. 17 B).

In left lateral view the endocranium has a depth of about 9.9 mm similar to what is seen in *Gogonasus* (Long et al. 1997 fig. 10A), with the greatest depth to the posterior of the specimen. The depth of the skull tapers anteriorly, without a constant depth as demonstrated in *Osteolepis* (Thomson, 1965 fig.1) and *Gogonasus* (Long et al. 1997 fig. 10). This shape of the endocranium is a similarity in the 3 types of “osteolepid” skulls found in the formation. In lateral view the basipterygoid process (Fig. 16C,D) is situated posteriorly on the endocranium wall up against the processus connectens. This arrangement is most similar to *Styloichthys*. The basipterygoid process in *Gogonasus*, *Medoevia* and *Cladarosymblema* is not as far back as in ANU V3339, and in *Psarolepis* the basipterygoid process has a very anterior position along the side of the skull. On the left lateral side of ANU V3339 the olfactory tract extends from the deepest section of the fenestra endochoanalis as in *Cladarosymblema* (Fox et al. 1995 fig. 24). The small conical teeth are held in the premaxilla lamina and are in a ‘recessed’ position. The premaxilla extends down in front of the teeth and they are hidden behind this bone wall. The specimen has the vomerian tusks partly preserved. The vomer is situated mesially to the fenestra endochoanalis on the palate similar to *Gogonasus* (Long et al. 1997 fig. 10C) and *Youngolepis* (Chang, 1982 fig. 7B). The lateral endocranium wall shows several other features of importance. A large foramen approximately mid-length to the specimen is identified as cranial nerve II (CII). Just above this is a small foramen presumably nerve III (CIII). Ventral to these is a larger foramen, possibly an eye stalk/muscle attachment (?eys). Several other small openings in the side walls of the endocranium are presumed to be damage during mechanical preparation of the specimen.

The second specimen referred to this genus ANU V3346, an incomplete fronto-ethmoidal shield (Fig. 17C). The posterior has been weathered along with parts of the anterior skull roof. The specimen exposes the small vessels in the anterior of the snout.
In dorsal view the anterior margin is fairly complete, but the left side is slightly damaged. The right lateral margin back up to the postorbital corner is complete. Posterior to this the specimen is incomplete with a small impression left in the rock matrix for part of the posterior end. The left lateral side is very weathered with no bone margins preserved. The posterior right side may have broken along the frontal pit line (pl. Fr). On the left side a small part of the frontal pit line is preserved (pl. Fr Fig. 17A). The supraorbital sensory canal (soc) is preserved on the right side in a similar position to ANU V3339. In dorsal view the orbital notch is quite deep, with a prominent postorbital corner. On the left side, where the bone has been weathered, small 'holes' and tubes are preserved in the sponge layer of the bone. The posterior margin is incomplete except for the section preserved across the midline.

In anterior view, the specimen is dome-shaped. The right nasal opening as preserved is quite different to the previously described taxa. The nasal opening is in the margin of the bone producing a 'sub-narial gap' (Fig. 17) as in *Latvius porosus* (Greiner, 1977 fig. 3) and slightly like *Styloichthys* (Zhu & Yu, 2002 fig. 1e). This subnarial gap is unable to be confirmed on the holotype (ANU V3339) as the nasal margins are incomplete. There is a distinct curve to the anterior of the shield like *Latvius* (Greiner, 1977 fig. 3). The median part of the anterior margin is the deepest; this is similar to *Psarolpeis* (Friedman, 2007 fig. 3F). The orbital notch is greater than *Latvius porosus*.
Figure 16. Fronto-ethmoidal shield of new Genus & Species 2, ANU V3339. A, Dorsal view, showing the well developed frontal pit line (pl. Fr), well developed orbital notches and nares seen from above. B, Ventral view showing the structures identified which include the post nasal wall (pnw), basipterygoid process (bp pr) parasphenoid (psp) and the crista suspendens (cr sus). C, Right lateral view identifying the cranial nerve II and III (CII, CIII), basipterygoid process (bp pr). D, Left lateral view exposing the olfactory ridge, cranial nerve II (CII) and a possible eyestalk (?eys).
Figure 17. A. line drawings of ANU V3339. A. Ventral view B. Dorsal view showing a similar soc pattern to *Thursius wudingensis*. C. Lateral view showing the possible eye stalk. D. ANU V3346 showing the weathered bone surface exposing the spongy bone. E. Reconstructed anterior view of ANU V 3339, Showing the premaxilla suture on the right side and the midine suture.
Lower Jaws

ANU V3313 (Fig. 18A- C) was prepared by Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China. The margins of the jaw are all complete and it has very well exposed internal structures.

The jaw tapers slightly anteriorly similar to NG 1 and unlike Gogonasus. Generally the lower jaw is similar to Medoevia (Lebedev, 1995 fig. 11). The dermal bones (dentary, infradentaries 1-4) are fused with no sutures visible between them (Fig. 18B), but the arrangement of these bones is presumed to be as in Eusthenopteron. The horizontal pit-line (pl Id) extends over three quarters of the specimen as in Gyroptychius, Thursius and Osteolepis (Jarvik, 1948). The horizontal pit-line lies in the suture between the dentary and the infradentaries according to Jarvik (1980). If so, the horizontal pit-line in ANU V3313 defines a dentary which deepens anteriorly as in Eusthenopteron (Jarvik, 1980 fig. 125A). However the dentary in Eusthenopteron (Jarvik, 1980 fig. 125A) tapers posteriorly terminating above the area overlapped by the quadratojugal. In ANU V3313 it is unknown if the dentary continues as in Eusthenopteron or follows the infradentary 4 pit-line. Along the ventral margin the mandibular sensory canal (p mcp) is seen as pores extending close to the ventral surface of the jaw. Small groups of sensory pores are seen at the anterior of the jaw in the dermal bones (gr sp Fig. 18B). The posterior has lost the dermal bone towards the tip, however the overlap for the quadratojugal (oa Qj) is still preserved.

The jaw has an extremely deep adductor fossa (ad fo), much deeper than NG 1 australis (Fig. 14) with a relatively large glenoid fossa (gl fo Fig. 18A), similar to ANU V3128 described below. The post glenoid process (gl pro ie articulation) is not well preserved but shows good margin definition. Between the articulation and the infradentary 4 a small foramen for the dorsal mandibularis externus nerve VII is noted (CVII Fig. 18C), in the same position as in Gogonasus (Long et al. 1997 fig. 37). The opening for this nerve in Cladarosymblema consists of three small foramina (Fox el al. 1995 fig. 47). The posterior of the articulation is not well preserved and could not be determined if there was a lateral line canal (llc) opening in this position as in Gogonasus (Long et al. 1997 fig. 37).

There are three coronoids in the lower jaw as in Gogonasus (Long et al. 1997 fig. 26) and other ‘osteolepids’. Each coronoid has a single tusk (Fig. 18A, C), there are no replacement tusks in the specimen similar to Medoevia (Lebdev, 1995 fig. 11). In
contrast, *Gogonasus* which has at least two tusks on the first two coronoids (see specimen ANU49259). Small depressions in ANU V3313 lie anterior to each tusk, and on coronoid 3 there are two depressions, a larger one (the most anterior) and a smaller one (closest to the tusk). The intercoronoid fossa (**int cor fo**) is elongate, extending between coronoid 1 and 2 (Fig. 18A), in the same position as *Gogonasus* (Long et al. 1997 fig. 37A), *Cladarosymblema* (Fox et al. 1995 fig. 47) and *Gyroptychius* (Thomson, 1968 fig. 3). Coronoids 1 and 2 are free from denticles. However the posterior coronoid (coronoid 3) has a ledge of small denticles which rests on the prearticular/adducctor fossa wall (Fig. 18A). The dorsal ledge of the prearticular (**pre**) also has a row of denticles, which in some places forms small clumps of denticles. This row may have continued the length of the prearticular, but this is difficult to determine due to poor preservation. A large foramen on the ventrolateral surface of the prearticular is for the epibrachial arteries as in *Gogonasus* (Long et al. 1997 fig. 37) and *Medoevia* (Lebedev, 1995 fig. 11B). The lateral surface of the prearticular lacks denticles and extends to the symphysis at the anterior of the jaw, whereas in *NG 1 australis* it is shorter and does not reach the symphysis. A groove runs along the length of the jaw between the prearticular and the meckelian bone. In this groove one foramen is seen in ventral view, probably for the intermandibularis nerve V (**CV**), and/or for epibranchial arteries. This foramen is about inline with the third coronoid tusk.

The biting edge of the dentary is filled with small conical shaped teeth, increasing in size anteriorly. A row of small marginal denticles extends from the adductor fossa to the anterior along the dentary. The parasymphysis plate (**ads**) is incomplete but was probably triangular in shape, there are denticles preserved in the specimen on the plate (Fig. 18A). It was probably narrower than *Gogonasus*.

On the anterior the mandibular symphysis of the jaw is preserved, triangular in shape (**m. sym**). The symphysis muscle scarring is seen, with a small foramen below, this is for the lateral line canal (**fo lle**). It is opened in part on the inner surface and can be traced following the same line as the sensory pores on infradentary 4.
Figure 18. Lower jaw of NG 2. A, B, C, right lower jaw ANU V3133, prepared by IVPP. A, showing the median surface, showing 3 coronoids and an intercoronoid fossa. The posterior coronoid contains 5-6 small denticles on its dorsal surface. The mandibular symphysis has been well preserved (m sym). The glenoid fossa (gl fos) is deep but poorly preserved. B, External view with a well developed horizontal pit line (ph ld) and a small area overlapped by the quadratojugal (oa Qj). The mandibular sensory canal is also preserved well (pmcp). C, Dorsal view illustrating the various structures of the jaw. The small parasymphisial plat is seen at the anterior (ads), the three coronoids and the denticled prearticular.
The previous description is based on the most complete lower jaw, but two other specimens are also referred to this species.

ANU V3128 is a left lower jaw (Fig. 19A). The jaw is complete, but only the exterior surface is in view, the inside surface being enclosed in rock matrix. Two measurements were taken from the jaw: the distance from the vertical pit-line of infradentary 2 to the posterior end of the lower jaw (k) and the distance from the vertical pit-line of infradentary 2 to the anterior end of the lower jaw (m). The jaw has a L/B of 4.75. The jaw is short and broad, as in *NG 1 australis* (V516a). Both horizontal and a vertical pit lines are deeply etched in the bone surface (pl ld, pl ld2 Fig. 19A). The horizontal pit-line (pl ld) extends about three quarters of total length from the posterior end of the jaw. This pit-line is also defining the dentary boundary as in ANU V3313. The vertical pit-line of infradentary 2 (pl ld2) extends vertically from the anterior end of the horizontal pit-line. This pit line is smaller and extends down through the line of mandibular sensory groove. This mandibular sensory groove (p mcp) gradually curves up as it extends from the posterior end to the anterior margin. The pores follow the curves of the pl ld, and lie in a single fine line. There is a large overlapped area for the quadratojugal on the posterior-dorsal margin of the jaw. The glenoid fossa is quite deep, as in *NG 1 australis*. The anterior margin differs from *NG 1 australis* being more curved. However variation in the anterior of the lower jaw was noted by Young & Gorter (1981: 119). ANU V3128 shows three conical teeth present about a third of the way back from the anterior margin in the dentary. The jaw structure in general also resembles that of *Thursius macrolepidotus, Thursius pholidotus* and *Gyroptychius milleri* (Jarvik, 1948 fig. 23C,E & G). ANU V3128 lacks the small foramina on the infradentaries as described above in *NG 1 australis*.

ANU V3337 (Fig. 19B–C) is an incomplete left lower jaw. The horizontal pitline (pl ld) is preserved well (Fig. 19B) along with the mandibular sensory canal (p mcp Fig. 19B). The posterior and anterior of the specimen have not been preserved. On the internal surface two coronoids have been preserved. The Third coronoid has 7-8 enlarged denticles (Fig. 19C) and a small depression is preserved anterior to these between coronoid 3 and 2 (Fig. 19C). This pattern is somewhat different to ANU V3133 as the third tusk seems not to be preserved, but has more denticles. However if could be that the third coronoid tusk is quite small and blends with the denticles, as is
the case in *Kenichthys*. The second coronoid has a large single tusk and a somewhat larger depression anterior to the tusk than the posterior coronoid (Fig. 19C). A row of denticles extend along the dorsal margin of the coronoids in the preserved section of the specimen (Fig. 19C).

ANU V3352 is an incomplete left lower jaw (Fig 19D) and placed in *NG 2* as it comes from the same locality as all other *NG 2* material. The posterior preserved. The specimen shows the horizontal pit-line (*pl Id*).
Figure 19. Lower jaws of NG 2 A, lower left jaw V3218 with a well developed pl ld defining the dentary. B, C, An incomplete lower left jaw V3337 prepared at IVPP showing the external surface of V3337 A, and the lingual surface of V3337 (B) with the posterior coronid preserved. D, V3352 an incomplete lower left jaw with part of the pl ld4 preserved.
Cheek Units

Four examples of the cheek unit were identified. Three of these (ANU V3307; ANU V3308; ANU V3309) come from the same locality 134 in horizon F with a further complete cheek plate (ANU V3348) coming from locality 142 belonging in horizon I.

ANU V3348 is a complete cheek (Fig. 21A). The dorsal margin shows a depression towards the anterior. The posterior margin is a rounded-square shape. A remanent propercular suture is seen near the posterior margin as in the incomplete cheeks (ANU V3307–ANU V3309). The ventral margin of the quadratojugal is flat with a small ridge following the margin. The margin which abuts with the maxilla is slightly recessed and gently concave. The margin which the jugal abuts is straight. A large concave margin is preserved where the postorbital overlaps. The cheek unit consists of the quadratojugal, squamosal and preopercular with only the small preopercular suture left. The pit-lines (pl. Qj, pl. Sq, pl. Pop Fig. 21B) are all preserved well on the surface of the cheek. The jugal sensory canal (juc Fig. 21B) extends up from the bases of the preopercular, through the squamosal along side the pl. Sq and continues on to the jugal margin. The cheek has a length of 24.8 mm with the anterior being 12.5 mm in depth and the posterior 13.8 mm in depth. The approximate length of the squamosal is 22.9 mm with a height of 14.5 mm.

ANU V3307 consists of the squamosal, quadratojugal, preopercular. The antero-dorsal margin is incomplete. The squamosal pitline is well developed in the specimen (Fig. 20A,B) and extends into the quadratojugal becoming the quadratojugal pit-line (pl. Qj). A small overlap is seen anteriorly for the maxilla (oa Mx Fig. 20B). The pores of the jugal sensory canal (juc) are clearly seen in the squamosal and preopercular. There is a possible foramen or suture between the squamosal and the preopercular (?s/fo Fig. 20B). This specimen has a broad square posterior similar in shape to Gyroptychius groenlandicus (Jarvik, 1950 figs. 18, 20). A small gap at the ventral end of the suture between the preopercular and the quadratojugal (Fig. 20B) is preserved.

ANU V3309 also comprises the squamosal, preopercular and the quadratojugal. The suture between the preopercular and squamosal is only visible ventrally (Fig. 20C). The jugal sensory canal (juc) again extends through the squamosal onto the preopercular. Two small well developed clusters of pores (gr sp
Fig. 20C) are seen on the preopercular and anteriorly to the quadratojugal pit-line (pl Qj Fig. 20C). The suture between the squamosal and the quadratojugal can not be seen. The squamosal and quadratojugal pit-lines are deeply indented into the bone (pl Qj, pl Sq Fig. 20C). The square posterior shape is similar to ANU V3307 (Fig. 20B).

ANU V3308 (Fig. 20E,F) is very similar to the previous specimens with the antero-dorsal margin incomplete. The sensory pores of the jugal sensory canal (juc) are well developed on the preopercular. The quadratojugal pit-line (pl Qj) is clearly developed. The squamosal pit-line (pl Sq) extends further back onto the preopercular as the preopercular pit-line (pl pop). As with ANU V3309 the anterior and dorsal margins are incomplete, but the posterior has a similar broad square shape.

Isolated Cheek Bones

ANU V3305 is identified as a possible quadratojugal (Fig. 21C), with a well developed quadratojugal pitline (pl Qj). There is a slight ridge along the ventral surface which forms a flat margin that possibly abuts with the lower jaw. There are two margins, on the quadratojugal which attach to the maxilla anteriorly and the preopercular posteriorly. The absence of sensory pores is consistent with identification as a quadratojugal. The sensory canal system extends behind the quadratojugal through the preopercular and down into the lower jaw in osteolepids (eg: Jarvik, 1948 fig. 37A).
Figure 20. Cheek unit of new genus & species 2. A, B ANU V3307 external surface of a cheek unit, with the jugal sensory canal (juc) extending down through the preopercular. The quadratojugal and squamosal pit lines well defined (pl Qj, pl Sq). A suture is preserved between the preopercular and squamosal. C, D, ANU V3309 is the posterior part of an incomplete cheek unit. The jugal sensory canal (juc) is also preserved well in the preopercular, the preopercular suture is partly preserved along with the quadratojugal/squamosal pit line. E, F ANU V3308 is also the posterior part of an incomplete cheek unit. The jugal sensory canal (juc) is also preserved well in the preopercular, the preopercular suture is partly preserved along with the squamosal pit line. 2
Jugal

ANU V3294 (Fig. 22A, C) is identified as a jugal from the smooth, fairly deep orbital margin. It is complete except for a small part of the anterior dorsal margin. The sensory pores have the distinct three direction branch typical of the bone. The sensory canals extend down from the postorbital and anteriorly to the lachrymal (ioc) with a posterior branch to the squamosal (juc). A small overlap on the dorsal margin for the postorbital (oaPo Fig. 22C) is preserved. A small notch on the posterior margin (Fig. 22C) marks the position of the infraorbital sensory canal (ioc). Jarvik (1948) in the Scottish 'osteolepids' such a notch on the jugals was not identified. This notch is probably of no significance between the different species and is just a recess in the bone where the infraorbital sensory canal (ioc) extends through two bones.

ANU V3296 is a second jugal similar shape to ANU V3294 (Fig. 22B&G) with a deep orbital margin and sensory canals with the distinctive branching into three directions (Fig. 22G). A group of sensory pores (grsp) lies just in front of the branching point (Fig. 22G). The relatively flat dorsal margin has a large overlap for the postorbital; unlike ANU V3294 no overlap for the lachrymal (oa La). There is also a notch (Fig. 22G) in ANU V3296. The jugal is longer than it is high.

ANU V3301 (Fig. 22D) is larger than the previous specimens and measures about 10mm in length and 7mm in height. The margins of the specimen are complete except for the ventral margin. ANU V3301 has similarities to ANU V3295 in having a notch on the posterior margin more or less at the point where the jugal sensory canal (juc) extends through to the squamosal. This notch is probably of no significance between the different species and is just a recess in the bone where the infraorbital sensory canal (ioc) extends through two bones. There does not seem to be an overlap for the postorbital as in ANU V3294, ANU V3295, and ANU V3296. However this may have been lost during preservation. There is a small overlap area for the lachrymal (oa La) at the anterior margin as in ANU V3294.

ANU V3295 (Fig. 22E,F) is a small incomplete jugal, with both internal and external surfaces. The posterior and ventral margins are mostly damaged. The dorsal margin shows more detail than the previous specimens (ANU V3294, ANU V3296). The jugal forms a major part of the orbital margin with the highest part of the jugal at
the orbital margin (Fig. 22F). There is a large overlap area on the dorsal margin for
the postorbital (oa Po) as in all the other specimens (V3296, V3295). On the internal
surface there is a recessed ridge which forms a socket for the maxilla to fit into (Fig.
22E). The orbit has a bevelled edge where eye ball must have been. On the internal
surface there are two ridges which extend anteriorly and dorsally which is probably
the jugal sensory canals (juc) and the infraorbital sensory canal (ioc Fig. 22F).

Postorbital

ANU V3239 is identified as a postorbital square in its shape (Fig. 23A) with a
slightly concave orbital margin. The jugal, postorbital and lachrymal all play a part in
forming the orbit. A small group of sensory pores (gr sp Fig. 23B) lies behind the
infraorbital sensory canal (ioc). The postorbital is more elongate than the
Canowindrids (which do not form part of the orbital margin; see Koharalepis; Young
et al. 1992 fig. 14), and in Kenichthys. There is a similarity in shape with Thursius
wudingensis (Fan, 1992 fig. 3C) and Thursius macrolepidoyus (Jarvik, 1948 fig.
58A). ANU V3359 (Fig. 23C) is an incomplete postorbital. The anterior margin has
been lost but the posterior margins are well defined giving a square shape as in ANU
V3293.
Figure 22. Jugals of new genus & species 2. A, C, right jugal ANU V3294. B, G, right jugal ANU V3296. D ANU V3301 left jugal, showing the infraorbital sensory canal (ioc), group of sensory proes (gr sp), jugal sensory canal (juc) and the overlap area for the lachrymal (oa La). E, F ANU V3295 free from rock matrix showing both external and internal sides of the jugal. All the jugals show a well developed jugal and infraorbital sensory canal (juc, ioc), they all have a group of sensory pores near the junction of the juc and ioc.
Figure 23. Various dermal bones of NG 2. A, B, ANU V3239 right postorbital, showing the concave orbital margin, a cluster of sensory pores (gr sp) and the infraorbital sensory canal (ioc). C, ANU V3359 is an incomplete postorbital. D, ANU V3357, right lachrymal with a well preserved jugal sensory canal (juc) and a curved anterior margin for the orbit. E ANU V3358, left maxilla. F ANU V3355 another left maxilla.
Lachrymal

ANU V3357 is a possible left lachrymal (Fig. 23D), with the jugal sensory canal (juc) crossing the specimen and rising towards the anterior. The lachrymal is rectangular in shape with the dorsal margin being undulating. The anterior margin is curved and inclined backwards. At the posterior of the specimen a curved margin is interpreted as the orbital margin (or mar Fig. 23D). It is quite distinctive in only the posterior margin forms the orbital margin. In other “osteolepids” eg Kenichthys (Zhu & Ahlberg, 2004), Osteolepis, Thursius, Gyroptychius (Jarvik, 1948) and Gogonasus (Long et al. 1997) it is the dorsal margin of the lachrymal which forms part of the orbital margin. This is not the case in this new specimen.

Maxilla

ANU V3358 (Fig. 23E) is identified as a small maxilla (about 2.5 cm in length). The ventral margin is flat presumably where the teeth may have been held in a recessed position as no teeth are visible. The anterior margin is incomplete. The specimen tapers gently anteriorly like ANU V3355 (Fig. 23F), identified as another maxilla. Again the ventral margin is straight and the posterior curved.

Opercular

Three incomplete operculars are provisionally identified as belonging to NG 2 as where found at the same locality as the fronto-ethmoidal shield ANU V3339. ANU V3353 (Fig. 24A) is elongate, tapering posteriorly. ANU V3297 (Fig. 24B) is incomplete, but also tapers posteriorly as in ANU V3353. ANU V3354 (Fig. 24C) is a roundish shape, may not belong to NG 2, but was found at the same locality as the skull (ANU V3339) and is placed here. ANU V3354 shows the internal bone structure of the operculum, part of the bone being weathered away exposing the spongy bone layer exposed in the centre (Fig. 24 C).

Subopercular

Two suboperculars are identified. The shape of the two differs slightly, but Jarvik (1948) notes individual variation, and this could explain the difference. ANU V3351 (Fig. 24D) is a large subopercular about 3 cm in preserved length. The preserved portions suggest a tapering posteriorly. ANU V3350 (Fig. 24F,G) is complete with a well developed overlap area on the dorsal margin (oa Op Fig. 24G).
The dorsal margin is quite straight suggesting that the opercular had a straight ventral margin.

Extrascapular Series

The extrascapular series in "osteolepiformes" (Jarvik, 1972) consist of paired lateral extrascapulars which overlap a median extrascapular. Jarvik (1948) states that the lateral extrascapular overlaps the opercular in the Scottish ostolepids, with the posterior margin of the median extrascapular generally concave, but may sometimes be convex. The same pattern is seen in NG 2 with the lateral extrascapular overlapping the median, and overlapping the opercular.

ANU V3347 (Fig. 24E), a right lateral extrascapular; is symmetrical bone which is preserved showing the visceral surface, but removing a fragment of bone revealed the cosmine surface (the fragment was then glued back in place). A large ridge extends through the centre of the specimen, branching off to the right (Fig. 24E). Small contact face on the inside margins indicate that this bone overlapped the opercular series and the median extrascapular in the arrangement documented by Jarvik (1948). The anterior of ANU V3347 is broad tapering to a point posteriorly.

Cleithrum

ANU V3349 (Fig. 25A) is identified as a cleithrum, showing both smooth cosmine and ornamented bone. A prominent ridge extends down through the specimen, which comes to a broad point.

ANU V3360 (Fig. 25B) is a small rectangular bone, probably representing a submandibular. ANU V3361 (Fig 25C) has a sensory canal extending through the specimen, and may come from the extrascapular series.
Figure 25. Various bones of NG 2. **A**, ANU V3349 cleithrum. **B**, ANU V3360 unidentified bone probably from the submandibulars. **C**, ANU ANU V3361 unidentified probably from the extrascapular series.
Discussion of *NG 2*

The fronto-ethmoidal shield differs from *NG 1 australis* as follows:

- The curvature of the anterior of the fronto-ethmoidal shield is greater in *NG 2* similar to *Latvius porosus* (Greiner, 1977 fig. 8) and *Muranjilepis* (Young & Schultze, 2005 fig. 6C).

- The orbit is quite deep, and from observation may be deeper than *NG 1 australis*.

- *NG 2* has a deep depression on the palatal lamina which is not as deep in *NG 1 australis*, although they are both similar in having the one depression where *Gogonasus, Medoevia* and *Cladarosymblema* have two small depressions on the palatal lamina.

- The postnasal walls in *NG 2* are convex, whereas in *NG 1 australis* they are concave. The postnasal walls in *Gogonasus* are gently sloping posteriorly, and are round in *Cladarosymblema*. *NG 2* lacks both the prenasal foramen and the nasal lamina seen in *NG 1 australis*. In these features *NG 2* is more similar to *Gogonasus*.

Both *NG 2* and *NG 1 australis* are unique in having the parasphenoid projecting posteriorly behind the processus connectens. *NG 2* has a breath/length index of 0.85 which is similar to *NG 1*. It has an e/b proportion of 0.92 which is similar to *NG 1 australis*. The postnasal walls are straight and ridged in *Kenichthys*.

The basipterygoid process is identified as a small round attachment area on the posterior of the endocranium like *Onychodus* (Andrews et al. 2006 fig. 56a). This differs from *NG 1* which has the basipterygoid process transversely attached to the endocranium.

The palaoquadrate articulations is placed slightly posterior than in *NG 1* and in transverse plane. This is somewhat similar to *Kenichthys*. Two rows of teeth are preserved in the premaxilla. This is not seen in other osteolepids (Chang & Zhu, 1993; Vorobyeva, 1981; Zhu & Ahlberg, 2004; Young & Schultze, 2005; Thomson, 1965; Long et al. 1997). The teeth are ‘hidden’–tucked under the premaxilla, with a small gap between the two rows. This small gap may allow for the lower jaw to fit in
between. The premaxilla probably overhung the lower jaw. The two rows of teeth in the premaxilla is also a major difference between NG 1 and NG 2.

A single depression on the palatal lamina is unique to the 'osteolepids' from this formation and may represent a small area where larger teeth from the lower jaw may have rested when the jaws were closed. However there is no evidence of larger teeth preserved in the lower jaws from the formation.

A possible eyestalk is seen on the left side of V3339. This differs to NG 1 which does not have this structure. The supraorbital sensory canal has a pattern similar to NG 1, Muranjilepis, Kenichthys and Thursius wudingensis.

These jugals differ from Gyroptychius (Jarvik, 1948 fig. 71A), in which the jugal is excluded from the orbit margin, unlike species of Osteolepis and Thursius (Jarvik, 1948 figs. 37A, 58A). In Gyroptychius it is the lachrymal and the postorbital which form the orbit (Jarvik, 1948. fig. 22 F,G). The jugals have two rows of sensory pores; the jugal sensory canal and the infraorbital sensory canal which is normal for all species. A small overlap area is present on the anterior of the jugal where the lachrymal attaches.

The jugals are similar in shape to Thursius philidotus, Th. moythomasi, and O. macrolepidotus form Jarvik (1948 fig. 22 A,D,E). The measurements (Appendix 4) show that they lie outside the range of Osteolepis macrolepidotus (which are 0.55-0.68, 1.65-1.90), Thursius moythomasi and Thursius philidotus. The jugals of NG 2 are similar to Thursius wudingensis (Fan, 1992 Fig. 3B) in having its dorsal anterior margin forming part of the orbital fenestra although Thursius wudingensis has a slightly different shape.

The Canowindrids (Koharalepis & Beelarongia) differ greatly in shape of their jugal they have an elongate jugal (Koharalepis see; Young et al. 1992 fig 10C; Beelorongia see, Long, 1987b fig. 5).

Youngolepis shows a very different shape (Chang, 1991 see fig. 9). It is illustrated as having a broad and open orbital margin. NG 2 is small and not as broad. However the sensory canals are similarly positioned as Youngolepis (Chang, 1991: 362), "the jugal
canal joins the infraorbital canal at an acute angle. Jarvik (1972, p. 136) thinks it is typical for porolepiforms”.

One specimen shows a complete cheek for NG 2. The posterior is broad and square in its shape. This is similar to *Gyroptychius groenlandicus* (Jarvik, 1950 figs. 18, 20). There is a small gap between the quadratojugal and the preopercular in all the NG 2 cheeks. This gap is not seen in the *groenlandicus* illustrations from Jarvik (1950). Other individuals to exhibit this feature are *Thursius wudingensis*, *Kenichthys*, *Youngolepis* and *Psarolepis*. The cheek is fused with only a small part of the preopercular suture preserved. The fused cheek unit is also seen in *Kenichthys*, *Youngolepis* and early “osteolepids”.

The cheek plates are similar to most early sarcopterygians (*Psarolepis*, *Youngolepis*, *Gyroptychius groenlandicus*, *Thursius wudingensis*) that have a fused cheek unit. The cheek of NG 2 (Fig. 20,21) is small and broad, square shaped, which is fairly wide posteriorly as in *G. groenlandicus*. The dorsal margin is curved with a recess for the extratemporal; this is different to *Osteolepis* and *Thursius* as represented by Jarvik (1948), but similar to *Thursius wudingensis* (Fan, 1992 fig. 3D). The preopercular is also held in a more horizontal position (Fan, 1992 fig. 3D) than a vertical as in *Osteolepis*, *Thursius*, *Gyroptychius* and *Latvius*. The jugal sensory pores extend through the preopercular, but not into the quadratojugal. It is presumed that the sensory system extends behind the quadratojugal in the normal position as in *Osteolepis* and the porolepiformes; *Holoptichius*, *Porolepis* as seen in Jarvik (1972 fig. 63).

The infraorbital, postotic, and jugal sensory canals in all three (NG1,23) ‘osteolepids’ fronto-ethmoidal shields have a pattern similar to *Muranjilepis* (Young & Schultze, 2005) and *Porolepis* (Jarvik, 1972 fig. 61A). The cheek complex is similar to *G. groenlandicus*. 

NG 2 shares few features in common with *Kenichthys*. They have:

- Similar lower jaw, with no foramina as in NG 1.
- Both have foramina in the cheek
- The cheeks of both have a slight depression on the dorsal margin.
However it differs from *Kenichthys* with some significant differences, as follows:

- Two rows of teeth in the premaxilla.
- One anterior nostril with a fully developed choana.
- Single depression on the palatal lamina.
- Short and square postorbital.
- Probable broad parasphenoid (to be confirmed; only attachment known)

*NG 1* and *NG 2* share several features which are unique to them. These features may be significant to erect a family for these Middle Devonian 'osteolepids'. The features are as follows:

- The processus connectus projects out from the back of the fronto-ethmosphenoid.
- A single depression on the palatal lamina.
- Two rows of conical teeth in the premaxilla.
- The orbital notch of all genera in the formation form at almost a right angle.

The minor differences which suggest *NG 2* may be another genus are:

- A longer prearticular – extends to the jaw symphysis.
- The fronto-ethmosphenoid is more compact in *NG 2*.
- The basipterygoid process has a different arrangement in the two forms.
- The postnasal wall convex in *NG 2*, concave in *NG 1*.
- Infradentary foramina absent on *NG 2*.

It is also possible, however, that these differences might indicate only a different species within one genus. More complete specimens are needed to decide this.
NG 3 gen. et sp. nov.

**Diagnosis**

NG 3 has a broad fronto-ethmoidal shield with a d/b of 1.14, and an e/b of 1.05. Prominent nares visible from above, nares grooved with a triangular – rounded shape; preorbital and postorbital corners acute. The area overlapped by lachrymal and maxilla is long. The cheek unit is fused and narrow posteriorly. The lower jaw is long, with a constant depth having a b/l of 5.8. The postnasal walls are straight. The parietal is elongate h/a of 24.9-31.5.

**Holotype**

ANUV3186 a fronto-ethmoidal shield.

**Other Material**

Three parietal shields (ANU V3187, ANU V3230, ANU V3362); Two lower jaws (ANU V3145, ANU V3311a); One maxilla (ANU V3311b); One cheek unit (ANU V3146); Two branchiostegal rays (ANU V3363, ANU V3364).

**Locality and Horizon**

All material described below came from one locality 138, on the western side of the ‘Western Creek’; (Fig. 2B). The material is preserved in an extremely hard grey siltstone.

**Remarks**

Three specimens a fronto-ethmoidal shield, cheek and a lower jaw (ANU V3186, ANU V3146, ANU V3145) were found within a 1 cm of one another on one bedding plane. These specimens may belong to one individual. The other specimens came from the same bedding plane, but were more scattered up to 1 m away.

In comparison with NG 1 and NG 2 this new genus can be distinguished by nasal openings only visible from above; the lower jaw of constant depth; the fronto-ethmoidal shield is more elongate with a greater d/b proportion of 1.14 and an e/b proportion of 1.05. The parietals are more elongate than NG 1.
Description

Fronto-ethmoidal Shield

Dorsal View

The right side of ANU V3186 is complete, the left is broken. The specimen has broken along the midline suture, and the suture is clearly seen in (Fig 26D). Six smaller pieces of the left side of the shield have been prepared from the rock matrix, but five of these can not be fitted back on to the specimen.

One piece has the frontal pit line (pl. Fr) and it can be attached at the posterior along the midline suture (Fig. 26B). It also has the suture between the frontal and the dermosphenotic plate extending anteromesially on the right side. Small pores from the supraorbital sensory canal (soc) are also preserved on the posterior right side, near the frontal pit line (pl. Fr Fig 26B,C). The surface of the cosmine has blisters (bli Fig. 26B) similar to those described by Jarvik (1948), and also seen in Kenichthys (Chang & Yu, 1997 fig. 1D). These blisters sit higher than the surrounding bones surface and are of irregular shape as described by Jarvik (1948). They are probably areas where cosmine absorption and re-absorption has occurred before death.

The anterior fenestra exonarina is visible from above (fe exa Fig. 7C). This feature was not thought to apply to NG 1 australis by Young & Gorter (1981); and differs from the current view of the nasal openings are seen from above and below in NG 1. The nasal opening is of rounded-triangular shape, similar to Platyethmoidia (Young et al. 1992 fig. 17A,B), and larger than NG 1 australis. The sutures of the tectal and rostral plates are unclear due to the high degree of fusing between the bones. The nares have a different orientation to NG 1 australis (Young & Gorter, 1981 fig. 25C).

The preorbital corner (proc) and subnarial corner are acute, and similar to Osteolepis and Thursius. The preorbital corner (proc) is very large in this specimen. The orbit is not as deep as in NG 1 australis. The postorbital process is well developed (ptoc Fig. 26C) and more prominent than that in Platyethmoidia (Young et al. 1992 fig. 17). The overhugged snout is less pronounced than in NG 1 australis. The overlap area for the lacrimal and maxilla is quite long and is also seen in dorsal view (i La+Mx Fig. 26C). There is no trace of the pineal foramen either externally or internally, and may have been closed (as speculated in Platyethmoidia antarctica Young et al. 1992: 25) or not preserved. The supraorbital sensory canal (soc) extends in a row of pores close to the margin of the posterior and lateral margins of the shield,
turning mesially behind the nasal opening. A similar pattern in the supraorbital sensory canal occurs in *NG 1, NG 2, Muranjilepis* (Young & Schultze, 2005), *Kenichthys* (Chang & Yu, 1997. fig. 1A). No pores for the infraorbital sensory canal were observed. The specimen has the largest breadth length index (d/b) of *1.14. This is greater than the Middle Devonian “osteolepids” of Scotland, (*Osteolepis, Thursius, Gyroptychius*; Jarvik 1948, Table 1). This breadth length index is also larger than *NG 1 australis* and *NG 2*.

Lateral View

In lateral view the specimen shows a very flat skull roof, with not a great deal of overhang with the premaxilla as in *NG 1*. The orbital notch is held almost at right angles (Fig. 26C) in lateral view; this seems to be a trait in all the “osteolepids” from the formation. A large overlap is preserved for the maxilla and lachrymal. The nasal opening is in a higher position the *NG 1 australis*, nearly above the level of the lachrymal overlap.

Ventral view

The ventral surface has been prepared out, but endocranial structures are not well preserved. Only a few parts are identifiable; the fenestra exochoanalis (*fe end* Fig. 26D), the postnasal wall (*pnw*) is straight, not concave as in *NG 1* or convex as in *NG 2*. The premaxilla shows large sockets for the conical teeth. The midline suture (*M suture*) is seen in ventral view with a small feathered overlap edge (Fig. 26D).
Parietal shield

There are three incomplete examples of the parietal shield.

ANU V3187 (Fig. 27A) has some complete margins. The two margins of the posterior corners (formed by the supratemporal) are complete. The spiracular notch (i.spir) is incomplete on both sides. On the left side the lateral margin is complete, but towards the anterior it has broken along the intertemporal margin (fig. 27A). The anterior margin is complete, with the posterior mostly incomplete. The shape differs from the broad square shape of *NG 1 australis* (ANU V525, ANU V2268). The shield is cracked. The postotic sensory canal extends anteriorly along each margin (poc Fig. 8A,C). The postotic sensory canal turns inwards to the centre of the shield towards the anterior end. There are 13 pores on the right hand side and 18 on the left for the postotic sensory canal. Jarvik (1948) states, the differing number of pores is not significant, and is attributed to individual variation. Scattered pores are seen in the lower posterior corner of the specimen. There are no sutures seen in the specimen apart from where the intertemporal has broken off. Both the posterior oblique parietal pit-line (pl.po.Pa) and the transverse parietal pit-line (pl.tr.Pa Fig. 27A,C). The pl.tr.Pa extends to the lateral margin on both sides of the shield. The pl.po.Pa also extends to the broken posterior margin. The pattern of the postotic sensory canal differs from that in *NG 1 australis* (ANU V525, ANU V2268). The postotic sensory canal also resembles those found in *Thursius moy-thomasi* (Jarvik, 1948 fig. 13D), *Kenichthys* (Chang & Zhu, 1993 fig. 2C). The specimen is broader posteriorly than *NG 1 australis* (Young & Gorter, 1981 fig. 25B).

V3230 is a large parietal shield. The anterior margin is preserved complete, and the posterior is sufficiently complete to permit a reconstruction as in Fig. 9C. The lateral margins are incomplete with a large piece missing from the spiracular notch area on the right side. The midline suture is preserved at the anterior and posterior (Fig 27B). There is no evidence of any other sutures on the specimen. Presumably these have been covered by the cosmine layer. The postotic sensory canal extends anteriorly along the lateral margins of the specimen. It turns inwards anteriorly as in V3187. On the anterior margin a small overlap area is seen for the dermosphenotic plate (oa Dsph Fig. 27B). The transverse parietal pit line (pl.tr.Pa) and the posterior oblique parietal pit line (pl.po.Pa Fig. 27B). A small group of sensory pores can be
Lower Jaw

ANU V3145 is referred to *NG 3*, on the assumption it comes from the same individual as the holotype (fronto-ethmoidal shield ANU V3186). ANU V3311 is placed here as it comes from the same bedding plane as ANU V3186 and ANU V3145.

ANU V3145 is separated in two pieces with only a small fraction missing (just enough for the jaw not to fit back together exactly Fig. 28A,B). The posterior margin is incomplete and has been broken. The anterior is complete along with the dorsal margin and the ventral margin. The jaws length is about 5 times its height (54mm in total length and 10.6mm in depth). These specimens may come from one individual. Along the ventral margin of the jaw extends the mandibular sensory canal (*p mcp* Fig. 28A). The horizontal pit-line is deeply etched into the bone (*pl id* Fig. 28A) defining the dentary. The posterior end, although weathered, seems slightly different to the jaws assigned to *NG 1 australis* (Young & Gorter, 1981 fig. 27). The area overlapped by the quadratojugal and maxilla is less evident (*oa Qj*) due to the incompleteness of the posterior end.

The internal structures are well preserved though the surface is fragmented. In ventral view the ventral surface has a groove running the length of the posterior piece of the jaw. This groove separates the infradentaries from the prearticular, and presumably is the meckelian bone, similar to what is shown by Long et al. (1997 fig. 38A) for *Gogonasus*.

In mesial view large sockets are preserved in the dentary which would have contained conical teeth. Three teeth are preserved at the posterior end. Below these conical sockets a row of marginal denticles extends the length of the jaw. The parasymphysial dental plate (*ads*) is flat with small denticles and attached to this row of marginal denticles. The denticles are larger at the posterior end of the parasymphysial dental plate (Fig. 28B). The posterior coronoid is well preserved with a large tusk, a small replacement tusk posteriorly, and a small depression anterior to the (posterior) coronoid tusk. The lateral portion of the posterior coronoid bears more than two rows of denticles. A similar pattern is seen in *Powichthys, Youngolepis, Kenichthys, Medoevia* and *Gogonasus*. Ventral to the posterior coronoid, part of the prearticular is preserved. The prearticular has large denticles along the lateral margin (Fig. 28C). The prearticular is inclined in a dorsal direction possibly a result of preservation. The
The jaw is fairly uniform in depth, with the posterior being slightly shallower than the anterior. This is the other way around in *NG 1 australis* and *NG 2* where the posterior is deeper. As in most osteolepids, no sutures are visible between the infradentaries; these have probably become fused.

**ANU V3311a** (Fig. 28D,E) is an incomplete left lower jaw. The mandibular sensory canal extends along the preserved part and the horizontal pit line is well defined *(p.mcp, pl Id* Fig. 28E). Part of the adductor fossa wall is preserved showing that it formed a very deep fossa *(ad fo* Fig. 28D).

During preparation, a small incomplete maxilla (V3311b) was discovered encased in the rock matrix with V3311a. The posterior margin which abuts the cheek unit and the anterior margin are incomplete. Small tooth sockets are seen on the inside of the ventral margin (Fig. 28F). Along the dorsal margin is an overlap area defined by a small ledge that would have been for the lachrymal and jugal.
Figure 28. Lower jaws of NG 3. A, B, C, D lower jaw V3145a and V3145b prepared by IVPP. A, B showing the external surface of V3145a+b. C, Showing the lingual surface of V3145a and V3145b. D, E V3133 also prepared by IVPP, showing a well developed horizontal pit line (plh ld) and mandibular sensory pores (p. mcp) in F and part of the adductor fossa in E.
Cheek Unit

ANU V3146 comprises the quadratojugal, squamosal and the preopercular (Fig. 29A,B). The cheek unit is fused with no sutures preserved. The margins of the cheek are mostly intact except where a large crack extends through to the dorsal margin. The dorsal margin shows a complete arch unlike NG 2 which has a slight concave recess. The jugal sensory canal (juc) extends through the preopercular and down into the quadratojugal (pop, Qj Fig 29B). A pit line extends through the quadratojugal and squamosal closely to the maxilla margin (pl. Qj, pl. Sq). Anterior and ventrally overlaps are preserved for the postorbital, jugal and the maxilla (oa Po, oa Ju, oa Mx Fig. 29B). The cheek unit is narrow compared to NG 2 in which the cheek is broader posteriorly with small gap in between the quadratojugal and preopercular. ANU V3146 also does not contain the small recess on the dorsal surface as in NG 2. It also differs from the cheeks of Osteolepis, Gyroptychius, Thursius (Jarvik, 1948). The cheek measures 26.7 mm in length, 9.4 mm in height posteriorly and 14 mm anteriorly. This also differs from NG 2 which had a cheek that is slightly wider posteriorly. ANU V3146 is narrow posteriorly. The squamosal approximate measurements are 19 mm in length and 13 mm in height. ANU V3146 differs from NG 2 in having a narrow posterior, whereas NG 2 is quite square in its posterior (Fig. 27). There is a large overlap dorso-anteriorly for the postorbital, with the overlap for the maxilla being very small in comparison. The margin where the jugal abuts is inclined, and a small overlap. The shape of the cheek unit is distinctive being similar to Thursius wudingensis and Kenichthys (Chang & Yu, 1997 fig. 2 B,C). However three small foramina in Kenichthys and Thursius wudingensis are not seen in ANU V3146.

Branchiostegals Ray

ANU V3364 is a complete right branchiostegal ray. The specimen is slightly wider posteriorly. The specimen has a straight inner margin (Fig. 29C). A prominent ridge (ri.Rbr Fig. 29C) extends through the specimen in close proximity to the dorsal margin, petering out towards the antero-dorsal corner. The anterior margin is not straight as in (Young & Gorter 1982, fig. 26C) the assigned NG 1 australis specimens, but has a curved anterior margin (Fig. 29C). The specimen indicates that the gular for this species had a straight margin with a slight notch in the postero-dorsal margin. The specimen is quite distinctive in having straight median margin,
most of the first branchiostegal rays are represented as having curved margins (Jarvik, 1948 figs. 43, 60, 69, 75, 80). The overlap for the subopercular is steeply inclined down into the rock matrix. A small overlap is identified in the anterior right corner for the preceding branchiostegal rays. The specimen gives a breadth/length proportion of 0.40.

ANU V3363 is another first branchiostegal ray from the left side (Fig. 29D) it also has a round posterior and a fairly straight medial margin as in ANU V3364. The complete dorsal margin shows a distinct antero-dorsal corner. The anterior shows a small overlap area for the second branchiostegal ray (oa Rbr2 Fig. 29D). The dorsal overlap area for the subopercular extends down into the rock matrix as in ANU V3364 and ridge (ri. Rbr) is similar.
Figure 29. Cheek unit and Branchiostegal ray of NG 3. A, B V3146 a cheek unit of comprising of the quadratojugal, squamosal and preopercular. C, D The first branchiostegal ray V3364 (C); V3363 (D).
Discussion of NG 3

The fronto-ethmoidal shield has a breadth/length proportion of 1.14 this is the largest proportion of the “osteolepids” shields in this study. It has a large e/b proportion of 1.05 which is also larger than NG 1 australis and NG 2. The v/w proportion is 0.6 within the range of NG 1, NG 2. NG 3 has a larger lio/dpio proportion of 4.83, this is much larger than the other “osteolepids” in the formation. The nasal openings are seen from above as in Osteolepis and Platylethmoidia. The shield is also quite flat like Platylethmoidia. The orbital notch does not appear to be as deep as in NG 1 australis, with the posterior notch curved as in Platylethmoidia. Blisters are seen on the shield’s surface as in Kenichthys.

The parietal is elongate similar to Thursius and Kenichthys; being broad posteriorly, and narrow anteriorly. The parietals (V3187, V3230, V3362) were noted to be quite different to NG 1 australis. The shields show characteristics of Kenichthys along with Thursius. They are quite broad and Thursius like. The postotic sensory canal pores and the transverse parietal pit-line resemble those found in Thursius (Jarvik 1948, fig. 13D), and Kenichthys (Chang & Zhu, 1993 fig. 2C). The reconstructed shape of NG 3 parietal shield gives a shape similar to Kenichthys (Chang & Zhu, 1993. fig 2C), and Thursius (Jarvik 1948 fig. 58).

The cheek unit is similar to NG 2; in having fused dermal bones (quadratojugal, preopercular, squamosal), but is narrower posteriorly, (broader in NG 2), and differs from NG 2 in not having a recess for the supratemporal. The cheek of NG 3 is like Thursius pholidotus (Jarvik, 1948 fig. 65A).

The lower jaw of NG 3 is quite different from NG 1 australis. The jaw does not have the large foramina on the infradentaries as in NG 1 australis. The jaw doesn’t taper anteriorly as in the other two. However the lower jaw shows some similarities with NG 1 and NG 2 these are, a marginal row of denticles, the parasymphisial dental plate is narrow and slightly more elongate compared to NG 1 & 2. The preserved coronoid is positioned centrally and projects out horizontally, whereas the coronoid tusks in NG 1 and NG 2 project dorsally. The prearticular
inclines dorsal toward the anterior, but this is probably due to displacement during preservation.

Chapter 7. Summary

This study identifies three forms of 'osteolepids' in the finer sediments of the Hatchery Creek Conglomerate; now identified as the Corradigbee Formation. The three forms of 'osteolepids' differ greatly to other described osteolepiforms, but at the same time show some similarities with forms like Gogonasus, Kenichthys, Medoevia and Cladarosymblema. The osteolepids differ in their basipterygoid process, the position of their postnasal wall, palaoquadrate articulation. NG 2 may have a feature which may be an eyestalk, this is not seen in NG 1. The three share a similar supraorbital sensory canal pattern to Muranjilepis and Porolepis.

The suggestion that G? australis may be similar to Kenichthys is unsupported. NG 1 has several features that are considerably different from Kenichthys. These include the parasphenoid, lower jaw, two teeth rows, the positioning of anterior and posterior tactual plates, and a single depression on the palatal lamina.

Also the idea that G? australis may be a canowindrid is unable to be concluded at this stage as the preserved material does not include the information needed. However the postorbital plate of NG 2 is quite different in shape from Koharalepis.

The several unique characters which are only seen in NG 1, 2 and 3 may indicate a close relationship between the three, and they may belong to a single family grouping. NG 1 & NG 2 may also be considered as two species within the one genus. Some of these features include, the single depression on the palatal lamina, the process connectens overhangs the back of the fronto-ethmoidal shield, two tooth rows in the premaxilla. NG 1 and NG 2 are the only known 'osteolepids' to contain two rows of teeth in the premaxilla. Some dermal bones of NG 1, 2 and 3 are still not clear. Their body plan remains unknown and is assumed to be similar to Osteolepis.
References


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JARVIK, E 1972. Middle and Upper Devonian Porolepiformes from East Greenland with special reference to Glyptolepis Groenlandica and a discussion on the structure of the head in porolepiformes. Meddelelser om Grønland, 187:2


### Appendix 1 ANU V numbers and collected material

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### Appendix 3 Measurements of Specimens

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