

SPECIAL PAPERS IN PALAEONTOLOGY

Number 9

FISH FROM THE FRESHWATER  
LOWER CRETACEOUS OF VICTORIA,  
AUSTRALIA, WITH COMMENTS ON  
THE PALAEO-ENVIRONMENT

BY

MICHAEL WALDMAN

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BY  
MICHAEL WALDMAN

With 18 plates and 37 text-figures

THE PALAEOLOGICAL ASSOCIATION  
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DECEMBER 1971

# CONTENTS

Abstract	Page v
Introduction	1
The Mesozoic sediments of Victoria	3
Geology of the Korumburra-Leongatha Region	4
The fauna of the continental Lower Cretaceous of Victoria	4
Classification	5
Abbreviations	5
Systematic Descriptions	7
Order Ceratodiformes, Family Ceratodontidae	8
<i>Ceratodus</i> sp.	8
Order Palaeonisciformes, Family Coccolepididae	10
<i>Coccolepis woodwardi</i> sp. nov.	11
?Coccolepididae	19
Order Pholidophoriformes, Family Archaeomaenidae	20
<i>Wadeichthys oxyops</i> gen. et sp. nov.	22
The relationships and derivation of the Family Archaeomaenidae	33
Order Clupeiformes, Family Koonwarriidae	35
<i>Koonwarria manifrons</i> gen. et sp. nov.	35
Family Leptolepididae	43
<i>Leptolepis</i>	46
<i>Leptolepis koonwarri</i> sp. nov.	46
The Affinities of <i>Leptolepis koonwarri</i>	58
The Koonwarra fish fauna	61
The invertebrate fauna	92
The flora	93
The geology of the Koonwarra fish-bed and surrounding sediments	95
Stratigraphy	95
The lamination and its origin	96

Disturbance of the sediments	100
Mineralogy	100
The origin and termination of the fish-bed	101
The palaeo-environment of the fish-bed	103
The mortality mechanism and the connection with preservation	106
The palaeo-ecological evidence from the vertebrates: the evidence derived from preservation	110
Comparable preservation in other assemblages	114
The biological evidence	115
Winterkill	117
Acknowledgements	118
References	119



ABSTRACT. 5 families of fish are known from Koonwarra: Ceratodontidae (Dipnoi), Coccolepididae (Palaeonisciformes), Archaeomaenidae (Pholidophoriformes), Koonwarriidae nov., and Leptolepididae (Clupeiformes). The third and fourth families appear to be limited to Australia.

The Ceratodontidae are known from a single specimen, referable to *Ceratodus* sp. The Coccolepididae are sparsely represented by *Coccolepis woodwardi* sp. nov. Only one species of archaeomaenid is known from the site, *Wadeichthys oxyops* gen. et sp. nov. This is the most primitive archaeomaenid known, possessing enamelled scales overall, an unossified notochord, an uncompacted caudal skeleton, and preopercular pit-lines and sensory canals similar to those of some parasemionotids.

*Koonwarria manifrons* gen. et sp. nov., type genus of the new family Koonwarriidae, appears to be derived from the archaeomaenids and is considered to be a teleost. The caudal skeleton is compact and homo-heterocercal, with elongate uroneurals and well-formed hypurals. The scales are cycloid and skull pit-lines are greatly reduced.

A new species of *Leptolepis*, *L. koonwarri*, is closely related to *L. talbragarensis* from the Jurassic of New South Wales. It may also have affinities with the Cretaceous *L. diasii* from Brazil and *Clupavus brodiei* from the English Upper Jurassic. *L. koonwarri* is a mosaic form with 'advanced' skull features such as the loss of the post-orbital and possession of few preopercular canal branches, but the axial and caudal skeleton is of primitive leptolepid form.

The palaeo-environment was lacustrine or paludal, and mass mortality occurred periodically due to anoxic winter conditions beneath an ice-cover; the phenomenon known as 'winterkill'. The graded laminations present in the fish-bed are thought to be seasonal and to represent successive spring floodings, with settling of sediment during the years of the fish-bed. They may therefore be described as varves. Although such laminae are most common in deep, cold lakes, the widespread aquatic arthropod fauna is characteristic of a modern shallow-water environment. The number and variety of terrestrial insects and the small size of the fish also indicate shallow waters.

## INTRODUCTION

THE Koonwarra fish-bed was discovered in 1962 by workmen engaged in straightening a bend in the South Gippsland Highway for the Country Roads Board of Victoria. The site of this discovery is located 2.5 km west of the town of Tarwin and 4.0 km east of Koonwarra; 150 km by road from Melbourne. The site is 230 m west of the north-east corner of allotment 87, parish of Leongatha. The grid-reference is 3966E. 2457N., on the Wonthaggi one mile sheet (text-figs. 1, 2).

At the time of discovery, the University of Melbourne, Department of Geology made a considerable collection of fossil material from the site, most of it being taken from the northern side of the road. The Mines Department of Victoria and the National Museum of Victoria also possess smaller collections made during that period.

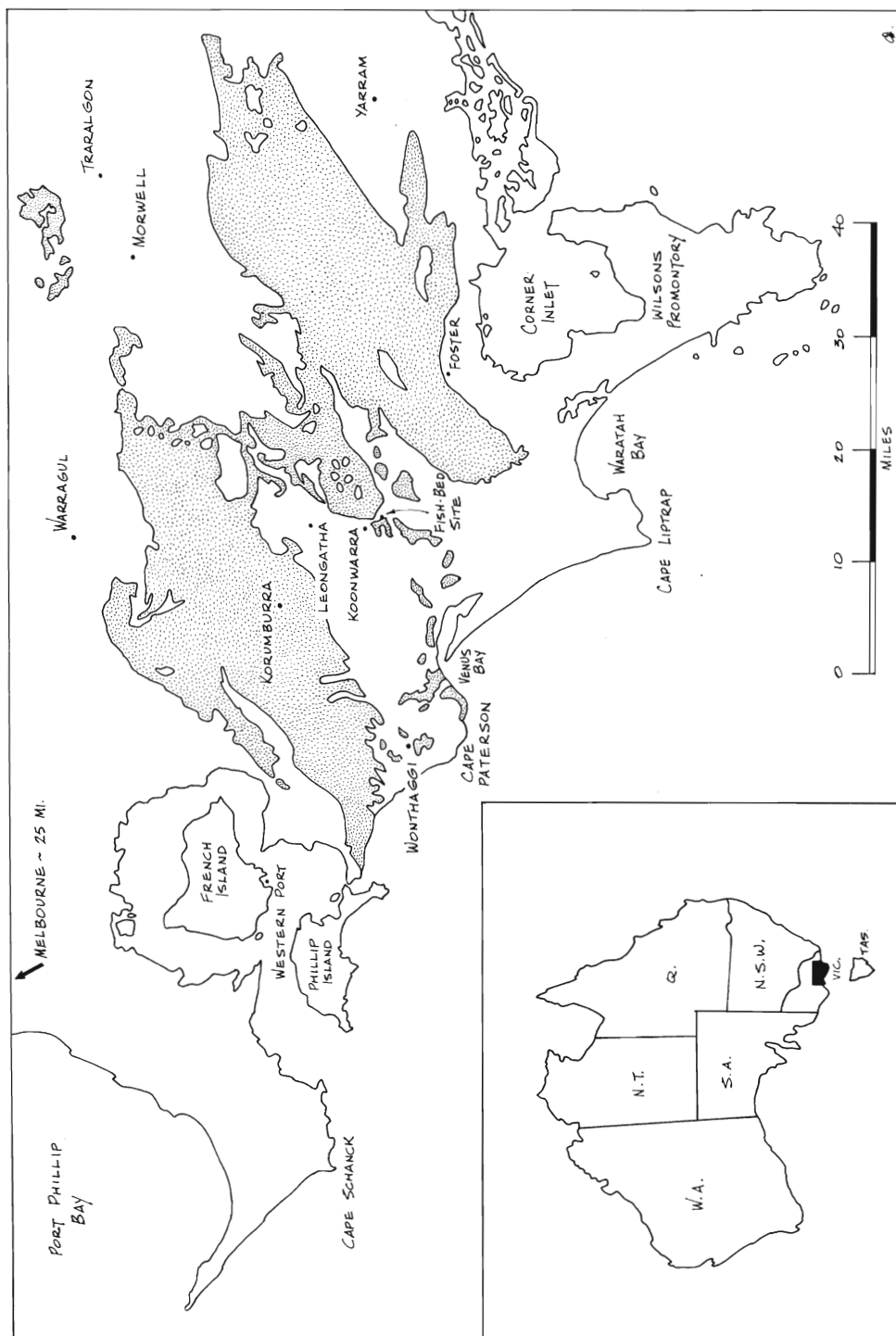
The fish-bed occurs within a 7.1 m true thickness of mudstone and represents a still-water environment in the predominantly fluviatile sediments of the Lower Cretaceous Korumburra Group. It is made up of graded laminae which are composed of alternate layers of siltstone and claystone. The mudstones are contained within a succession of fluviatile arkoses.

When the present study commenced in 1965, a small excavation had been made on the northern side of the road, in the area from which most of the fossils had been obtained. This region is limited in extent, being bounded along the strike by the highway and a railway cutting. Permission was therefore obtained from the Country Roads Board to excavate on the western side of the road, above the road-cutting. This was carried out in early 1966 by bulldozing, overburden being removed from an area of about 600 m<sup>2</sup>. The fish-bed horizon was then relocated and removal of rock commenced, following the strike and excavating down to a level of 5–6 feet. The depth of the trench was governed by the dip of the bed (37°) into the spur through which the road-cutting had been driven. About 14–16 m<sup>3</sup> of fossil-bearing rock was removed from this south-western exposure. The distance between the northern and southern sites is approximately 18.6 m. A trench was subsequently dug at 90° to the strike to enable the beds to be mapped stratigraphically. A further, smaller trench was driven along the strike in the lower region of the fish-bed.

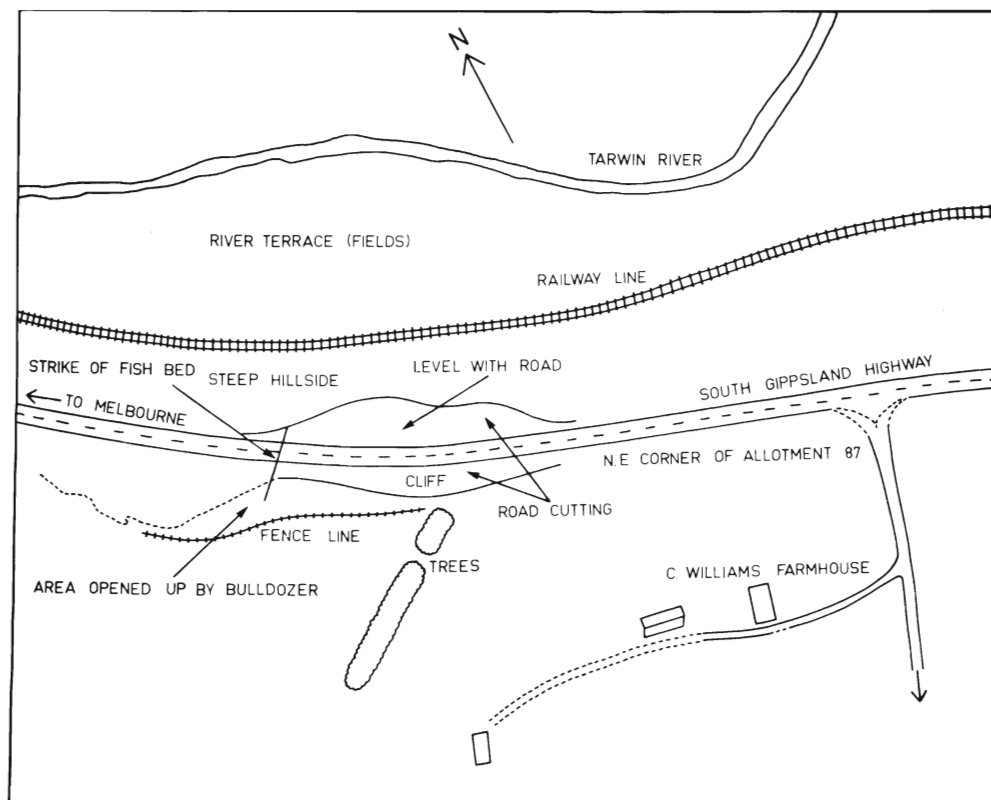
Apart from the fish, the only other remains of vertebrates found have been those of birds, represented by three feathers. The presence of other vertebrates is indicated, however, by the finding of two widely differing types of fleas.

Invertebrates are abundant, consisting mainly of aquatic and terrestrial insects, aquatic crustaceans, and an arachnoid. The invertebrate fauna is to be described by E. F. Riek, of the Commonwealth Scientific and Industrial Research Organization.

Plant material occurs in quantity and over 30 species are present, including angiosperms. (Dr. J. G. Douglas, Mines Department of Victoria; personal communication 1970.)



TEXT-FIG. 1. Main outcrops of Lower Cretaceous strata (stippled on map) south-east of Melbourne in southern Victoria, showing position of fish-bed site. Inset shows location in Australia.



TEXT-FIG. 2. Plan view of the Koonwarra fish-bed locality. Scale: 1:2000.

### THE MESOZOIC SEDIMENTS OF VICTORIA

Kenley (1954) stated that since 1900 the Victorian Mesozoic has been attributed to the Jurassic with 2 small Triassic exceptions. Medwell (1954*a*) gave a predominantly Lower Jurassic age to these sediments, although she stated in a second paper (1954*b*) that some of the Mesozoic exposures near Casterton in western Victoria were probably Lower Cretaceous. Dettmann (1963) published the results of her investigations into the microflora of the SE. Australian Upper Mesozoic, assigning it to 3 Lower Cretaceous assemblages, the lowest probably being Valanginian or younger and the highest Albian. More recent macrofloral studies by Douglas (1969) have agreed for the most part with Dettmann's work. Regrettably, the fauna of the Victorian Upper Mesozoic is not sufficiently diagnostic of age to be used successfully.

The main divisions of the Lower Cretaceous in Victoria are: Merino Group, Otway Group, Barrabool Sandstone, Tyers Group, and Korumburra Group (Medwell 1954). Talent (1965) estimated the total thickness of the above units to be more than 3000 m. The Koonwarra fish-bed represents a still-water environment within mainly fluvial sediments.

## GEOLOGY OF THE KORUMBURRA-LEONGATHA REGION

This area of the South Gippsland Highlands, and beyond Leongatha to Koonwarra, Tarwin, and Meenyan, is composed of block-faulted sedimentary rocks (Hills 1959), mainly sandstones, siltstones, and claystones. These are overlain in many places by Cainozoic sediments and volcanics.

These lithologies produce a landscape of rolling hills, dissected by meandering rivers, such as the Tarwin which flows near the Koonwarra site. The terrain is poor in rock exposures except at the coast where the strata are very well exposed in sea cliffs around Cape Paterson.

For the most part road-cuttings, earth dams, well-diggings, and cores from water borings provide the only access to the sediments. The coal mines in the Korumburra Group at Wonthaggi are unfortunately now closed, only the tip-heaps remaining. It was in a road-cutting that the Koonwarra fish-bed was originally discovered.

Although scattered plant and animal remains have been found in the region in the past, the Koonwarra find is the only one of any magnitude. This is probably due to three factors: 1. The lack of natural exposures; 2. The general paucity of fossil material (even at Cape Paterson); 3. The failure of finders to notify institutions of their discoveries.

The third of these points is worthy of consideration. Reliable informants from near Leongatha have told me of a discovery of fossil fish made on a near-by property during dam-construction about 30 years ago. Although a number of local people recalled the discovery, none knew what had become of the fossils. The original South Gippsland Highway ran almost at right angles to and over the strike of the fish-bed, and yet no fossils from that construction ever reached Museum or University as far as is known.

## THE FAUNA OF THE CONTINENTAL LOWER CRETACEOUS OF VICTORIA

*Vertebrates.* The first record of vertebrates from the group was by Krausé (1886, cited by Kenley 1954) who noted '... the homocercal tail of a ganoid fish (? leptolepis)' and '... a large portion (neural plate) of the carapace of a chelone'. These specimens were taken from the railway cutting on the east bank of the Glenelg River at Casterton, western Victoria. In 1900 Hall described *Leptolepis crassicauda* from the same locality, and in that paper also defined *Psilichthys selwyni*, which he considered a chondrosteian fish, from Carapook (Muntham), Victoria. In 1906 and 1907 (reprint) Woodward described a dipnoan splenial tooth as *Ceratodus avus*, and a dinosaur claw which he referred to the carnosaur *Megalosaurus*, both from Cape Paterson. Chapman in 1912 noted a lungfish scale from Kirrak (Wonthaggi), S. Gippsland, which he referred to *Ceratodus(?) avus*, and in 1914 erected the subgenus *Metaceratodus* to house both scale and tooth, plus another tooth from the Cretaceous of Walgett, N.S.W. Until recently the only other described vertebrate remains were those of a chelonian from Carapook (Chapman 1919), described as *Chelycarapookus arcuatus* by Warren (1969). A bore core from Kirrak (P.26117) (Wonthaggi), S. Gippsland, contains the undescribed trunk and fins of a fish. On the label the specimen has been tentatively identified as 'cf. *Hypsocormus*', but this is incorrect and the specimen is now being re-examined.

Hills (1958) has mentioned the presence of possible reptilian gizzard stones in the Victorian Mesozoic, but these have yet to be found in association with fossil reptiles. Talent, Duncan, and Handby (1966) described 2 feathers from the Koonwarra fish-bed and subsequently a third feather has been recovered (Waldman 1970).

*Invertebrates.* The invertebrates of the Korumburra Group are represented by rare lamellibranchs, which until recently had been described as *Unio*. McMichael (1956) investigated these and found their systematic position (and often their exact provenance) indeterminable. While examining the type-locality of *Leptolepis crassicauda* (see above) I discovered a few poorly preserved bivalves apparently of two separate genera previously unknown from the Victorian Mesozoic. The only other published work on invertebrates has been a brief description of 2 insects from the Koonwarra fish-bed (Carroll 1962), and a paper on the conchostracans (Crustacea) of the same bed, by Talent (1965).

### CLASSIFICATION

It has been found impracticable to use any one classification of previous authors due to the problems involved, for example, with the family Archaeomaenidae.

I have followed Berg (1958) in using the family Coccolepididae, even though I tend to agree with Lehman (1966) on the dubious nature of that family. I have re-defined the family Archaeomaenidae to include 4 genera for which Wade (1941) erected the suborder 'Cenogenoidei' and have placed one newly discovered genus within that family. A new family, the Koonwarriidae, has been erected to house the new teleost *Koonwarria*.

The Leptolepididae have been placed within the Clupeiformes in accordance with Berg, Lehman, and the recent work of Patterson (1967).

The familial ending '-idae' has been adopted from Gardiner (1967, 1967a) where applicable.

Details of individual classifications are given in the 'Systematic Descriptions' section.

#### Abbreviations

MUZ	Monash University, Department of Zoology
MUGD	University of Melbourne, Department of Geology and Mineralogy
NMV, or P.	National Museum of Victoria (Palaeontology)
MF, or AMF	Australian Museum, Sydney, N.S.W. (Palaeontology)
PMD Collection	P. M. Duncan, 152 Maryvale Road, Morwell, Victoria
MDV	Mines Department of Victoria

#### Abbreviations—Anatomical

ang. art.	angulo-articular
ant.	antorbital
ap.	anterior pit-line
asc. pr.	ascending process of parasphenoid
bbr.	basibranchial
bpt. pr.	basipterygoid process of parasphenoid
brs.	branchiostegal ray

cbr.	ceratobranchial
chy.	ceratohyal
cl.	cleithrum
co.	coracoid
cr.	cranial rib
de. spl.	dentalo-splenic
dpt.	dermopterotic
dsph.	dermosphenotic
ect.	ectopterygoid
ent.	entopterygoid
ep.	epural
eph.	epihyal
eth.	ethmoid (dermethmoid + mesethmoid)
ethc.	ethmoid commissure
ext.	extrascapular
f.	fulcral scale
for.	scapular foramen
fpr. op.	facet for hyomandibular processus opercularis
fr.	frontal
g.	gular
ga.	gill-arch
gf.	gill-filaments
gr.	gill-rakers
h.	haemal arch
hc.	anterior division of the supramaxillary pit-line
hhy.	hypohyal
h. sp.	haemal spine
hy.	hypural
hybr.	hypobranchial
hyo.	hyomandibular
hyo. VII.	hyomandibular branch of cranial nerve 7
ifc.	infraorbital sensory canal
ifo.	infraorbital
iop.	interopercular
lep.	proximal segment of lepidotrichia
ll.	lateral line
lls.	lateral line scale
md.	mandible
mdc.	mandibular sensory canal
mp.	middle pit-line
mpt.	metapterygoid
mx.	maxilla
n.	neural arch
na.	nasal
n. sp.	neural spine
orp.	postmaxillary pit-line
op.	opercular
pa.	parietal
pal.	palatine
pal. VII.	palatine branch of cranial nerve 7
pcl.	postcleithrum

pg.	pelvic girdle
pmx.	premaxilla
po.	postorbital
poc.	preopercular sensory canal
pop.	preopercular
pp.	posterior pit-line
p.p.h.	postero-dorsal process of hypural
pr. op.	hyomandibular processus opercularis
ptr.	postrostral
pu.	preural vertebra
q.	quadrate
ra.	radial
ro.	rostral
rp.	rostral process of antorbital
r. pmx.	rostro-premaxilla
sc.	scapula
scl.	supracleithrum
s. com.	supratemporal commissure
smx.	supramaxilla
sn.	supraneural
so.	supraorbital
soc.	supraorbital sensory canal
sop.	subopercular
sr.	sclerotic ring
ssc.	suprascapular
u.	ural vertebra
ud.	urodermal
ur.	uroneural

## SYSTEMATIC DESCRIPTIONS

## Order CERATODIFORMES

Family CERATODONTIDAE

Genus CERATODUS

*Ceratodus* sp.

## Order PALAEONISCIFORMES

Family COCCOLEPIDIDAE

Genus COCCOLEPIS

*Coccolepis woodwardi* sp. nov.? *Coccolepis* sp.

## Order PHOLIDOPHORIFORMES

Family ARCHAEOMAENIDAE

Genus WADEICHTHYS nov.

*Wadeichthys oxyops* sp. nov.

## Order CLUPEIFORMES

Family KOONWARRIIDAE

Genus KOONWARRIA nov.

*Koonwarria manifrons* sp. nov.



## Family LEPTOLEPIDIDAE

## Genus LEPTOLEPIS

*Leptolepis koonwarri* sp. nov.

## Order CERATODIFORMES

*Diagnosis.* Lehman 1966, pp. 247–248.

## Family CERATODONTIDAE

*Diagnosis.* Lehman 1966, pp. 247–248

## Genus CERATODUS

*Diagnosis.* Lehman 1966, p. 247

Since the erection of the genus *Ceratodus* by Agassiz (1838), a large number of species have been described, mainly on the basis of isolated teeth. Lehman (1966) has summarized the known species. Within the family Ceratodontidae there are three extinct genera: *Ceratodus* Agassiz, *Paraceratodus* Lehman, *Microceratodus* Texeira; and the extant *Neoceratodus* Castelnau.

A summary of the Australian fossil and recent lung-fish was given by Hills (1958), but the Victorian Mesozoic occurrences are stated here in more detail.

Woodward (1906, 1907) described a splenial tooth of *Ceratodus* from beds then thought to be of Lower Jurassic (in fact Lower Cretaceous) age at Cape Paterson, S. Gippsland, and named it *C. avus*. In 1912 Chapman noted a scale from a bore-core in the 'Upper Jurassic' (Lower Cretaceous) of Kirrak (Wonthaggi), S. Gippsland, and referred it to *C. (?) avus*. The same author in 1914 described an opalized tooth from New South Wales as *Ceratodus wollastoni* and named it as a new sub-genus, *Metaceratodus*, '... in view of the intermediate or annectant [*sic*] character of the Jurassic and Cretaceous with the living species of Australia ...'. Until now, no further fossil lung-fish material has been described from Victoria.

*Ceratodus* sp.

Plate 1; text-fig. 3b

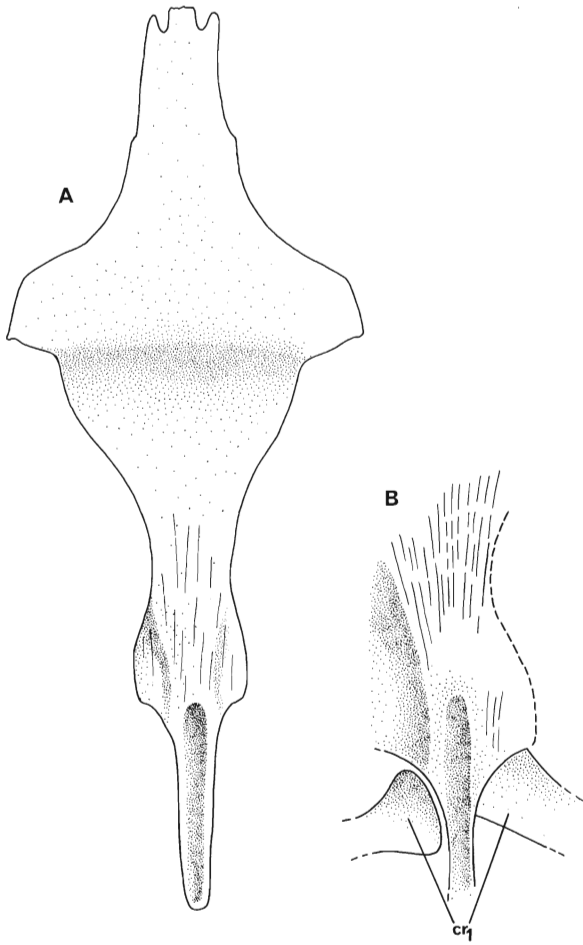
*Horizon.* Koonwarra fish-bed, L. Cretaceous.

*Locality.* Koonwarra, S. Gippsland, Victoria.

*Material.* 1 incomplete axial skeleton (Pl. 1, fig. 2) plus a fragment of a parasphenoid (text-fig. 3b) (MUZ 3343).

The specimen is large and consists of an incomplete posterior axial region, with the remains of the median fins, and a small part of a pelvic fin. The anterior region is largely missing and the remains consist of fragments of scales, isolated axial elements, and a part of the parasphenoid. Regrettably it is not known how complete was the preservation of the skull region and how much was destroyed. The specimen was in the process of weathering to clay and was penetrated by small (recent) plant roots, which have destroyed much of the structure. It was collected (including counterparts) in over 150 fragments and only about half of these have been fitted together. As it seems that few more additions may be made to the skeleton, it is considered desirable to describe the specimen as it is.

*Parasphenoid.* This is the only part of the skull which may be identified with any certainty, although it is incomplete. Only the postero-ventral region is preserved, and this resembles the condition in *Ctenodus*



TEXT-FIG. 3A. Parasphenoid of the extant Australian lung-fish *Neoceratodus forsteri* Krefft, MUZ 3343, ventral view,  $\times 1.2$ . B. Postero-ventral region of the parasphenoid of *Ceratodus* sp. from the fish-bed,  $\times 1.2$ .

*cristatus* Agassiz, from the British Carboniferous (Lehman 1966, p. 270, fig. 26) and the living *Neoceratodus* (text-fig. 3A). The well-defined longitudinal groove on this region is well preserved, together with part of the bilateral expansion of the bone alongside it. Anteriorly the bone is destroyed, but the beginning of the anterior parasphenoid expansion (to abut against the pterygoids) is visible.

The few remaining ribs are long and slender, taper ventrally, and are aligned at progressively narrower angles to the notochord proceeding posteriorly. They are indistinguishable from those elements in *Neoceratodus* (Günther 1871, pl. 30). Beyond these lies the triple series of bones made up of haemal arches, axonosts, and baseosts (Pl. 1, fig. 2). The haemal arches and fused spines are rod-like, about 25 mm in length, and expanded at both ends. Each is succeeded distally by an axonost of similar shape, but which may be nearly twice its length, measuring 40–50 mm. Distally there are the small baseosts, about 20 mm in length, with their extremities more expanded than those of the axonosts. Attached to these are the delicate, curving camptotrichia.

The neural arches and their fused spines are curved, fairly long elements, expanded distally. Articulating on to each one is a long, waisted axonost up to 60 mm long. Distally the axonosts abut against the

poorly preserved baseosts which resemble their ventral counterparts. The camptotrichia of the median dorsal-anal fin articulate on to these elements and greatly outnumber them.

All axial elements decrease proportionally in size progressing posteriorly, as far as may be seen. The extreme tip of the tail is known, and the scale-covered notochordal lobe extends right to the posterior tip of the fin (Pl. 1, fig. 1).

*Paired fins.* Part of the posterior region of one of the pelvic fins is visible, but is very poorly preserved and little structure may be made out. It is in a similar position to that of *Neoceratodus* (Günther 1871, pl. 30).

*Squamation.* The scales have been reduced to a white chalky material which does not preserve the structure in any detail. In one or two cases, however, scales close to the margin of the body show some of their typical 'mosaic' appearance. They resemble those of *C. formosus* (Wade 1935), and *C. (?) avus* (Chapman 1912). The scales are often rounded-rhombic in shape except in the axial lobe of the caudal fin where they appear to be circular, and exhibit fine, 'fingerprint-like' markings (Pl. 1, fig. 1).

*Remarks.* Little information may be obtained from this specimen as even the axial skeleton is very badly damaged. The parasphenoid appears to resemble that of *Ctenodus* and *Neoceratodus*. As previously noted, the median scaled lobe, which extends along the line of the notochord posteriorly, divides the caudal lobe terminally. A similar condition exists in *Ceratodus formosus* (Wade 1935) from the Triassic of Brookvale, New South Wales, and appears to be present in the Triassic genera *Paraceratodus* (Lehman *et al.* 1959) and *Microceratodus* (Texeira 1954, see Lehman *et al.* 1954) to judge from their illustrations.

The latter character may represent an earlier type of organization than that found in *Neoceratodus*, and this is borne out by the intermediate nature of the parasphenoid. This element is robust as in *Ctenodus*, but its general form is somewhat like that of *Neoceratodus*.

Until teeth (and in particular a splenial tooth) are found at Koonwarra, it is of little value to speculate as to whether this form may be referred to *C. avus* (Woodward 1906, 1907).

#### Order PALAEONISCIFORMES

#### Suborder PALAEONISCOIDEI

#### Family COCCOLEPIDIDAE

#### Genus COCCOLEPIS Agassiz 1843, p. 300, pl. 36, figs. 6, 7

*Diagnosis.* Gardiner 1960, p. 243

*Type species.* *Coccolepis bucklandi* Agassiz

Liu (1957) summarized the known occurrences and descriptions of *Coccolepis* and these are here amended. *Coccolepis* was first described and named by Agassiz in 1843, the species being *C. bucklandi* from the lower Kimmeridgian (Upper Jurassic) of Bavaria. Woodward defined *C. liassica* (1890b) from the Lower Lias (Lower Jurassic) of Dorset, England, and in 1891 and 1895 noted *C. andrewsi* from the Lower Purbeck beds (Upper Jurassic) of Wiltshire, England. The latter species was further described in 1916 by Woodward. *C. australis* was erected by Woodward in 1895(a) for specimens from the ?Jurassic beds of Talbragar, N.S.W., Australia, and in 1911 Traquair named *C. macroptera* from the Wealden (Lower Cretaceous) of

Bernissart, Belgium. Gorizdro-Kulczycka described *C. aniscowitchi* and *C. socialis* in 1926, from the Upper Jurassic of Karatau, Turkestan, U.S.S.R. White (1934) defined the species *C. cockerelli*, from the Jurassic of Galkino, Turkestan; and in the same year Sewertzoff noted *Palaeoniscoidus turkestanensis* from the same region. In 1940 Berg created the new family Coccolepididae to house the genus *Coccolepis*. *Coccolepis martynovi* Berg was figured and described by Eremeyeva in 1940, but I have been unable to trace the original paper by Berg. Ghekker (1948) also described *C. martynovi* from Karatau, U.S.S.R. Berg in 1948 considered *C. socialis*, *C. cockerelli*, *Coccolepis* sp. (Eremeyeva 1940), and *Palaeoniscoidus turkestanensis* to be synonyms of *C. aniscowitchi*.

Liu introduced a new genus into the family in 1957, *Sunolepis yumenensis*, from the probable Lower Cretaceous of Western Kansu, China. Griffith (1958) redescribed *Browneichthys ornatus* Woodward (1889), thought by the latter to be a saurichthyid, and concluded that it should be placed in the Coccolepididae.

Gardiner (1960) gave a detailed description of *Coccolepis liassica*, and in 1966 systematically described the Subclass Chondrostei, placing the Coccolepididae within the Order Palaeonisciformes. Jakovlev (pers. comm. 1966) stated that *C. martynovi* and *C. socialis* are synonymous with *C. aniscowitchi*, and has further stated (pers. comm. 1967) that there is only one species of *Coccolepis* from the Karatau region. Takai (1944, p. 231, fig. 3) briefly described a specimen of ?*Coccolepis* from near Keizyo, Korea, in the Middle-Upper Jurassic freshwater Daido Group, noting that the specimen was lost, only a photograph then existing. The photograph originally appeared in Tokunaga (1925), see Takai (1944), and if the specimen was correctly identified (and this is doubtful) then it would represent the most easterly occurrence of *Coccolepis* in the Northern Hemisphere.

*Coccolepis woodwardi* sp. nov.

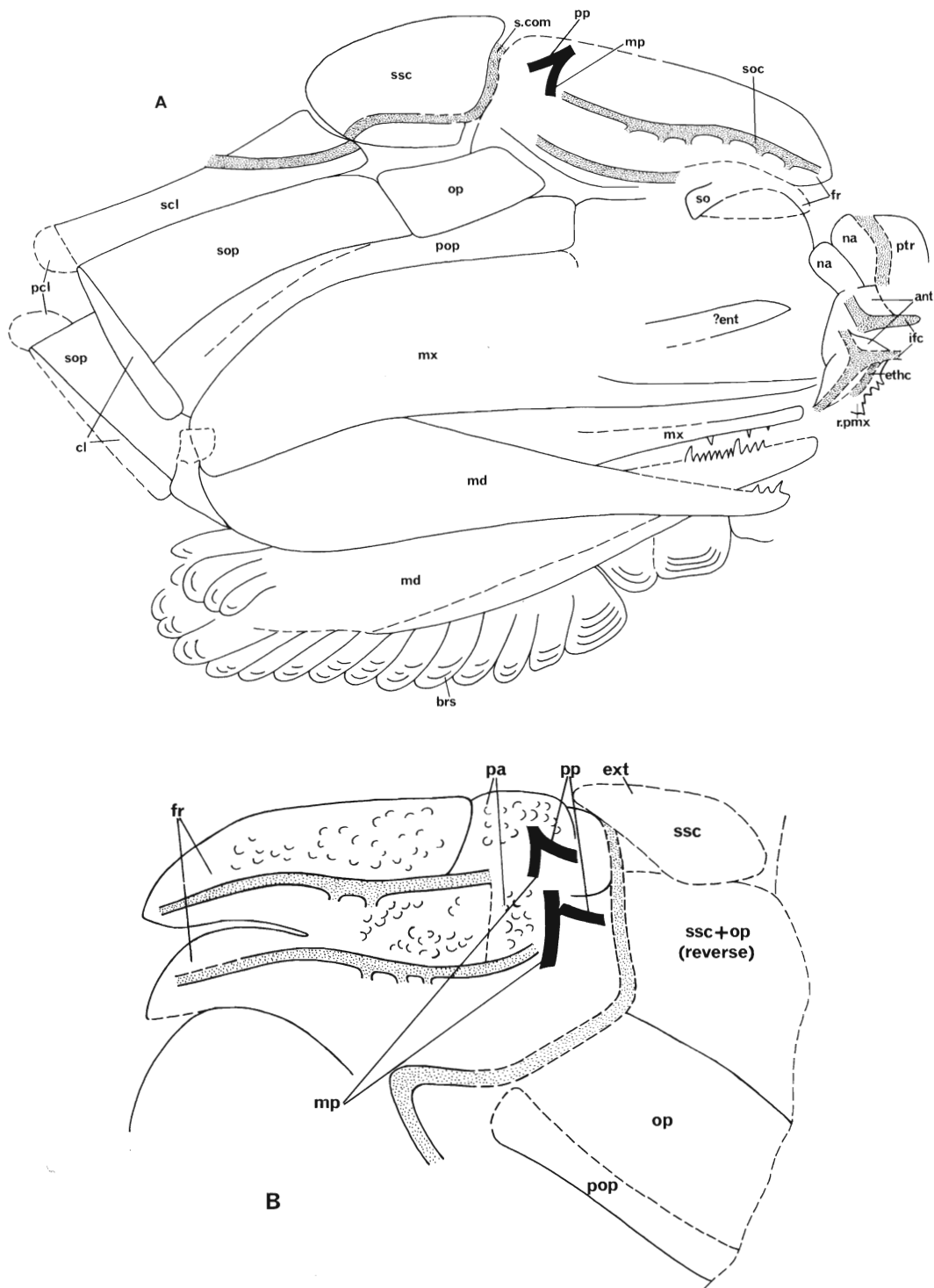
Plates 2, 3; text-figs. 4–6, 36

*Diagnosis.* A *Coccolepis* of medium-large size, length of the skull being contained about  $4\frac{1}{2}$  times in the standard body length, and approximately equalling the maximum body depth. Subopercular elongate, rectangular, larger than opercular; pit-lines on parietal; slender, curved mandible. At least 22 non-tuberculate branchiostegal rays; gill arches with denticulate platelets. Pectoral fins elongate, narrow based, containing about 18 lepidotrichia; pelvic fins situated midway between pectorals and anal fin, widebased, with 30–35 lepidotrichia. Dorsal fin opposed to origin of pelvic fins, and is largest of all the fins; anal fin slightly closer to caudal fin than to pelvic fins, contains 31–34 lepidotrichia, its rear margin concave posteriorly. Caudal fin with 78 lepidotrichia; unjointed rays at origin of dorsal and anal fins, 30 fulcra on dorsal lobe of caudal fin; 'caudal inversion angle'  $156^\circ$  (see Liu 1957).

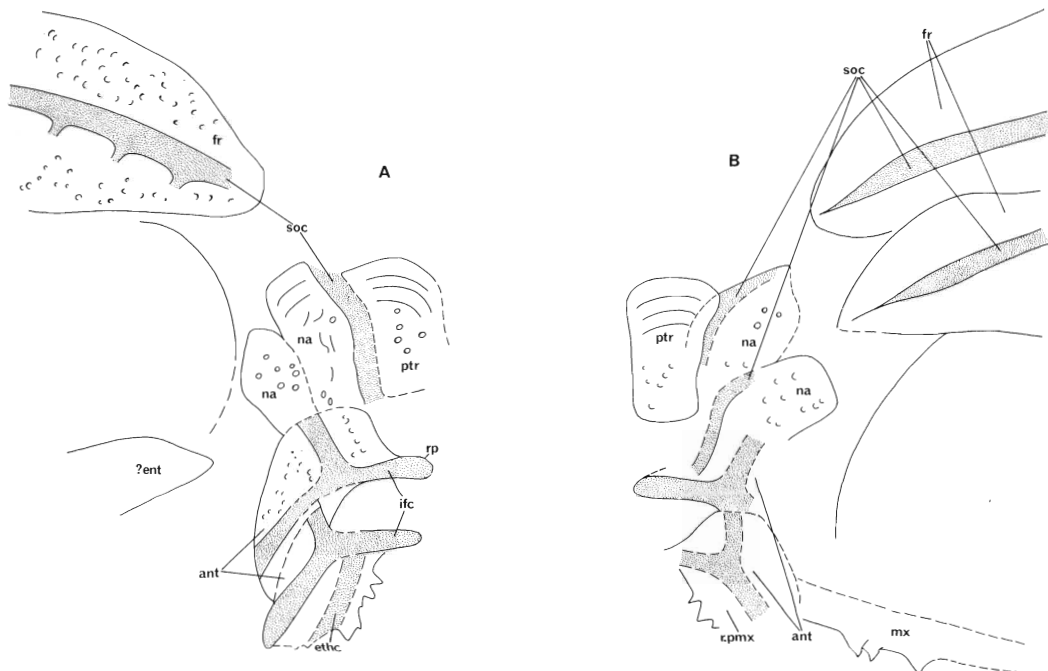
*Holotype.* MUZ 3167AB (Pl. 2, fig. 1).

*Paratypes.* MUGD 3631AB; 3632AB; 3633; NMV P.24682 (counterpart in P.M.D. Collection); P.26062; MUZ 1220 and 2511AB (comprising all known material of *Coccolepis woodwardi*).

*Horizon.* Koonwarra fish-bed, L. Cretaceous.



TEXT-FIG. 4A. *Coccolepis woodwardi*, MUZ 3167A, holotype. Skull and pectoral girdle,  $\times 5$ . B, Counterpart of A,  $\times 6$ . (See also Pl. 3, fig. 4.)



TEXT-FIG. 5A, B. *Coccolepis woodwardi*, MUZ 3167AB, counterparts, holotype,  $\times 10$ . (See also Pl. 3, fig. 4.)

*Locality.* Koonwarra, Victoria, Australia.

*Origin of Name.* Named for the late Sir Arthur Smith Woodward, who described many of the early collections of fossil fish from Australia.

*Description.* The skull has a shallowly inclined dorsal margin with a rounded snout resembling that of *C. liassica* (Woodward 1890b, Gardiner 1960). The preservation of the skull is generally incomplete, but in MUZ 3167A, B a considerable amount of detail is visible (text-figs. 4A, B, 5A, B; see also skull reconstruction (text-fig. 36).

The rostro-premaxilla (r. pmx.) can only be made out in MUZ 3167A, and is obscured by other elements. It appears to be small and quite narrow. It carries the ethmoid commissure (text-fig. 5B).

The nasal bones (na.) are visible in MUZ 3167AB, but unfortunately overlap, obscuring details of their exact shape. They are tuberculate, longer than broad, and originally would have rested each side of the postrostral. The postrostral (ptr.) is almost rectangular, but is slightly broadened posteriorly, and bears rugae posteriorly which parallel its rear margin, as well as tubercles (text-figs. 5A, B).

The tuberculate frontals (fr.) begin at the antero-dorsal orbital level and terminate behind the level of the posterior margin of the orbit. Anteriorly they taper to a point and the suture between them appears curved (text-fig. 4B).

The supraorbital (so.) elements are poorly known, there being vague indications of such a bone in MUZ 3167A (text-fig. 4A).

A ?dermosphenotic (?dsph.) may be discerned at the postero-dorsal margin of the orbit of MUZ 3167A immediately anterior to the preopercular, but its shape is uncertain and identification tentative. The parietals (pa.) are small, apparently square and are tuberculate (text-figs. 4A, B).

The form of the dermopterotic (dpt.) is not known.

The extrascapulars (ext.) rest against the parietals, but their shape is not accurately known. They would seem to have been narrower elements than the parietals (text-figs. 4A, B).

*Cheek Region.* The maxilla (mx.) is of the typical palaeoniscoid shape, expanded below the preopercular and with a slim process extending anteriorly beneath the orbit. The maxilla bears the usual double series

of teeth, the larger ones being evenly spaced and a little curved. Teeth extend posteriorly to the angle of the jaws (text-fig. 36).

The antorbitals (ant.) (text-figs. 5A, B) are visible together in the disarticulated snout of MUZ 3167AB, and are triangular, with a rostral process (rp.) for articulation with the rostro-premaxillary. The arrangement of the antorbitals was probably similar to *Nematoptychius greenocki* (Traquair) (Gardiner 1963, fig. 7).

The infraorbital series is not known.

The curved preopercular (pop.) overlies the postero-dorsal margin of the maxilla and tapers posteriorly, terminating at the rear margin of the maxilla. The subopercular (sop.) lies against the postero-dorsal margin of the preopercular, and is approximately rectangular, lacking the marked curvature of the posterior margin present in *C. liassica* (Gardiner 1960, p. 244, fig. 1). In MUZ 2511A and 3167A the opercular (op.) is visible. It is smaller than the subopercular, of a rounded-rectangular shape, and in 2511A bears fine concentric ornamentation.

*Lower Jaw.* The mandible (md.) is best seen in MUZ 2511A (Pl. 3, fig. 1), 3167A (Pl. 3, fig. 4) and P.26062 (text-fig. 4A and Pl. 3, fig. 2). It resembles that of *C. liassica* (see above), but may have extended a little further anteriorly than in that species. It is toothed in similar fashion to the maxilla. Gardiner (loc. cit.) stated that the teeth of the larger series in the lower jaw of *C. liassica* were 'somewhat stouter' than those of the upper jaw, and this is also apparent in *C. woodwardi*.

*Sensory Canal System.* The sensory canals of the skull region may be most clearly observed in MUZ 3167AB (text-figs. 4A, B; 5A, B and Pl. 3, fig. 4). The supraorbital canal (soc.) traverses the nasal, continues longitudinally through the frontal, and terminates on the parietal, ending in the anterior pit-line (ap.). The infraorbital canal (ifc.) is known from the antorbital, where it possesses the triradiate 'Y'-shape mentioned by Gardiner (1963, p. 310). The canal pathway beneath the orbit is unknown, but is visible behind the orbit in MUZ 3167B for a short distance before abruptly turning through about 80° to run posteriorly along the dermopterotic.

*Cephalic Division of Main Lateral Line* (text-figs. 4A, B). The posterior region of the parietal bears two well-developed pit-lines, the middle pit-line (mp.) inclined laterally, and the posterior pit-line (pp.) posterolaterally. The main canal gives off the supratemporal commissure (s. com.) into the extrascapular on leaving the dermopterotic and extends posteriorly along the lateral margin of the suprascapular. The preopercular sensory canal (poc.) may be represented by a longitudinal groove in the posterior region of the preopercular, but this is not certain. The mandibular sensory canal (mdc.) runs the length of the lower jaw, fairly close to the ventral margin.

*Hyoid Arch.* Only the branchiostegal rays (brs.) are known, plus small toothed platelets which are probably derived from the gill-arches.

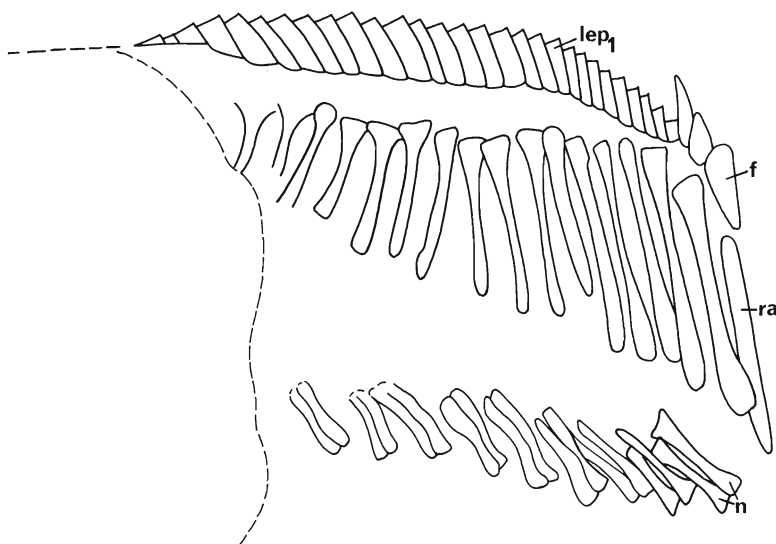
The branchiostegal rays number at least 22 per side and bear striae which parallel their distal margin. Their shape seems variable, those anteriorly being broader than the posterior elements of the series (text-fig. 4A). In P.26062 the hyobranchial region has been slightly disturbed and a single branchiostegal ray separated from the series. Scattered about this ray in the matrix of the same bedding plane are denticulate platelets. Platelets such as these are known in a number of fish (see p. 41) and are generally associated with the gill-arches.

*Palate.* This is not known apart from the anterior region of an ?entopterygoid in MUZ 3167A, but see ?*Coccolepis* (p. 19).

*Neurocranium.* Unknown.

*Pectoral Girdle and Fins.* The suprascapular is most clearly seen in MUZ 3167A. It is a large element with a well-rounded posterior margin and has a curved suture with the extrascapular (text-fig. 4A).

The cleithrum is a robust element and from its contact with the supracleithrum at an angle of about 100° it expands ventrally and curves round beneath the subopercular. The supracleithrum is very much like that of *C. liassica* except that its suture with the subopercular is straight rather than curved. A small postcleithrum is visible in MUZ 3167A (text-fig. 4A). The pectoral fin (Pl. 2, fig. 1; Pl. 3, fig. 4) is quite long and narrow on a short base and has about eighteen lepidotrichia which bifurcate distally. No fulcra are present.



TEXT-FIG. 6. *Coccolepis woodwardi*, MUZ 3167A, holotype. Dorsal fin-supports and neural arches,  $\times 7$ . (See also Pl. 2, fig. 1.)

*Pelvic Girdle and Fins.* No trace of the pelvic girdle remains in any specimen, but the fins are composed of 30 to 35 lepidotrichia, which are branched and jointed distally. MUZ 3167 exhibits a row of poorly preserved radials. In MUZ 2511B a few radials are preserved towards the anterior margin of the fin. They appear to be thicker at the fin base and taper dorsally, unlike those of *C. liassica* (Gardiner 1960, fig. 2). The pelvic fins are situated about halfway between the pectoral fins and anal fin and are broadly based, being roughly triangular in shape with a concave rear margin.

*Unpaired Fins.* The dorsal fin begins at the level of the pelvic fins and ends immediately anterior to the level of the anal fin. It is large and in younger individuals (e.g. MUZ 3631AB) its height may equal the depth of the body (Pl. 2, fig. 3). It has the form of a right-angled triangle with a rounded apex, the right-angle being between the posterior margin of the fin and the body. At the origin of the fin there are about 10 simple rays, increasing in size posteriorly to the maximum height of the fin (MUZ 3631AB). A similar phenomenon is mentioned by Woodward (1895b, p. 146) for *C. andrewsi*. In MUZ 3167AB, a well-preserved teardrop-shaped scale is present between the first radial and the lepidotrichia. Above this scale there is another smaller one, followed by the first simple fin-ray (cf. *C. liassica*, loc. cit., pp. 246–247, fig. 3). The dorsal fin contains about 34 lepidotrichia, plus the 10 rays previously mentioned. The lepidotrichia are well jointed and bifurcate distally. 25 radials are present. 17 of these are visible in 3167A (text-fig. 6). The first one is a simple rod-shaped bone and does not exhibit the strong bow-shape of the same element in *C. australis* (Woodward 1895a and AMF.27070). It is followed by 5 larger elements expanded at each end, these being succeeded by a further 9 which tend to be expanded distally rather than proximally. The last 2 bones preserved are notable for their broad, fan-shaped distal terminations, similar to those of *Psilichthys selwyni* (Hall 1900). In 3167A the seventh bone in this series is possibly malformed as its shaft is a good deal shorter than those of its neighbouring elements (text-fig. 6). In general the series shows a regular decrease in length, progressing posteriorly. The anal fin contains 31 to 34 lepidotrichia which are jointed and branch at least twice. The fin is well preserved in MUZ 2511AB, and its posterior margin is deeply concave (Pl. 3, fig. 1). The fin originates slightly behind the level of the posterior margin of the dorsal fin. There are 3–4 simple rays at the anterior margin of the fin as well as a teardrop-shaped fulcral scale. In advance of this scale is the imprint of another, stout and curving to a point (MUGD 3631B). Radials number 13–15, which are inclined and sometimes curve in an antero-dorsal direction.

The heterocercal tail is deeply cleft, with the dorsal lobe only slightly longer than the ventral (Pl. 2, fig. 2). The fin is made up of 78 lepidotrichia, compared with about 41 in *C. liassica* (Gardiner 1960, p. 247). There are about 30 stout fulcras on the dorsal margin of the upper caudal lobe. The fulcras of the lower



caudal lobe are much smaller than those of the upper, but each lobe has a large lanceolate scale at the origin of the fulcral scale-row. Woodward (1895a, pl. II, fig. 4) showed similar scales in *C. australis*. Lying alongside these in the dorsal lobe axis are 4-5 long rows of tapering, diamond-shaped scales, which reach almost to the posterior tip of the lobe. The number of such scales seems to be at least 35 per row. Gardiner (1960, p. 247) gave the number of scales per caudal lobe row as 12 in *C. liassica*.

*Axial Skeleton.* Most specimens show traces of the axial skeleton, and in general this resembles that of *C. australis* (Woodward 1895a) and *C. liassica* (Gardiner 1960). In the anterior region the curved neural spines remain unfused with their arches, and spines are absent beneath the dorsal fin radials. In MUZ 3167A the arches beneath the dorsal fin are not fused, as in *C. australis* (Woodward 1895a), but posteriorly there are fused neural spines and arches. Delicate ?neural spines support the upper caudal lobe (MUZ 3167A). Nothing is known of the haemal arches of the anterior region, but these must have been very small. At the level of the middle of the dorsal fin base, well-developed haemal arches are fused with long haemal spines. The most posterior of the series are robust in support of the lepidotrichia of the lower caudal lobe and number at least 14, the first 6 being the sturdiest. These expanded elements closely resemble those of *Psilichthys selwyni* (Hall 1900; and personal observation) from the Lower Cretaceous of western Victoria, and *Coccolepis australis* (Woodward 1895a). In MUZ 2511B some have infilled cores of white, clayey material, similar to infillings common in Jurassic fish from Talbragar, N.S.W.

*Squamation.* The squamation of *Coccolepis australis* is well known (e.g. Woodward, 1895a, figs. 1c, 1d). That of *C. woodwardi* is most clearly visible in MUZ 3167AB and is also preserved in other specimens to a lesser extent. Isolated scales of *Coccolepis* are fairly common in the deposit and a broad size-range occurs. The smallest scales may only have a few tubercles on the posterior region (Pl. 2, fig. 4) (sometimes as few as 2 or 3) whereas the largest may have 30 or more (Pl. 4, fig. 6). Isolated lateral line scales are also known (Pl. 2, fig. 5). The scales are cycloid, slightly longer than broad and in common with all other species of *Coccolepis* are divided into two regions. The anterior region, which is overlapped when *in situ*, occupies about two-thirds of the scale and is covered with fine, sinuous radii which emanate from the focus of the scale. On reaching the margin of the scale the radii protrude over the edge by a minute amount (less than 0.1 mm). These protrusions would probably have been embedded in tissue. The posterior third of the scale is roughly rhombic in shape and is defined by the presence of elongate tubercles of enamel which are arranged with their long axes parallel in an anterior-posterior direction (see Woodward 1895a). The most posterior tubercles extend beyond the scale margin as small spines. The tubercles are 0.5 mm in length on a scale 4 mm long and 3 mm broad. The scale may also possess well-marked circuli, which lie more closely together posteriorly than anteriorly. There are about 60 oblique rows of scales, reaching their maximum length at the level of the anterior portion of the dorsal fin. In life the tubercled areas of the scales were the only parts exposed to the exterior and must have provided an effective light armour. The lateral line is visible to some extent in all the specimens, both sides being present due to lateral compression. It is represented by a series of parallel, elongate nodes or the corresponding depressions (Pl. 2, fig. 5).

*Measurements of Holotype.* MUZ 3167AB

	mm
Body length (excl. head)	54
Head length	28
Total length (incl. tail)	110
Head depth (corrected) max.	18
Body depth	?
Depth of caudal pedicle	11

*Growth Series in Coccolepis woodwardi.* Although only a very few specimens are known it is possible to cite features that may indicate immaturity. These are:

- (i) Size.
- (ii) Scale characters.
- (iii) Length of fin-ray joints.
- (iv) Fin-ray dichotomy.

A size gradation is known in the species, there being eight specimens which may be definitely assigned to *C. woodwardi*, ranging from the 'fry' P.24682, 30 mm in length by extrapolation (Pl. 3, fig. 3) to MUZ 2511AB, about 220 mm long by extrapolation (Pl. 3, fig. 1). Should the fragmentary specimen MUZ 3144A-J designated as ?*Coccolepis* be included in this species, the size range would be vastly extended. P.24682 is the smallest fish known from Koonwarra, and is worthy of special mention (Pl. 3, fig. 3). It is scaleless, and at Koonwarra such a condition is unlikely to be due to non-preservation or disturbance. The jaws are well developed, mandibles and maxillae bearing large laniaries and smaller teeth. The lower jaws also show tuberculation and the anterior extremity of the right mandible shows some of the openings of the mandibular sensory canal. The obliquity of the mandibular suspensorium is clearly visible.

The positions of the eyes are well defined as circular, carbonaceous stains. Judging by their present positions, the skull has been crushed somewhat obliquely, the 'eye-stain' of the left side appearing below that of the right side. Little else of the skull is preserved, apart from the general outline. The lateral lines are preserved as curved, dark lines and the dorsal fin is present, as well as parts of the pelvic fins.

The scales of the species bear tubercles on their exposed portion, the number of tubercles per scale being in proportion to the size of that scale and hence the size and age of the fish. It is, therefore, possible to give an accurate estimate of the size of a specimen of *Coccolepis woodwardi* from the size of an isolated scale and the number of tubercles carried. However, this is not translatable into terms of years at the present state of knowledge of the species.

Woodward mentioned (1895a, p. 5) that two specimens of *C. australis*, '... seem to differ only in the relatively great length of the joints of the fin-rays, a character regarded with good reason as denoting immaturity along Palaeoniscidae'. It is evident from Woodward's figures (1895a) that the fin-ray joints of the smaller examples are much longer than those of larger individuals. Gardiner (1960) figured the pelvic and anal fins of *C. liassica*, and the dorsal fin of *C. andrewsi*, all of which have small-jointed fin-rays, which would imply, according to Woodward (loc. cit.), that they have attained a degree of maturity. A similar phenomenon is exhibited by *C. woodwardi*.

In the smaller specimens there is little dichotomy of fin-rays (Pl. 2, fig. 3) except in the caudal fin, whereas in larger individuals such as MUZ 2511A this is marked. This may be a purely functional process, in that the juvenile fin-ray structure is so delicate that distal dichotomy would serve no useful purpose. It is only in the larger (i.e. older) fish of this species that fin-ray dichotomy is functionally necessary in order to give the fins their vital delicacy and accuracy of action.

These characters seem to be diagnostic of the immaturity of most of the specimens of *Coccolepis* found at Koonwarra.

Another ?juvenile character is also apparent, but it is not known how reliable or widespread this may be. In the immature specimens of *C. woodwardi* there is a rise in the dorsal margin of the fish beneath the dorsal fin, giving a 'humped' appearance (Pl. 2, fig. 3). This is absent in more mature individuals, e.g. MUZ 2511AB, and P.26062. Woodward (1895a) figured a similar 'hump' in a specimen of *C. australis* (MF. 247) which he considered to be immature. This structure is not exhibited by

the more mature individuals of that species. It may possibly be regarded as a juvenile character of uncertain distribution.

*Remarks.* The problem of comparing *C. woodwardi* with *C. australis* is complicated by preservation of different features in each species, but Table 1 compares six features known in both species.

TABLE 1

<i>C. woodwardi</i>	<i>C. australis</i>
Pectoral and pelvic fins well apart	Fins closer together
Pelvic fins at level of dorsal fin origin or slightly posterior to it	Pelvic fins originate in advance of level of dorsal fin origin
30 fulcral scales on the dorsal margin of the upper caudal lobe	54 scales on this lobe
5 scale rows on upper caudal	6 scale rows on this lobe
'Caudal inversion angle' (Liu 1957) 156–158°	Angle 162°
Branchiostegal rays with concentric striae; tubercles absent	Branchiostegal rays with tubercles

With reference to *C. australis*, the pectoral fin referred to an unidentified coelacanth (Woodward 1895a, pl. II, fig. 1) is almost certainly that of a large *Coccolepis* (Berg 1948). My only available comparison is the illustration of *Coccolepis* sp. by Eremeyeva (1940, p. 336), referred to *C. anisowitchi* by Berg (1948) and the correspondence between the two specimens is certainly very great.

With regard to the status of the family Coccolepididae (Berg 1940), it is necessary to clarify three main points. Firstly, Berg based the erection of the family on the presence of a single row of dorsal fin-supports. However, Stensio (1921, p. 247, footnote) suggested he was able to find traces of baseosts in *C. bucklandi*. If this is correct, then either the family definition must be altered (which would effectively reduce its taxonomic status to nil), or alternatively *C. bucklandi* (the type species) must be removed from the Coccolepididae. It seems likely that the loss of the baseost elements in the coccolepids was a gradual evolutionary process, and that in *C. bucklandi* the last traces of the process are still visible (Stensio 1921).

Secondly, Liu (1957) placed *Sunolepis* within the coccolepids on the basis of this single row of radials, even though the squamation of that genus differs from all other members of the family in that tubercles are absent. This may be relevant in the case of the chondrosteian *Psilichthys selwyni* (Hall 1900) which has a double row of dorsal fin-supports, as well as cycloid scales with circular ornamentation (personal observation).

Thirdly, Jakovlev (pers. comm. 1968) believes that *C. liassica* does not belong in the genus *Coccolepis*. As that species is the only one of the genus to be adequately described and figured to date (Gardiner 1960), it seems somewhat unusual to remove it from the genus at this time.

Lehman (1966) may well be justified in not recognizing the Family Coccolepididae, and, if baseosts are present in the type species and the taxonomic status of another well-described species is called in question, the validity of the family must be doubtful. I have continued to use the family name here, however, as I have not seen all of the material concerned.

## Family ?COCCOLEPIDIDAE

## ?Coccolepis sp.

## Plate 4

*Horizon.* Koonwarra mudstone succession, between lower part of the fish-bed and the lower arkose.

*Description.* Remains consisting of the broken fragments of parts of the jaws, palate, and hyoid regions of a large fish.

Part of the right mandibular ramus is preserved in four main pieces (MUZ 3144A-D). It is 125 mm in length and gently arcuate, particularly in the tapered anterior region. 8 teeth occur within this length, evenly spaced about 15 mm apart. They are large and conical in shape, curving to a point. The longest measurable tooth is 12 mm in length, and 6 mm wide at its junction with the jaw. The tip of a much smaller tooth is present in the matrix between the fourth and fifth teeth, suggesting the presence of other smaller teeth in the unexcavated matrix. A thin lamina of bone is given off in a mesial direction, lying nearly parallel to the inclination of some of the teeth and reaching about half their height. Part of the original bone surface of the dentary remains, and this draws attention to the mode of implantation of the teeth. They have the appearance of 'sprouting' from the jaw and are situated on the extreme lateral margin of this bone. The fourth tooth demonstrates this condition particularly well (Pl. 4, figs. 2, 5).

A large boomerang-shaped bone (MUZ 3144E-F) (Pl. 4, fig. 1) is present and along its shallowly concave margin there is a row of pointed teeth carried on a long slender bone which meets it with a straight suture. One end of the bone terminates in an oblique suture. A thinner lamina of bone is attached to the convex margin of the large bone, but it is broken and poorly preserved. By comparison with *Namaichthys schroederi* (Gardiner 1962) it seems likely that this element could be an entopterygoid and the attached lamina part of the metapterygoid (or suprapterygoid series, Watson 1925, 1928). If so, then the tooth-bearing element is a palatine.

On the same slab as 3114E is 3114G, an impression of a tooth-bearing bone 23 mm long and 10 mm wide, considered to be a coronoid (Pl. 4, fig. 3). Parallel with the long margins are 4 rows of 8 vertical impressions of teeth apparently only slightly smaller than those in the jaw. They are inclined towards the long margin of the bone, and penetrate deeply into the matrix. The impressions have radial ornamentation around their base, giving a stellate appearance. The whole surface of the specimen is covered with a delicate 'lace-work' of matrix which represents infilled cancellous bone. The stellate structure of the tooth impressions may indicate vertical striations of the tooth surface near the base. This is reminiscent of *Saurichthys* from the Triassic of Spitzbergen, where the 'plici-dentine' around the base of the teeth is preserved in similar fashion (Stensio 1925). In several tooth impressions there are conical crystalline cores representing infillings of the centres of the teeth. These too have plicate margins.

A small, poorly preserved fragment of a toothed bone is present which bears part of two rows of curved and pointed teeth, portions of 6 teeth being preserved. There is a disparity in size between the teeth of the 2 rows. This could be part of a coronoid, premaxilla, maxilla, or dentary. The hyobranchial region is represented by a number of disarticulated and broken elements, mainly hypobranchials and ceratobranchials (cf. *Centrolepis*, Gardiner 1960). These are elongate, cylindrical bones, expanded at their extremities and bearing a longitudinal groove. They possess annulations at right angles to their long axes. A particularly robust ?hypobranchial on 3144I (Pl. 4, fig. 4) has retained a little of the actual surface bone which is striated parallel to its length. Also on 3144I there is a slightly waisted rectangular plate of bone with what appears to be a strong cylindrical process at one corner. By comparison with *Mesonichthys* (= *Elonichthys* in part) *aitkeni* (Gardiner 1963; Watson 1925, pp. 862-863, fig. 29) and *Centrolepis aspera* (Gardiner, loc. cit.) this bone seems to be a basibranchial. The 'cylindrical process' may be the remains of a hypohyal, hypobranchial, or ceratobranchial impressed upon it.

3144I also contains an elliptical-semicircular element (Pl. 4, fig. 4) with concentric ornamentation and an apparent suture along its main axis. This is identical to an anterior branchiostegal ray of *Coccolepis woodwardi* sp. nov., with the exception of its great size.

Several very small spinose platelets are scattered through the matrix of 3144I and the strong ?hypobranchial previously noted has at least 6 of these close to it (Pl. 4, fig. 4). Similar but smaller platelets are present beneath the disturbed branchiostegal series in *C. woodwardi* (P.26062).

*Classification.* The characters available for classification are: (1) A large, gently arcuate mandible bearing 2 different-sized series of teeth; (2) small coronoids with 4 rows of strong teeth; (3) an ?entopterygoid, with a narrow toothed ?palatine attached to its oral border and a thin ?metapterygoid attached to its aboral margin; and (4) toothed platelets in the hyobranchial region. Many widely different types of fish possess similar toothed platelets, including: coelacanth—*Sassenia* (Stensio 1921) and *Latimeria* (Ørvig 1957); osteolepids—*Eusthenopteron* (Lehman 1966, from Jarvik); amiids—*Amia* (personal observation); and palaeoniscids—*Acrorhabdus* (Stensio 1921). The combination of listed characters, however, rules out the osteolepids and the coelacanth. An *Amia*-like fish is a possibility but in *Amia* there is no inner lamina from the jaw as described for this specimen. Also, *Amia* does not possess an element in the upper or lower jaws resembling the ?entopterygoid of the Koonwarra fish.

There is, however, a considerable resemblance to the palaeoniscoids. The jaw may be assumed to belong to the mandible as the inward-projecting lamina corresponds closely to the description of that element in the palaeoniscoids *Nematoptychius greenocki* (Watson 1928) and *Centrolepis aspera* (Gardiner 1960). The maxilla of some palaeoniscoids also bears a shelf to support the posterior palatines and ectopterygoid but this seems to have been horizontal, for example *Watsonichthys* (= *Elonichthys* in part) *pectinatus* (Gardiner 1963; Watson 1925). The lamina does not resemble that formed by the ectopterygoid and palatines in *E. binneyi*, which is a tooth-bearing structure. In this context Watson's statements on the parallelism of the structures of upper jaw/palato-quadrate with those of the lower jaw in *E. caudalis* should be considered (Watson 1925, pp. 860–862).

The element carrying four rows of teeth is probably a coronoid rather than a palatine, with regard to the number of tooth rows.

MUZ 3144 seems most likely to be a palaeoniscoid and as it shows affinities with and no differences from *Coccolepis woodwardi* sp. nov., except in size, it may be classified as ?*Coccolepis* sp., particularly with reference to the platelets which are identical with those of *C. woodwardi*.

The only other large ?predatory fish so far found in the Victorian Upper Mesozoic is *Psilichthys selwyni* Hall (1900), of which the skull is unknown. As I consider *Psilichthys* to be a palaeoniscoid it is possible that the above remains belong to that genus.

Regarding the predatory habits of this fish (MUZ 3144), 2 very small scales of *Koonwarria* n. gen. are present amongst the branchial debris, as well as a minute opercular of *Leptolepis*. Very small ?shoal fish were, therefore, amongst the last food eaten by this predator.

#### Order PHOLIDOPHORIFORMES

*Diagnosis.* Berg 1940, p. 214; but alter in accordance with Griffith and Patterson 1963, p. 6.

#### Family ARCHAEOMAENIDAE

*Diagnosis* (emended from Wade 1941). Small to medium-sized fish with fusiform to deep bodies. Suspensorium inclined anteriorly, orbit fairly large, placed well

forward. Premaxillae small, triangular; rostral small to medium-sized; nasals large, meeting in mid-line; frontals large, wide behind orbits. Parietals medium to large, quadrangular; dermopterotics of moderate size; extrascapulars broader than long. Maxillae long, arcuate, bearing one or two small supramaxillae; one large infraorbital in series of smaller elements; postorbital large. Opercular larger than subopercular; interopercular narrow and triangular, extending anteriorly from subopercular; preopercular large, arcuate; ventral limb extending anteriorly. Lower jaw probably consisting of at least articular, angular, and dentalo-splénial elements; large median gular present. Mandible may be deepened in coronoid region; branchiostegal rays few to moderately numerous. Pit-lines present on parietal, dermopterotic and preopercular; supraorbital sensory canal ends on frontals or parietals. Notochord persistent; ribs ossified; dorsal lobe of caudal region slightly produced; caudal fin forked. Paired fins smaller than unpaired fins; fin rays with long proximal and short distal joints, branched distally. Fulcra present on all fins, scales rhomboid with smooth or pectinate rear margin, or both rhomboid with cycloid together, or cycloid with a trace of enamel. Where present, rhomboid flank scales deepened.

*Historical summary.* 2 species of *Archaeomaene*, *A. tenuis* and *A. robustus*, were originally described by Woodward (1895a) together with *Aetheolepis* and *Aphnelepis* from the ?Jurassic of Talbragar, N.S.W. The first genus was placed in the Pholidophoridae and the last two genera in the Semionotidae.

In 1909 Goodrich incorrectly noted the genus *Archaeomaene* as *Archaeonemus*, and placed it in the new family Archaeonemidae [sic].

Wade (1941) cited the above information and reclassified the 3 genera, creating a new genus, *Madariscus*, for *A. robustus*, in a new suborder Cenogenoidei. 3 families were erected to house these genera, *Archaeomaene* and *Madariscus* being placed in the Archaeomaenidae, *Aetheolepis* in the Aetheolepidae, and *Aphnelepis* in the Aphnelepidae.

Arambourg (1958) referred all these genera to the one family Archaeomaenidae. Gardiner (1960) believed that the Archaeomaenidae and the Pholidophoridae were derived from a common ancestor. Griffith and Patterson (1963) suggested that the 4 genera 'appear to fall into 2 groups' depending on scale type, and which infra-orbital below the dermosphenotic is enlarged. The authors also noted the possible presence of 'chondrosteian' characters in *Archaeomaene* and *Aphnelepis*.

Arambourg (pers. comm. 1966) has asserted his belief that one family is enough to house these 4 genera, and that the imperfectness of the material does not allow for further 'splitting'.

Lehman (1966) placed *Archaeomaene* and *Madariscus* within the Archaeomaenidae, while *Aphnelepis* and *Aetheolepis* were placed in the Pholidophoridae.

*Terminology.* With regard to the snout region of *Wadeichthys*, the bone carrying the ethmoid commissure is referred to as the rostral (Rayner 1948, p. 339; Griffith and Patterson 1963, p. 39). The rostral is separate from the neurocranium. In *Koonwarria* and *Leptolepis koonwarri* the rostral is apparently fused into the ethmoid ossification, and I have followed Rayner (1948, p. 339) in describing this coalescence as the ethmoid.

The terminology of the caudal skeleton of the Archaeomaenidae and the Clupeiformes is that of Patterson (1968). The hyoid region is described in usual palaeoichthyological style for ease of comparison with the work of others.

Genus *Wadeichthys*, nov.

*Type species. Wadeichthys oxyops*, nov.

*Diagnosis.* A medium-sized fish known to reach at least 120 mm in length. Length of skull contained 3 times in standard body length. Skull large, roofed mainly by large frontals and parietals; median rostral; nasals meet in mid-line. Orbit large, placed well forward; 6 infraorbitals, numbers 5–6 (occasionally 4) and dermosphenotic with cusped rear margins. 2–4 supraorbitals; infraorbital 3 enlarged. Long, slightly curved maxilla, carrying a single supramaxilla. Opercular  $2\frac{1}{2}$  times as deep as subopercular, meeting it along a horizontal suture. Preopercular crescentic; horizontal and vertical limbs symmetrical. Lower jaw with slight anterior droop in juveniles; large triangular median gular. Jaws lacking teeth; 10–12 branchiostegal rays present. Supraorbital sensory canal ends on parietal; pit-lines present on parietal and dermosphenotic, very well developed on preopercular. Notochord persistent; no ossification of centra known. All fins with fulcra; pectoral fins with 12–13 rays, pelvic with 7–8, dorsal and anal with 9 each, and caudal with about 22. Number of radials in dorsal and anal fins equal to fin-ray count. Proximal fin-ray joint long; unpaired fins larger than paired fins; dorsal fin situated between origins of pelvic and anal fins. Scales rhomboid, heavily enamelled; flank scales deepened, one row notched and tunnelled by lateral line; dorsal and ventral ridge-scales.

*Wadeichthys oxyops* sp. nov.

Plates 5, 6, 7, fig. 1; text-figs. 7–17, 34

*Diagnosis.* As for genus (sole species).

*Holotype.* MUZ 3075AB (text-figs. 7A, B; pl. 5, fig. 1).

*Paratypes.* MUGD 3625, 3627–3630, 3647, 3650–3651, 3658, 3660. MUZ 2338, 2385, 2879, 3049, 3059, 3219, 3230, 3232, P.24676.

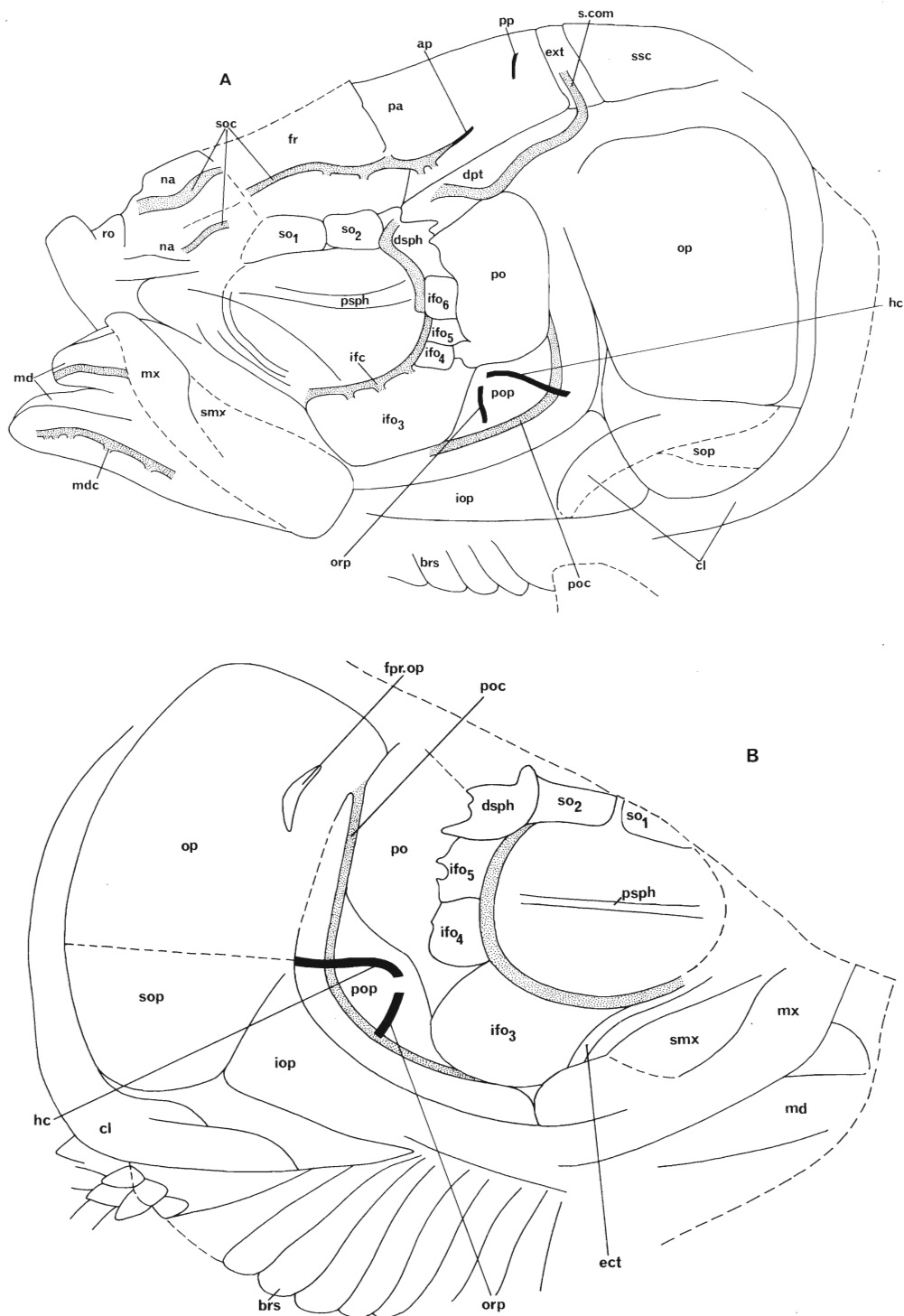
*Material.* A number of specimens in the following collections: MUGD, MUZ, NMV, P.M.D.

*Horizon.* Koonwarra fish-bed, L. Cretaceous.

*Locality.* Koonwarra, Victoria, Australia.

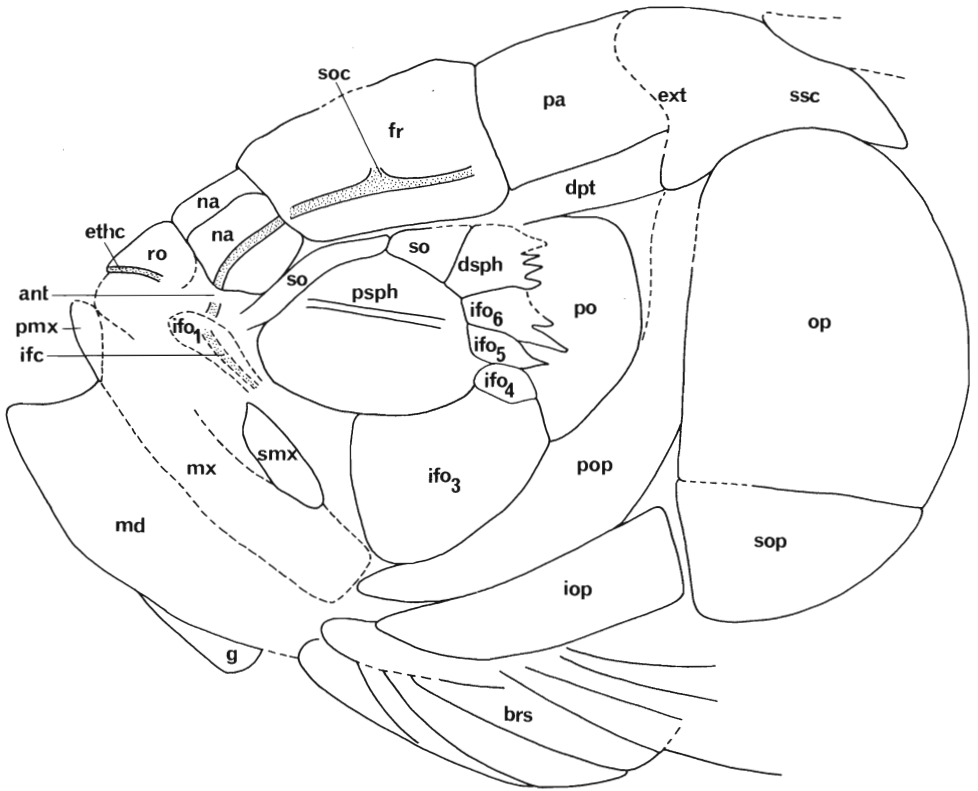
*Origin of Name.* Generically named for the late Revd. R. T. Wade, who described many of the Australian Mesozoic fish from New South Wales, including the Talbragar Archaeomaenidae. The specific name (Gr. 'Spike-cheek') refers to the cusped circumorbital bones posterior to the orbit which are characteristic of this species.

*Description.* Skull roof (text-figs. 7AB, 8–10, 13, and 14). The premaxilla (pmx.) is represented in P.26063 (text-fig. 8) by a toothless lanceolate element. It lies immediately antero-ventrally to the median rostral (ro.) (P.24676A, 26063AB, MUGD 3626A). Posterior to this the broad, shield-like nasal (na.) meets its fellow in the mid-line. The frontal (fr.) is narrow at the anterior dorsal margin of the orbit, and expands posteriorly. There are 2–4 supraorbital bones. This variation in supraorbital number seems to depend on mode of preservation on some occasions where the elements have been telescoped on to each other, but in other cases where preservation appears normal the variation is probably ontogenetic. The first (so<sub>1</sub>) is an extended quadrilateral, slightly expanded anteriorly, and the remainder are usually much smaller. The dermosphenotic (dsph.) is a fairly large element, compared with other bones surrounding the orbit (with the exception of the large third infraorbital), and bears up to 5 cusps on its posterior margin. It is similar to that element in *Catervariolus* (Saint-Seine 1955). According to Lehman (1966, pp. 133–134, fig. 124) *Catervariolus* resembles both the *Parasemionotiformes* and the *Amiiformes*. The parietal (pa.) meets the posterior margin of the frontal with a straight suture and is almost square, being as broad as the frontal. The narrower, rectangular dermosphenotic (dpt.) articulates with the frontal antero-mesially, the dermosphenotic antero-laterally, the postorbital laterally, and the extrascapular posteriorly. The extrascapular (ext.) is a narrow element shaped rather like an isosceles triangle lying with its apex mesially. (Skull reconstruction fig. 34.)



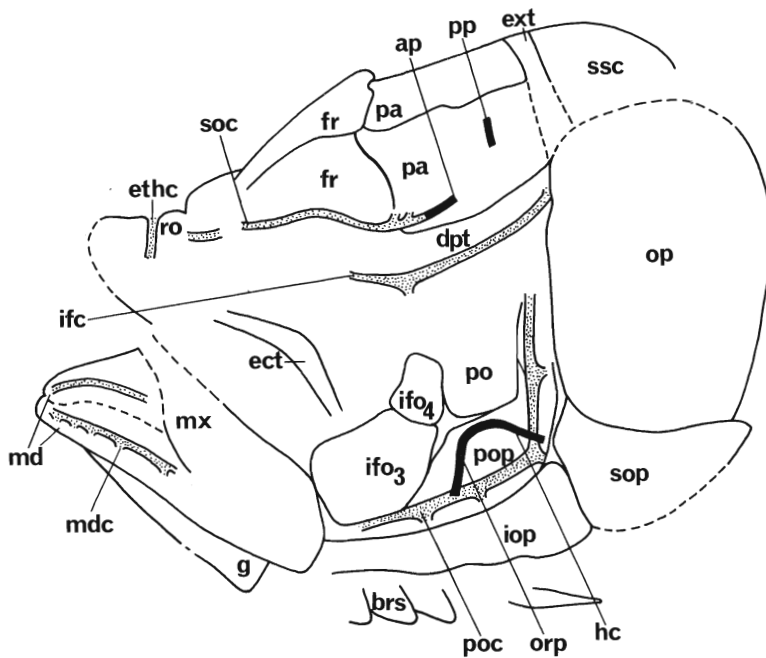
TEXT-FIG. 7A, B. Lateral views of the skull of *Wadeichthys oxyops*, part and counterpart. MUZ 3075AB, holotype,  $\times 4.5$ . (See also Pl. 5, fig. 1.)



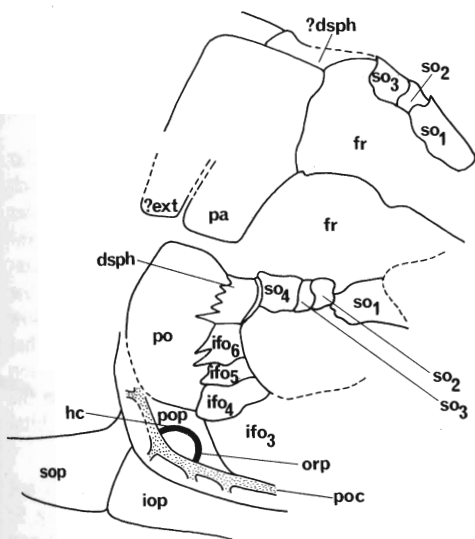


TEXT-FIG. 8. *Wadeichthys oxyops*, P.26063, lateral view of skull,  $\times 3.5$ .

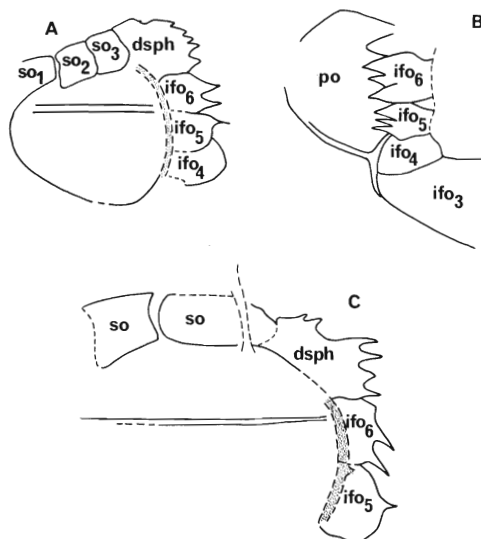
**Cheek Region.** (Text-figs. 7-15, 34; Pl. 5, fig. 2.) The maxilla (mx.) is long and slightly curved, tapers anteriorly, and is toothless. A single, lanceolate supramaxilla (smx.) is inserted in its dorsal margin, and bears small longitudinal rugosae, visible in MUGD 3625B. The antorbital (ant.) is not well known in any specimen. The infraorbital series consists of 6 elements, of which the first 2 are indistinctly preserved in the available material (i.e. lachrymal, ifo<sub>1</sub>, (text-fig. 8) and infraorbital 2 (ifo<sub>2</sub>)). Infraorbital 3 (ifo<sub>3</sub>) is the largest of the series, and is a broad element occupying the posteroventral margin of the orbit, much as in *Pholidophorus* (?) *caffii* (Nybelin 1966, fig. 5). It is bounded by the dorsal margin of the ventral preopercular limb, dorsally by infraorbital 4 and the ventral margin of the postorbital, and extends anteriorly to the posterior dorsal margin of the maxilla. Infraorbital 4 (ifo<sub>4</sub>) is a small, curved, quadrilateral, generally non-cusped element, with ventrally convex and dorsally concave margins. Infraorbitals 5 (ifo<sub>5</sub>) and 6 (ifo<sub>6</sub>) are of comparable size, and are markedly cusped, the number of large serrations varying from individual to individual (text-figs. 7, 8, 10-14). This variation extends to the number of cusps on similar bones on separate orbits of the one specimen. Infraorbital 5 commonly possesses a single, well-marked point, as in MUZ 3230A, 3059B, 3049, 3075A, and 2106AB, but in MUGD 3625B it is tricuspid. Infraorbital 6 is bicuspid in MUZ 3059B, 3049, and 2106A, but MUGD 3625B is again different, being tricuspid. Infraorbital 6 lies against the ventral margin of the dermosphenotic. The variation in the shape and sometimes number of the posterior infraorbitals may be due to fusion of elements, or possibly to the suture between 2 such bones having been destroyed during fossilization. Nybelin (1966) noted a possibly similar occurrence in *Pholidophoroides crenulata* which he thought might have been caused by 'ontogenetic disturbance' or regeneration following injury. In *Wadeichthys* similar variations occur often on each side of the skull of a single individual (cf. lateral line pores in *Wadeichthys*). I consider the normal number of infraorbitals in *Wadeichthys* to be 6.



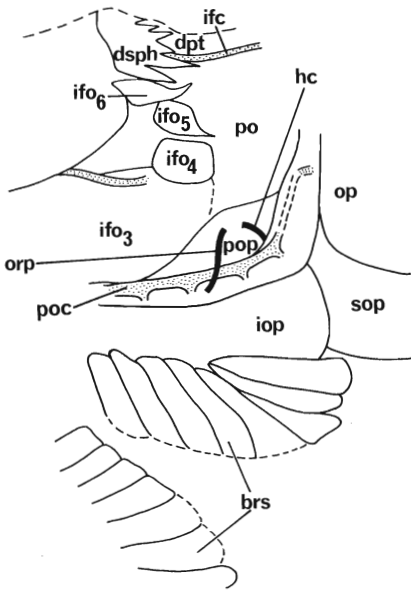
TEXT-FIG. 9. *Wadeichthys oxyops*, MUZ 3232A, lateral view of skull,  $\times 4$ .  
(See also Pl. 5, fig. 2.)



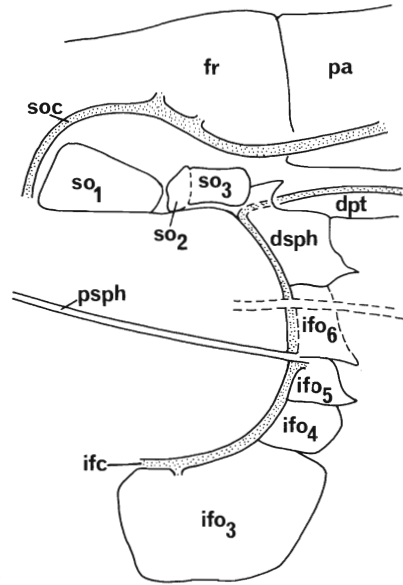
TEXT-FIG. 10. *Wadeichthys oxyops*, MUZ 3106A, skull roof and cheek region,  $\times 3.5$ .



TEXT-FIG. 11. A-C. *Wadeichthys oxyops*, orbital region. A, MUZ 3049,  $\times 4$ . B, MUGD 3625A,  $\times 4$ . C, MUZ 3059B,  $\times 11$ .



TEXT-FIG. 12. *Wadeichthys oxyops*, MUZ 3106B, distorted cheek and branchial region,  $\times 4$ .

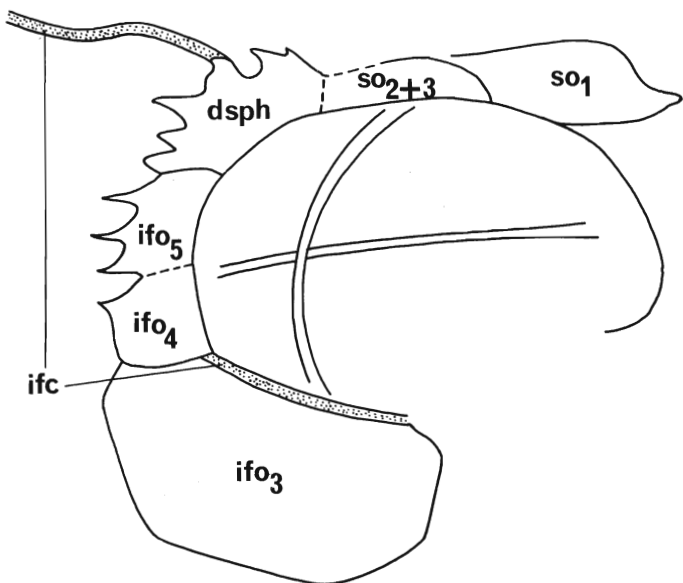


TEXT-FIG. 13. *Wadeichthys oxyops*, MUZ 3230A,  $\times 7$ . (See also Pl. 5, fig. 3.)

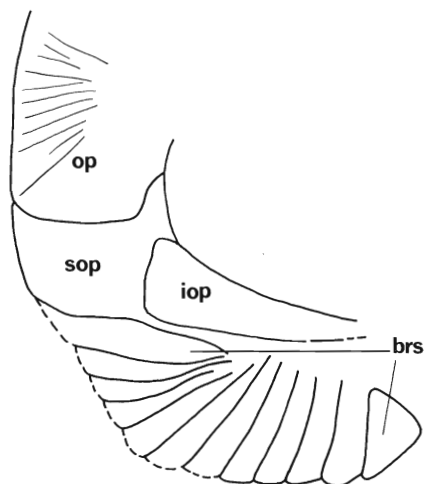
The opercular (op.) is large, the height being  $1\frac{1}{2}$  times the length, with curved posterior and dorsal margins. The anterior and ventral margins are virtually straight. The opercular exhibits a subtle ornamentation of fine lines which radiate posteriorly from a point a little above its centre. On MUZ 2879AB, consisting of fragmentary material, an isolated opercular is visible and shows the inner surface (text-fig. 16A). Close to the anterior margin in the dorsal third of the element there is a short vertical groove, the articulation for the processus opercularis of the hyomandibular (fpr. op.). It corresponds exactly in size to that process in a hyomandibular preserved on the same bedding plane. The anterior margin of the opercular is developed into a small process at this point, similar to the opercular of *Ichthyokentema* (Griffith and Patterson 1963).

The postorbital (po.) is about half the length of the opercular and two-thirds its height. The subopercular (sop.) is less than half the height of the opercular, and possesses a small process anterodorsally, which runs for a short distance along the anterior margin of the latter element (text-figs. 7A, 15). The subopercular is nearly semicircular, and from its anteroventral border the triangular interopercular (iop.) tapers anteriorly below the ventral limb of the preopercular, terminating behind the posterior margin of the maxilla (text-figs. 7A, 8, 15). The preopercular (pop.) (text-figs. 7-10, 12, 16C) is large, and at the level of the opercular-subopercular suture its posterior margin is bent anteriorly through about  $130^\circ$ , giving a shallow parabolic appearance. The anterior margin comes to a crest opposite this angle, and the bone somewhat resembles a scimitar in shape. The preopercular tapers rapidly towards its extremities, the dorsal portion extending along the anterior margin of the opercular, while the ventral limb extends anteriorly to the posterior margin of the maxilla. The latter limb lies between the ventral margin of the third infraorbital and the dorsal margin of the interopercular.

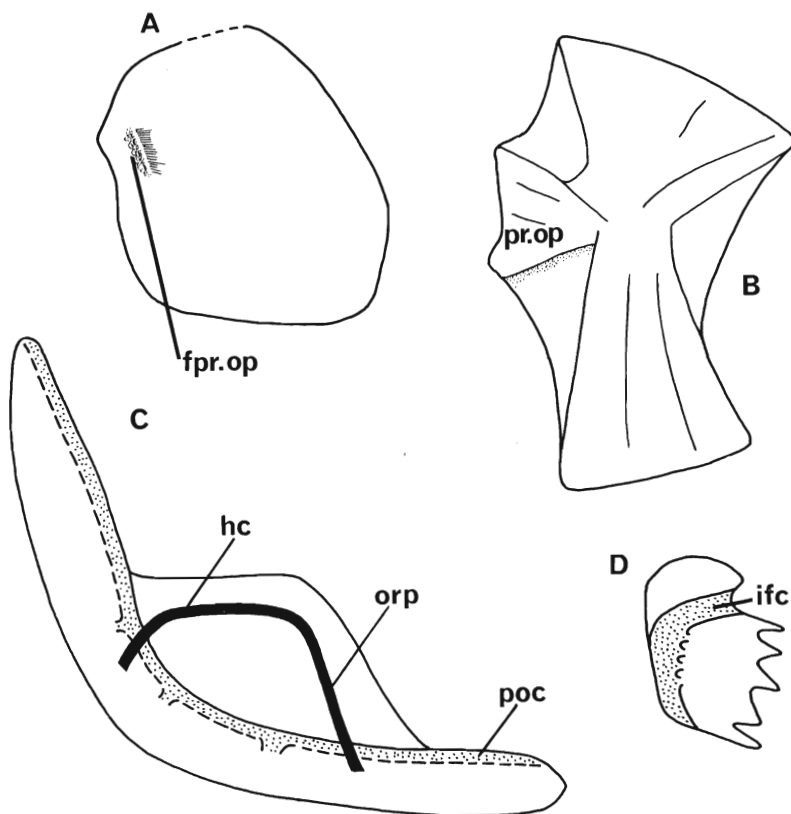
**Lower Jaw.** The mandible (md.) is visible to some extent in several specimens, but its structure is not entirely clear due to the lack of disarticulated specimens. It is best observed in MUZ 3232AB (text-fig. 9; Pl. 5, fig. 2). In MUGD 3629B, the mandible bears small longitudinal rugae. The jaw exhibits a slight droop anteriorly and proceeding posteriorly the dorsal margin is elevated. It appears to be toothless, although in MUZ 3230A very fine granules near the tip of the mandible imply the possibility of minute denticles, but this may be merely cancellous bone. The droop of the jaws is often exaggerated due to the superimposition of both lower jaw rami with their curved sensory canal infillings. In more mature and



TEXT-FIG. 14. *Wadeichthys oxyops*, MUZ 3059A, orbital region,  $\times 10$ .



TEXT-FIG. 15. *Wadeichthys oxyops*, MUZ 3232B. Opercular and branchial regions,  $\times 5$ .



TEXT-FIG. 16. A-D. *Wadeichthys oxyops*, MUZ 2879AB. A, Opercular,  $\times 5$ . B, Hyomandibular,  $\times 12$ . C, Preopercular,  $\times 12$ . D, Dermosphenotic,  $\times 10$ .

presumably adult specimens this jaw-droop is less marked or totally absent (e.g. MUGD 3647AB; 3626A, P.26063 (text-fig. 8)). I have also observed that this droop is most marked in the smaller specimens of *Aphnelepis* (Woodward 1895a, Wade 1941) from Talbragar, N.S.W. It seems, therefore, to be a juvenile phenomenon.

A large, triangular, median gular (g.) is present, with the apex anteriorly. It is most clearly visible in P.24676, MUZ 3232A, and P.26063 (text-figs. 8, 9; Pl. 6, fig. 1).

*Sensory Canal System.* The supraorbital sensory canal (soc.) traverses nasal, frontal, and parietal bones (text-figs. 7A, 8, 9, 13). In the nasal it crosses the bone in arcuate fashion, convex mesially. The canal then enters the anterior region of the frontal and runs posteriorly in an almost straight line to the middle of this element. There it changes direction, passing in a shallow arc, which straightens to meet the posterior limit of the frontal at right-angles. There appear to be 5 tubules issuing from the canal on the frontal, one situated on the anterior section, and the remainder spaced fairly regularly along the posterior portion. On entering the antero-lateral part of the parietal the canal gives off one large tubule mesially, and two smaller ones laterally before diminishing to a shallow groove, the anterior pit-line (ap.) (text-figs. 7A, 8). The infraorbital sensory canal (ifc.) is represented on the rostral by an arched ethmoidal commissure (ethc.), which presumably joined the canals of each side of the snout (text-figs. 8, 9). The antorbital is crushed in every specimen, but a section of the canal carried on that bone may be seen in P.26063 (text-fig. 8) and MUZ 3219. In the latter the characteristic Y-shape of the canal is visible (cf. Pholidophoridae; Nybelin 1966) with a short postero-dorsal branch being present. In P.26063 the canal is visible on infra-orbital 1 (lachrymal). Infraorbital 2 is unknown. Infraorbital 3 possesses 3 approximately equidistant and very short tubules. Infraorbitals 4 and 5 may have one tubule each, but number 6 does not show the canal. The dermosphenotic is visible in many specimens (text-figs. 7, 8, 10, 11A, 12-14) but in MUZ 2879A an isolated example of this bone is preserved, with an infilling of the sensory canal (text-fig. 16D). The canal runs close to the orbital margin of the element, and then turns through a right-angle to leave the postero-mesial margin through a broad notch. It runs posteriorly into and through the dermopterotic, giving off two tubules in its anterior region, but the arrangement of tubules posteriorly is obscure.

*Cephalic Division of Main Lateral Line.* A small, anteriorly concave groove is present on the postero-mesial area of the parietal, and probably represents the posterior pit-line (pp.) (text-figs. 7A, 9). The middle pit-line (mp.) runs in a shallow arc from the postero-lateral region of the parietal to close to the lateral margin of the dermopterotic. The lateral line (ll.) contacts the anterior border of the extrascapular and then turns mesially through 90° to run parallel with that border (fig. 5A). This is the supratemporal commissure (s. com.), and may bear 4 tubules. Close to the lateral margin of the extrascapular the cephalic lateral line continues posteriorly into the suprascapular, running close to the lateral margin of that bone. At least one short tubule is given off close to the posterior margin of the suprascapular. The canal is then deflected ventrally into the supracleithrum, and a single small tubule may be seen at the mid-point of that bone. The preopercular sensory canal (poc.) runs parallel with the posterior margin of the preopercular element. In no specimen are all the branches of the preopercular sensory canal clearly exposed but it would seem that there were about 5 short tubules (text-figs. 9, 10, 12; Pl. 5, fig. 2). The preopercular also bears on its anterior expansion 2 well-developed grooves which represent pit-lines (text-figs. 7AB, 9, 10, 12, 16C; Pl. 5, fig. 2). They almost form a parabola, convex anteriorly. The dorsal limb of the parabola is formed by a groove running antero-dorsally, and this curves ventrally to join the lower limb which runs vertically. The dorsal groove represents the posterior part of the anterior division of the supramaxillary pit-line (hc.), and the vertical groove the postmaxillary pit-line (orp.) (cf. Nybelin 1966).

The mandibular sensory canal (mdc.) is clearly shown in MUZ 3232A and 3075A (text-figs. 7A, 9) and has 5 short tubules which become progressively larger and more widely spaced, traced posteriorly.

*Lateral Line (ll.).* This is visible to some degree in a few specimens, but the apertures to the exterior are most clearly visible in MUZ 3230AB, 3232AB, and the holotype. MUZ 3230AB is a juvenile specimen and MUZ 3232AB only a little older. The scales tunnelled by the lateral line are the deepest, the pores occurring in the dorsal third of the scale. These apertures are irregularly spaced and they vary in number from 12 to 16. On MUZ 3232AB they are spaced as follows, scales numbering from the posterior margin of the pectoral girdle:

3232A—2.4.6.10.13.16.19.21.24.27.32.34.37.41. (14 pores)

3232B—2.3.5.8.11.13.15.17.19.21.26.28.30.32.35.40. (16 pores).

In the holotype (MUZ 3075AB) they are spaced as follows:

3075A—2.3.9.12.18.23.24.28.32.35.36.39.40. (13 pores)

3075B—3.4.8.11.14.16.20.28.33.37.38.40. (12 pores).

In MUGD 3628 some of the actual scales (not merely impressions) of the lateral line are present and pores seem to occur in nearly every one of these where preserved, with a few exceptions. In the caudal region, for example, there are 11 consecutive scales bearing lateral line perforations. The apertures are not only irregularly spaced, therefore, but there is considerable variation in their number and arrangement on each side of the fish and from individual to individual. In the posterior caudal scales (e.g. numbers 40–41) the lateral line pore is represented by a cylindrical infilling.

*Hyoid Arch.* The only elements known are the hyomandibular (hyo.) and the branchiostegal rays. The former is known from the fragmentary MUZ 2879AB (text-fig. 16B). It is a sturdy structure, although in all probability not very thick, and may be basically described as three triangles, joined apically. The head of the hyomandibular is a wide-based triangle with the apex directed ventrally, and the whole is tilted slightly anteriorly. The main shaft of the bone forms an upright isosceles triangle, about twice as long as the head. At the waist formed by the 2 apices is inserted the apex of a third, much smaller, equilateral triangle, the processus opercularis (pr. op.). Linking these triangles are very thin flanges of bone.

The branchiostegal rays (brs.) lie beneath the interoperculum, and are well represented in several specimens (text-figs. 7–10, 12; Pl. 6, fig. 1). There are 10–12 branchiostegals, resembling those in *Archaeomaene*, which Wade (1941) described as 'strap-like'. The first ray is very broad, almost semicircular, with the anterior margin being convex. Subsequent rays are about 4 times as long as they are broad, and the last ray is lanceolate in form. This last branchiostegal is bounded dorsally by the interopercular and the lower margin of the subopercular, and posteriorly by the anterior margin of the lower limb of the cleithrum.

*Palate.* Little is known of the palate, as this region is always covered by the dermal bones of the cheek in the available material. In the disintegrated 2879AB, no palatal elements are distinguishable. In one or two specimens, however, the tapering, antero-dorsal wing of the ectopterygoid (ect.) is visible.

*Neurocranium.* Of the neurocranium only the parasphenoid (psph.) is visible, crossing the orbit; but no details of this element are known.

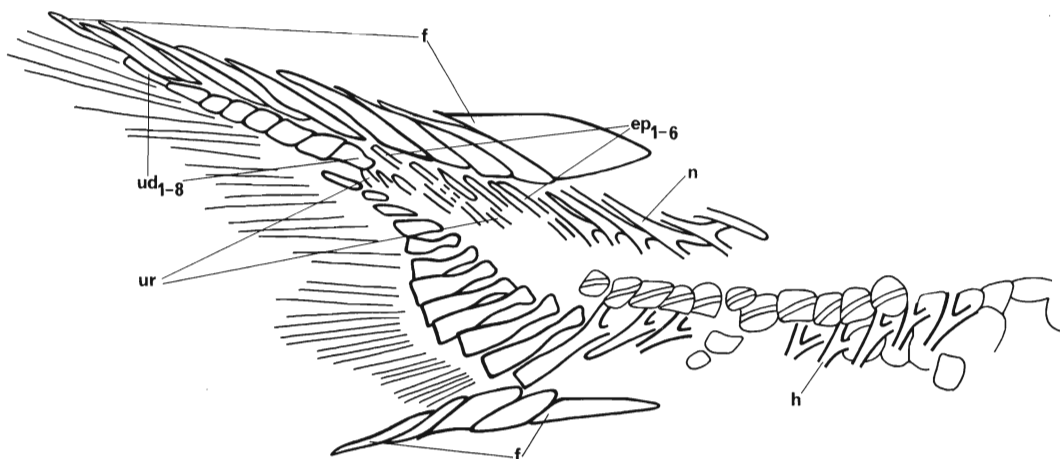
*Pectoral Girdle and Fins.* The cleithrum (cl.) is a sigmoid-shaped bone, articulating with the supracleithrum about halfway along the posterior margin of the opercular. The suture between the two elements is steeply inclined antero-dorsally. In 2385AB there is a partly preserved ?coracoid which is strongly formed and expanded distally. No radials are visible.

The pectoral fins are the least well preserved of all the fins, and contain about 12–13 jointed lepidotrichia (lep.) (MUZ 3232B, 2106AB) which bifurcate distally. The leading ray is fringed with fulcra.

*Pelvic Girdle and Fins.* The pelvic fins appear to be approximately similar in size and arrangement to the pectorals, but possess only 7–8 lepidotrichia (3232B). The structure of the pelvic girdle is unknown.

*Unpaired Fins.* The dorsal fin (Pl. 5, figs. 2, 3; Pl. 6, fig. 3) arises approximately mid-way between the level of the pelvic and anal fins and has 9 jointed, branching lepidotrichia, the leading one bearing at its base several strong fulcral scales and rays. The skeletal supports are waisted toward their distal margins and broaden to articulate with an equal number of lepidotrichia (Pl. 5, fig. 3; Pl. 6, fig. 3). The anal fin possesses the similar triangular shape of the dorsal fin, is about the same size and contains a similar number of lepidotrichia and radials (Pl. 5, fig. 3; Pl. 6, fig. 3). The latter are far more slender than those supporting the dorsal fin, but also expand distally.

The caudal fin is forked and symmetrical, although there is a scale-covered area extending for about one-third of the length of the dorsal lobe. Both dorsal and ventral lobes of the caudal fin have well-developed fulcra (f.) along their margins, about 14 being present on each. The dorsal fulcra are the more robust. There are 22 jointed lepidotrichia. The radials of the dorsal and anal fins, and the caudal fin supports are clearly visible in a number of juvenile specimens (Pl. 5, figs. 2, 3; Pl. 6, fig. 3). Among these are MUGD 3647AB; 3648AB; MUZ 3230AB; 2385AB and P.24676. The whole caudal structure is visible in 2385AB (text-fig. 17; Pl. 7, fig. 1).



TEXT-FIG. 17. *Wadeichthys oxyops*, caudal region of axial skeleton, MUZ 2385B,  $\times 6$ .

*Axial Skeleton.* (Text-fig. 17; Pl. 7, fig. 1.). This is not well known, as in most specimens the scales have remained in place. In MUZ 2385AB, the posterior region is free of scales and the axial skeleton is visible.

The neural (n.) and haemal (h.) arches are very similar in size and shape until the caudal fin is reached, being slender shafts fused to deeply incised arches. This arrangement terminates beneath the second fulcral scale of the dorsal caudal lobe and gives way to 6 slender epurals (ep.) which underlie the fulcral series. This appears to be a primitive number (Patterson 1968). Beneath these lies another row of smaller bones, also arranged 'en echelon', the ural neural arches (ur.).

Posterior to this in the axis of the caudal fin lie the 8 well-developed urodermals (ud.) which are parallelogram-shaped with the exception of the first one and the last 2, which tend to be elongate.

This arrangement is very similar to that of *Archaeomaene tenuis* (Woodward 1895a, and personal observation) where there are at least 6 such urodermals and 5 epurals, and to the British Lower Liassic pholidophorid *Pholidophoropsis* (Nybelin 1966), which has 5 epurals and 8–10 urodermals (Patterson 1968).

The last haemal spine before the lepidotrichia are reached is distally expanded, as are the succeeding 8 spines. The last 3 are small slivers of bone, making 11 haemal spines supporting the fin. No centra are known in any specimen.

*Squamation.* The rhomboid scales (Pl. 5, fig. 2) are thick and heavily enamelled, with a smooth posterior margin, and possess peg-and-socket articulation. The flank scales are deepened, the longitudinal row carrying the lateral line being the deepest. There are 47 transverse rows of scales on the body, counting from the rear of the opercular to the middle of the caudal fin (see Nybelin 1966, p. 402). It is necessary to add a few more incomplete rows in the dorsal caudal region, giving about 56 rows in all. There are 10 longitudinal rows, of which the fifth has the deepest scales and carries the lateral line. The lateral line scales are notched on their posterior margins (Pl. 6, fig. 3), somewhat in the fashion of *Parasemionotus labordei* (Lehman 1952, fig. 123). No thinning of scales or concentric striation is present.

A number of scales of *Wadeichthys* have been sectioned and these show very similar structure to those of *Pholidophorus higginsii* (Gardiner 1960), except that the enamel layer appears thinner and the cell spaces smaller. Canals of Williamson are present but are reduced.

*Measurements of Holotype.* MUZ 3075AB.

	mm
Body length (to end of lower caudal lobe)	51
Head length (to rear of opercular)	23
Total length (incl. tail, approx.)	95
Body depth (max.)	20
Head depth	18
Caudal pedicle depth	9

*Growth Series of* *Wadeichthys oxyops*. A growth series was described by Wade (1935) with reference to scale development of the Triassic catopterid *Brookvalia*. Gardiner (1967) showed similar development of scales in the palaeoniscoids *Sceleto-phorus* Frič, *Phanerosteon* Traquair, and *Carboveles* White.

The scales of *Brookvalia* first appear along the lateral line from behind the pectoral girdle to the axis of the tail, and Wade stated (loc. cit., p. 27): '... a fish 84 mm long is almost completely covered with scales. The small uncovered areas are adjacent to the dorsal and anal fins and the infero-posterior corner of the caudal pedicle. The last portion to be covered is that lying beneath the dorsal fin.'

This is similar to the case in several small specimens of *Wadeichthys oxyops*, e.g. MUZ 2385AB, 3230AB, 3231AB; MUGD 3647AB, 3648AB.

The largest of these (by extrapolation) is MUGD 3648, which consists of a trunk, missing most of the paired fins and nearly all of the skull. The growth series is incomplete in its earlier stages, as the smallest example of *Wadeichthys* (MUZ 3231AB) (Pl. 6, fig. 2) shows only minor differences from slightly more adult specimens.

MUZ 2385AB (Pl. 7, fig. 1) has only the posterior half of the body intact. It shows the least number of horizontal scale rows of any specimen, about 5 beneath the remains of the dorsal lepidotrichia, and 2-3 rows posterior to this region in the caudal axis. It is not clear whether or not this is a vagary of preservation, as below the posterior rows there are a few isolated scales which may have drifted from their original position. This fish is intermediate in size between MUZ 3230 and 3231 and it seems more likely that the missing scales were once present and were carried away before, or during, preservation. The most mature fish (*Wadeichthys*) developed a dorsal convexity or 'hump back', e.g. Pl. 5, fig. 4.

Lehman (1952, pl. 33A and C) illustrated what may well be a similar phenomenon of sub-adult growth in *Parasemionotus labordei* and *Pteronisculus cicatosus*, where the dorsal and anal fin supports are not covered by the scales.

*Discussion.* The systematic position of *Wadeichthys* is a problem with regard to the classifications of previous authors. Having studied all the material available to both Woodward (1895a) and Wade (1941), together with the new specimens from Koonwarra, I am convinced that the following genera are very closely related: *Archaeomaene*, *Madariscus*, *Aphnelepis*, *Aetheolepis*, *Wadeichthys* nov. The confused situation has been rather like that previously existing in the family Pholidophoridae, except that fewer species were involved. The stumbling block in archaeomaenid taxonomy from the point of view of earlier authors has been the squamation. The rhomboid squamation of *Aetheolepis* (in part) and *Aphnelepis* led Woodward (1895a) and presumably Romer (1966) to place them in the Semionotidae. It is evident after careful examination that those 2 genera do not belong in that family. Such evidence as the structures of the snout (Griffith and Patterson 1963), the toothless jaws, and the cheek bones, mark both genera out as pholidophoroids. Griffith and Patterson (1963) stated that the Archaeomaenidae (general sense) fall into 2 groups, depending on whether the second or third infraorbital below the dermosphenotic is enlarged, and whether the scales are rhomboid or cycloid. With reference to the latter of the two criteria, Woodward (1895) remarked that both *Aetheolepis* and *Aphnelepis* bore scales which became thin posteriorly, and that in *Aetheolepis* these



were really cycloid. Nybelin (1966), on the other hand, has noted that in some members of the family Pholidophoridae (*sensu stricto*) enamel has begun to disappear, the reduction beginning anteriorly, and the enamel being retained in the caudal peduncle for a longer period of time. *Aetheolepis* scales (Schultze 1966) from the anterior region of the body are rhomboid whereas the posterior scales are cycloid. It may be assumed, therefore, that the scales in the Archaeomaenidae represent an argument only in that they are one way of determining which of the members of the family are more 'advanced' and which more 'primitive'. It is of interest, however, to note the different manner in which the archaeomaenids and pholidophorids have evolved toward the cycloid scaled condition; the former first losing the enamel covering posteriorly and the latter anteriorly.

Regarding the enlargement of infraorbitals, I have examined the relevant Talbragar material and conclude that the state of preservation of the infraorbital region of *Aetheolepis* and *Aphnelepis* does not allow a satisfactory conclusion to be reached concerning the infraorbital series. In *Wadeichthys* it is undoubtedly the third infraorbital (i.e. usually fourth below the dermosphenotic) which is enlarged. This may be significant as a specimen of *Archaeomaene* from Talbragar, MF. 761 (Wade 1941, fig. 2) shows that the second infraorbital below the dermosphenotic may not be 1 element. It could well be 2, making the enlarged infraorbital the fourth and not the third below. It is more logical, based on available evidence, to consider reduction and fusion of the infraorbital series (coincident with a change from rhomboid to cycloid scales); and loss of at least one element would be a reasonable supposition in an evolutionary gradation from the '*Wadeichthys* stage' to the '*Archaeomaene* stage'. This does not imply, of course, any direct evolutionary line between those 2 genera. There is also some infraorbital variation in *Wadeichthys*.

Nybelin (1966), Gardiner (1967a), and Wenz (1968) have discussed the use of the preopercular in taxonomic relationships. This involves both the shape of the bone and the arrangement of the sensory canal and its tubules. This element in the Archaeomaenidae is varied, and does not exhibit trends as does that of the Pholidophoridae *s. str.* (Nybelin, p. 428). It is possible, however, to state that in shape this bone is closer to the Jurassic than to the Triassic type of preopercular, as illustrated by Nybelin. In *Madariscus* and *Archaeomaene* the canal runs fairly near the anterior and centre of the preopercular, and the tubules are of moderate length, the preopercular being quite sharply angled. In *Aphnelepis* the preopercular is not so sharply angled and is slimmer, with the canal running in the posterior-centre of the dorsal limb. The canal in *Aetheolepis* runs centrally and has fairly long tubules, and the preopercular of *Wadeichthys* is symmetrical, with the canal running close to the anterior margin (text-fig. 16c).

Pit-lines are present in the preopercular of at least *Wadeichthys*, and (to a lesser extent) in *Archaeomaene*. It seems, therefore, that the evolutionary 'advancement' of the preopercular and its canals ties in with the change from rhomboid to cycloid scales in this family as well as in the Pholidophoridae (Nybelin 1966). Another feature is the presence of well-developed fulcra in those genera with rhomboid scales and the lack of reduction of fulcra in the cycloid-scaled genera.

Generally speaking it is proposed that the diagnosis given for the family Archaeomaenidae in this study reveals sufficient constancy of structure, particularly in skull

anatomy, for the family to be regarded as a single unit, comprising the following genera: *Archaeomaene*, *Aetheolepis*, *Aphnelepis* Woodward (1895a), *Madariscus* Wade (1941), and *Wadeichthys* n. gen.

*The Relationships and Derivation of the Family Archaeomaenidae.* Griffith and Patterson (1963) have commented on derivation of this family and were in some doubt as to whether the Pholidophoroidea (Halecostomi) were derived from the Parasemionotidae. However, Gardiner (1960) was convinced of this derivation. I have been unable to study the neurocranium of the Archaeomaenidae (due to the mode of preservation) and am unable, therefore, to comment on artery and nerve pathways which Griffith and Patterson considered significant.

Comparison of *Wadeichthys* with the Pholidophoridae (*sensu* Nybelin 1966) reveals a similarity in the following characters.

The sensory canals resemble their counterparts in *Pholidophorus* (?) *caffii* (Nybelin 1966, fig. 5) and *Ichthyokentema purbeckensis* (Griffith and Patterson 1963, figs. 1 and 6). The resemblance is largely one of simplicity in that the branches (tubuli) of the canals are few in number and comparatively short. The form of the pit-lines on the parietal and dermopterotic is almost identical to that in some pholidophorids (Nybelin 1966).

With regard to supramaxillae, *Wadeichthys*, *Archaeomaene*, and possibly *Aetheolepis* have 1 (as in *Ichthyokentema* and *P.* (?) *caffii*); and *Madariscus* and *Aphnelepis* have 2 (as in the Pholidophoridae, with the exception of *P.* (?) *caffii*).

The infraorbitals have a very similar arrangement, the third being greatly enlarged, and its relationship with the postorbital being much the same as in *P.* (?) *caffii*. The infraorbital series between the dermosphenotic and infraorbital 3 is also closely similar to the pholidophorids generally, and in particular to *Pholidophoroides* (Nybelin 1966, figs. 9 and 12). Griffith and Patterson (1963) have previously remarked on the archaeomaenid snout being typically that of a primitive pholidophorid (*non* Nybelin 1966); i.e. Median rostral with ethmoid commissure, premaxillae in contact below rostral, and nasals meeting mesially. *Wadeichthys* bears this out. These authors (p. 39) also refer to 2 features which, if present, would in their opinion 'indicate that the archaeomaenids originated independently from forms like the parasemionotids . . .'. These are a surangular in *Aphnelepis* and a pit-line in the preopercular of *Archaeomaene*, as described by Wade (1941). Having examined both the original material and casts, I believe that Wade was incorrect in designating a surangular for *Aphnelepis*. The preservation is such that no actual bone is left and many cracks are present in the matrix which lend themselves to diverse interpretation, particularly when combined with the overlying impressions of the maxillary region. There is no element which I would definitely designate a surangular. Pit-lines are present in the preopercular of *Archaeomaene*, but are much smaller than the well-developed pit-lines found in the same element in *Wadeichthys*. Those of the latter are similar to those of *P.* (?) *caffii* (Nybelin 1966, fig. 5). On at least one count, therefore, Griffith and Patterson's argument may be upheld, but if so, then the same will hold for the Pholidophoridae *sensu stricto*, which also have pit-lines on the preopercular (Nybelin 1966).

The erection of the suborder Cenogenoidei by Wade (1941) is invalid. It was

based entirely upon the supposedly unique cheek region of the fish included within the taxon, but this area is closely similar to that found in the Pholidophoridae *sensu stricto*. Is it reasonable, therefore, to separate the Archaeomaenidae as an independent family, or should it be incorporated into the Pholidophoridae?

Although it is clear that both families have a common ancestry, there are certain differences between them which warrant their separation. The 2 most important differences are the distinctiveness of the structure of the preopercular in the 2 families and the discrepancy in the mode of replacement of enamelled scales by cycloid scales. These taxonomic criteria serve to strengthen the hypothesis that perhaps migration and geographical isolation within the original pholidophorid-archaeomaenid stock established the Archaeomaenidae as a separate entity sometime in the Upper Triassic or early Jurassic (see also p. 92). The Archaeomaenidae may, therefore, be regarded as taxonomically replacing the suborder Cenogenoidei of Wade (1941).

A comparison of evolutionary grade is justifiable between *Wadeichthys* on the one hand, and *Pholidophorus latiusculus*, *P. cf. pusillus* and *P. (?) caffii* on the other. One might also compare *Archaeomaene* and *Madariscus* with *Pholidolepis* and *Pholidophoropsis* (Nybelin 1966). In many ways *Wadeichthys oxyops* is the most primitive member of the Archaeomaenidae known to date, despite its Lower Cretaceous age, though in this connection it should be remembered that the dating of the Talbragar beds as Jurassic (Woodward 1895a, Dulhunty 1937) is uncertain. The preopercular of *Wadeichthys* is possibly the most primitive example of this element found in the archaeomaenids and it resembles that of the parasemionotids. In *Watsonulus eugnathoides* (Lehman 1952) the characteristic boomerang-shape of the posterior preopercular region which carries the sensory canal is identical with that of *Wadeichthys*. The main anterior flange of the preopercular is larger than in the latter and while pit-lines are present (Lehman, loc. cit., fig. 106), they are arranged differently. *Jacobulus novus* is also very similar, and given no anamestic fragmentation of the element carrying the sensory canal from the inferior preopercular (loc. cit., fig. 126), a condition resembling *Wadeichthys* would be arrived at (see Westoll 1937). The arrangement of pit-lines is similar to *Wadeichthys*. It is, however, in *Thomasinotus divisus* that the clearest resemblance is found, particularly with reference to the pit-lines (Lehman 1952, fig. 129). In fig. 129A (loc. cit.), the pit-lines are shown as being joined, almost exactly as in *Wadeichthys*. It is apparent that the preopercular of *Wadeichthys* corresponds at least to the preopercular element carrying the main canal together with the bone bearing the pit-lines in the Parasemionotidae.

*Wadeichthys* is primitive, therefore, in the pattern of the preopercular, in its squamation, which does not exhibit thinning of scales at any point on the body (Pl. 6, fig. 3), and in the structure of the axial caudal skeleton. This may validate, at least in part, Gardiner's phylogenetic tree (1960) of the holosteans, the Archaeomaenidae branching off some time in the early Upper Triassic from the stream leading from the Parasemionotidae to the Pholidophoridae.

## Order CLUPEIFORMES

## Family KOONWARRIIDAE nov.

*Diagnosis.* Medium-large sized fish reaching a maximum known length of 294 mm. Length of head contained  $3\frac{1}{2}$ –4 times in standard body length. Nasals small, separated by large excavated frontals; anterior margins of frontals dactylate or deeply serrated; posterior margin of ethmoid similarly serrated. Parietals small; infraorbital 3 enlarged; a single, long supraorbital; sclerotic ring present. Maxilla long and curved, bearing 2 supramaxillae. Opercular twice as deep as subopercular; suture strongly oblique. Preopercular large, sharply angled; lower jaw with slight anterior droop; jaws toothless; 16 to 17 branchiostegal rays. Parasphenoid with basipterygoid process; palatine with maxillary process. Supraorbital sensory canal ends on anterior margin of parietal; small pit-lines present on parietal only. Notochord persistent; well-developed centra in maturity, numbering at least 50. Caudal skeleton with well-developed hypurals and uroneurals; supraneural and intermuscular bones present antero-dorsally. Fulcra absent; pectoral fin with 12–14 rays, pelvic with 10, dorsal with 12, anal with 22, and caudal with 22. Radials numerically equal to fin-rays; anal fin very long-based; origins of dorsal and anal fins opposed. Scales cycloid, without enamel, and bearing anteriorly directed radii.

## Genus: KOONWARRIA, nov.

*Type Species.* *Koonwarria manifrons* sp. nov.

*Diagnosis.* As for family, sole genus.

*Koonwarria manifrons*, sp. nov.

Plate 7, figs. 2, 3, Plate 8; text-figs. 18–21, 33, 37

*Diagnosis.* As for genus.

*Holotype.* MUZ 2797A, B; a complete adult fish (text-fig. 19 (skull only); Pl. 7, fig. 2).

*Paratypes.* MUZ 2798; 2799A, B, C; 2126AB (this comprises all the known material).

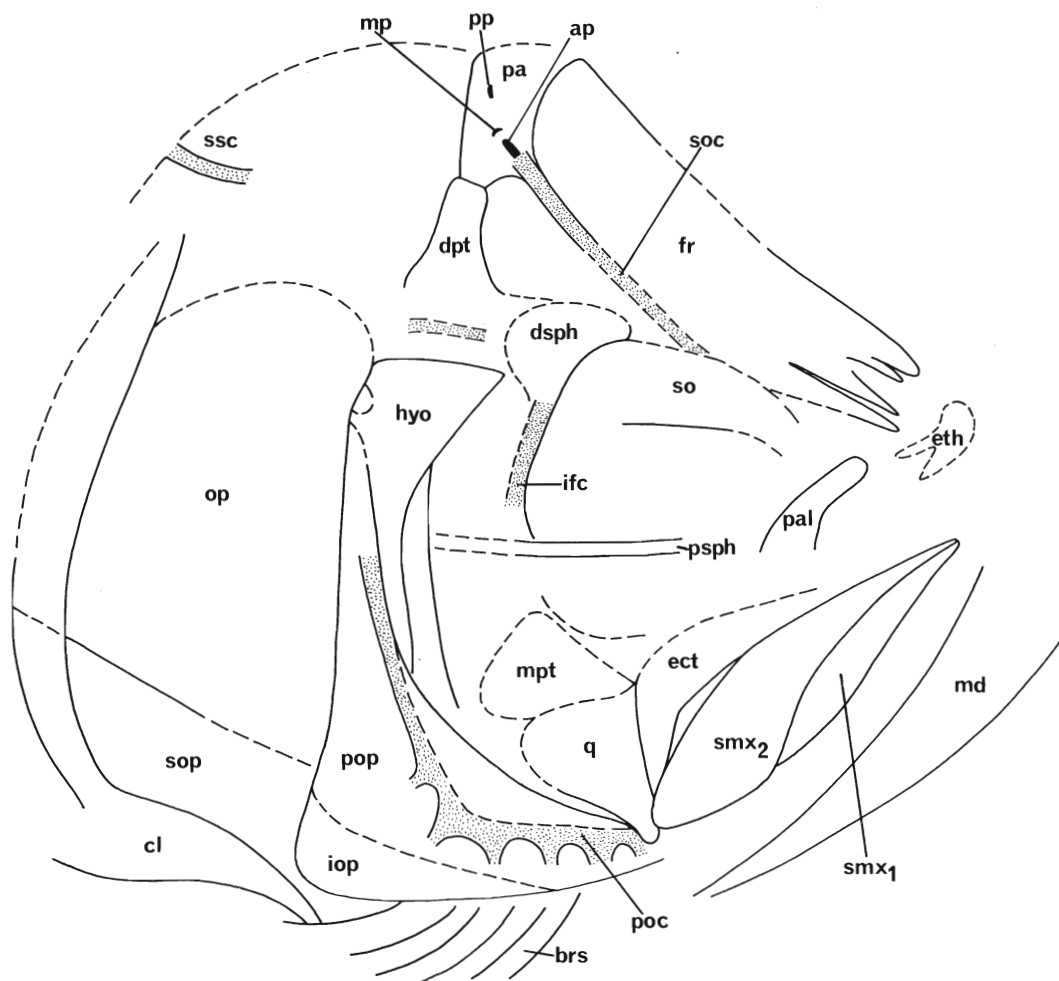
*Horizon.* Koonwarra fish-bed, L. Cretaceous.

*Locality.* Koonwarra, Victoria, Australia.

*Origin of Name.* The generic and family name is derived from the hamlet of Koonwarra. (Aboriginal: 'Place of Swans'.) The specific name refers to the hand-like suture between ethmoid and frontal bones.

*Description.* Only one paratype, MUZ 2799 (Pl. 8, fig. 1), is in any way complete, but is poorly preserved regarding details. MUZ 2126 is a headless trunk (Pl. 8, fig. 2) and MUZ 2798 (text-fig. 18; Pl. 7, fig. 3) is represented by a distorted skull, several ribs, pectoral and pelvic fins. Although the holotype is about four times the size of any of the paratypes it is not possible to distinguish differences which may be considered specific. MUZ 2797AB, is, therefore, regarded as the adult form of the paratype material.

*Skull Roof.* The frontals (fr.) are narrow anteriorly, but expand as they pass back over the orbit. They are of large size and extend posteriorly beyond the level of the orbit. The shape of the suture between the frontals is not known accurately. The posterior margin of one frontal is visible in 2798 and is comparatively straight (text-fig. 18). The anterior region is very deeply serrated, giving a dactylate appearance, the processes increasing in size laterally. This condition is visible in 2798, but more clearly in 2797A where there are five processes on each frontal, the most lateral being spatulate whereas the mesial ones are pointed



TEXT-FIG. 18. *Koonwarria manifrons*, MUZ 2798, slightly distorted skull in lateral view,  $\times 7$ .

(text-fig. 19). The frontals are slightly excavated interorbitally and this may be a mucous cavity as in some living teleosts (Patterson, pers. comm. 1968). Immediately anterior to the digitate margin of the frontals is the ethmoid (eth.). The exact shape of this element is not known as it is considerably crushed and its margins have been destroyed. The posterior border is partly visible, however, and is serrated, possibly not as deeply as the anterior frontal margin. There is no trace of the ethmoid commissure (text-figs. 18, 19).

A single large supraorbital (so.) is present on each side, convex mesially and concave laterally. It is 4 times as long as it is broad, and contacts the lateral margin of the frontal along a curved facet. This element is clearly visible in 2797A (text-fig. 19).

Immediately anterior to that facet lies another which is occupied by the small nasal (na.). This element is bounded posteriorly by the frontal and supraorbital, mesially by the frontal, and laterally by the antorbital.

The antorbital (ant.) is of comparable size to the nasal and may bear an antorbital branch of the infra-orbital sensory canal, but this is uncertain, due to poor preservation. This bone seems to be rectangular, but may not be completely exposed (text-fig. 19).

The posterior bones of the skull roof are poorly preserved in the examples collected to date, and difficult to interpret; however, 2798 offers the most detail (text-fig. 18). The dermosphenotic (dsph.) is seen in

2797A and 2798, and although not entirely clear, appears to be semicircular, abutting against the supra-orbital and the frontal. A concavity on the frontal receives the convex mesial margin of the dermosphenotic.

The parietal (pa.) is a short bone, broader than long, with a small anterior process extending into the posterior region of the corresponding frontal. It resembles that of *Pachycormus macropterus* (Lehman 1966) by possession of the anterior process and in that the supraorbital sensory canal enters the parietal via this process. The dermosphenotic (dpt.) runs posteriorly from the dermosphenotic around the convex posterior margin of the frontal to meet the parietal along what is apparently a very short suture.

The short extrascapular (ext.) is poorly preserved, but has a well-curved posterior margin. (Skull reconstruction text-fig. 33.)

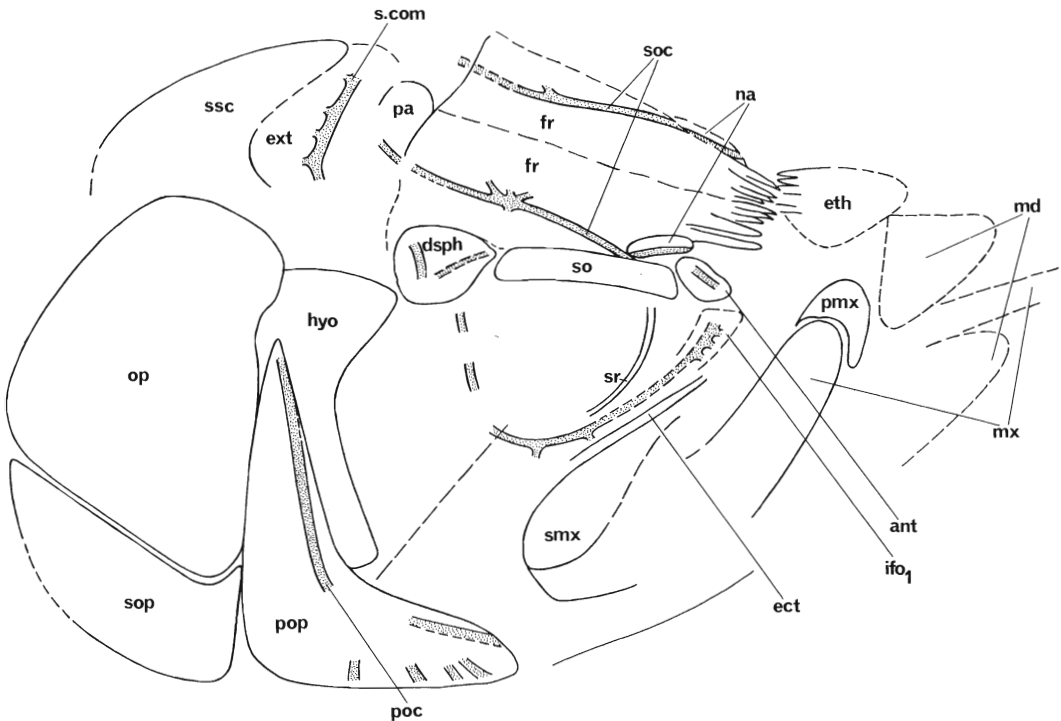
**Cheek Region.** The premaxilla (pmx.) is visible in 2797A, where it is in contact with the extreme tip of the maxilla. It is parabolic in shape and meets the maxilla along a strongly curved suture.

The maxilla (mx.) is a long, curved strip of bone which narrows anteriorly and appears to be entirely toothless. On its dorsal surface it carries 2 supramaxillae. The anterior supramaxilla (smx<sub>1</sub>) is lanceolate, being much longer than deep, and the posterior supramaxilla (smx<sub>2</sub>) is much stouter and anteriorly overlies smx<sub>1</sub> with a slender, tapering process similar to that element in *Leptolepis*. A sclerotic ring is present within the orbit.

The position of the infraorbitals is apparent only from the sensory canal which traverses them. No outlines are known, but there seems to be a large infraorbital at the postero-ventral margin of the orbit. It is not possible to determine whether or not a postorbital element was present.

The opercular (op.) is visible in 2798 and 2799A, B, but is most clearly seen in 2797A, B. It is large and quadrilateral, being  $1\frac{1}{2}$  times as high as it is long. The rear margin is convex posteriorly, and the dorsal edge curves ventro-anteriorly to the anterior rim. The latter is very nearly straight, and close to it, about one quarter of the way down, lies the facet for the hyomandibular process opercularis (text-fig. 19).

The opercular meets the subopercular (sop.) with an oblique suture, which runs ventro-anteriorly. The subopercular is about one-third as deep as the opercular.



TEXT-FIG. 19. *Koonwarria manifrans*, MUZ 2797A, holotype. Skull,  $\times 1.6$ .

The interopercular (iop.) is a triangular element tapering forward beneath the preopercular (text-fig. 18).

The preopercular (pop.) is preserved to some extent in all the specimens except 2126AB. It is a robust, sharply angled element, broadest in the angle and tapering rapidly on each limb. The vertical limb is longer than the horizontal (text-figs. 18, 19).

*Lower Jaw.* This is very poorly preserved in the material to hand. Only the anterior region is known, and that imperfectly, in 2799B and 2797A, but its dorsal margin rises steeply, much as in *Leptolepis*. Dentition is not determinable, but there are certain indications that minute teeth may have been present on the anterior region of the jaw, although this may be merely eroded bone. Insufficient material is available to decide whether or not a gular plate was present (text-fig. 19).

*Sensory Canal System.* The supraorbital sensory canal (soc.) runs through nasal, frontal, and parietal bones, but as the nasals are damaged in the available material, this part of the canal is not well preserved.

The frontal canal is visible in 2797A, 2798, and 2799B. It traces a linear path in the anterior half of the element and then curves in a very shallow arc until reaching the parietal suture. There are two tubules present in 2799B, one at the posterior part of the linear portion and one at the beginning of the arc. Both of these are directed mesially. In 2797A a small third tubule is present. On entering the anterior process of the parietal the canal terminates almost immediately in a small shallow groove, the anterior pit-line (ap.) (text-fig. 18).

The specimens are poorly preserved in the infraorbital region and little may be said of the infraorbital sensory canal (ifc.). Its path is seen in part beneath the orbit in 2797A but only 2 tubules are preserved. Parts of the canal are visible on what appear to be lachrymal (ifo.) and antorbital elements in the same specimen, and there appear to be 4 branches on the lachrymal. In 2798 a section of the canal may be seen on the last infraorbital (text-fig. 18). The canal pathway in the dermosphenotic is poorly preserved (2797A), but there is a small antero-dorsal branch, as well as the main canal to the dermopterotic.

*Cephalic Division of the Main Lateral Line.* The track of the canal on the dermopterotic is visible in 2798, but not in detail. It runs posteriorly in a straight line from the dermosphenotic suture and then, on entering the extrascapular, turns mesially through 90°. 2, or possibly 3, tubules are visible in 2798 about this angle. The canal is visible on the posterior of the suprascapular (text-fig. 18). Slightly posterior to the anterior pit-line there is a similar groove at right angles, representing the middle pit-line (mp.). Postero-mesially there are 2 minute projections of matrix, all that remains of the posterior pit-line (pp.) (text-fig. 18). 2799AB, and 2798 (text-fig. 18) exhibit 6 branches of the preopercular canal at the level of the angle and on the lower limb. The main canal runs approximately parallel to the anterior margin, closer to it than to the posterior. The branch tubules are fairly long, nearly reaching the posterior margin of the preopercular. No traces of pit-lines are present on this element.

The mandibular sensory canal (mdc.) is extremely poorly preserved.

*Lateral Line.* This is not visible in any specimen due to poor scale preservation.

*Hyoid Arch.* As the known skull material is comparatively undisturbed, little is known of the hyoid arch, except for details of the hyomandibular and the branchiostegal rays.

The hyomandibular (hyo.) is preserved in 2797A and to some extent in 2798 (text-figs. 18, 19). The head of the element is of a broad fan shape which narrows ventrally and then expands again as it runs ventrally along the anterior margin of the preopercular, ending at the angle of the latter. Much of the posterior ventral part of the hyomandibular is hidden beneath the preopercular. The hyomandibular shaft exhibits dorso-ventral rugae.

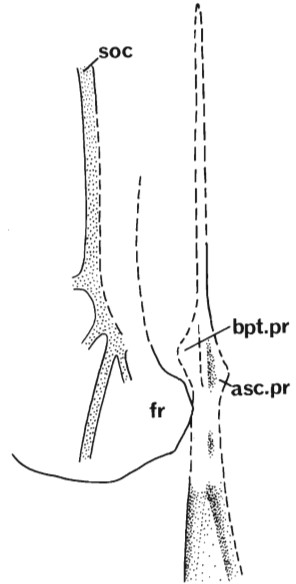
There are 16-17 crescentic branchiostegal rays (brs.), the most posterior rays being more expanded and sturdier than the anterior ones.

*Palate.* 2798 exhibits a small but sturdy arched process in the antorbital region, but the rest of the bone has been lost (text-fig. 18; Pl. 7, fig. 3). This process bears rugae, expands posteriorly, and is almost certainly the maxillary process of the palatine (pal.). It resembles that process in *Perca fluviatilis* (Goodrich 1909, fig. 456) and *Ichthyokentema purbeckensis* (Griffith and Patterson 1963, fig. 10).

The quadrate is seen in outline in 2798 as a small triangular element with its apex pointing ventrally, situated between the posterior margin of the mandible and the anterior limb of the preopercular. There is a groove aligned in a postero-dorsal direction which may be for articulation with the symplectic. The quadrate is also vaguely visible in 2799B.

*Neurocranium.* Of the neurocranium only the parasphenoid (psph.) is preserved, but in 2799B this element has been slightly displaced on its long axis and some structure is visible (text-fig. 20). The element is partly visible as an imprint. It is long and slender and along its axis there is the imprint of a groove, narrow and shallow anteriorly, but becoming deeper and broader posteriorly. This terminates at the posterior margin of the orbit. Posterior to this there is the imprint of a very small longitudinal groove and beyond this is the long, cone-like infilling of the tunnel between the posterior processes of the parasphenoid. These processes taper posteriorly and are bridged by a thin film of bone which formed the roof of the tunnel and probably the floor of the myodome. On one side of the impression are the broken bases of 2 processes. The anterior and narrower of the 2 may represent part of the basiptyergoid process (bpt. pr.) and the broader, posterior flange is probably part of the ascending process (asc. pr.). Regrettably no other parts of this important element are preserved.

*Pectoral Girdle and Fins.* The cleithrum (cl.) is a sigmoid element, broadest posterior to the margin of the opercular and extending ventro-anteriorly as a flanged, sinuously tapering process. Two-thirds of the way up the posterior margin of the opercular the cleithrum articulates with the supra-cleithrum along an almost vertical suture. The later expands dorsally, but its exact shape is not known. In 2798 the suprascapular (ssc.) is very poorly preserved and has a convex posterior margin. At the postero-ventral margin of the subopercular there is a blurred impression of an approximately hourglass-shaped element, with its long axis inclined postero-dorsally. The impression is probably incomplete and may represent the scapular, the anterior embayment being the scapular foramen. The pectoral fins are large and the lepidotrichia reach as far as the origin of the pelvic fins (2799B). There are 12–14 lepidotrichia which possess very long proximal joints. In 2797B more than half the total length of the fin is composed of these segments. The rays bifurcate twice distally, although the anterior ones may branch once only, and the first ray not at all.



TEXT-FIG. 20. *Koonwarria manifrons*, MUZ 2799B, parasphenoid in dorsal view,  $\times 6$ .

*Pelvic Girdle and Fins.* In 2798 this consists of a pair of bones, each broadly circular at its articulation with the fin-rays, then narrowing sharply and gently expanding anteriorly as a slender shaft (Pl. 7, fig. 3). Their length is about three-quarters of the length of the lepidotrichia. There are 10 lepidotrichia per fin, but in 2797B the fins have become partly detached from the girdle and it superficially appears that one fin has 14 rays. The pelvic fins are approximately the same length as the pectorals.

*Unpaired Fins.* The anal fin (Pl. 7, fig. 2; Pl. 8, figs. 1, 2) is long-based, extends almost to the beginning of the lower caudal lobe, and bears at its origin a single large scale. The fin is shaped like an elongate triangle with the hypotenuse as the body margin, and contains 24 lepidotrichia, each with a long proximal joint. The number of radials equals that of the lepidotrichia and the former are long and slender, reaching almost to the level of the distal margin of the haemal spines. The rays bifurcate in similar fashion to those of the pectoral fin.

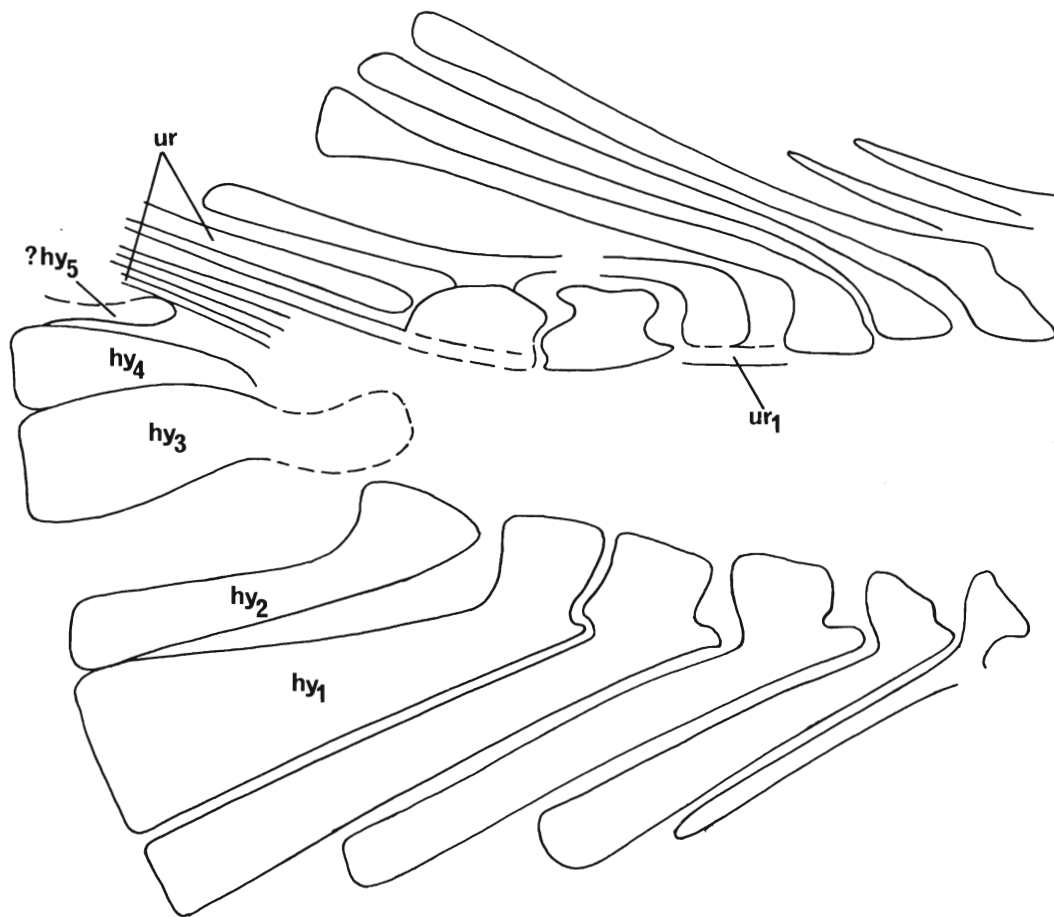
The cleft caudal fin is most clearly visible in 2797A but is seen to some extent in 2799C and 2126A. In the last two small specimens the tail is naturally fairly slender, but in the adult 2797AB, it is large and powerful (Pl. 7, fig. 2). Each lobe of the fin is composed of 11 segmented robust principal rays, each with a short proximal segment. The rays are branched distally, with the exception of the outermost principal ray of the ventral lobe and possibly also the 3 outermost lepidotrichia of the dorsal lobe. Preservation of the latter rays is, however, very poor and their exact structure is indeterminate. The proximal region of the caudal rays was probably covered by scales as these latter appear to be in place and not merely disturbed from the body. Weakly developed unbranched rays are present at the origins of dorsal, anal, and caudal fins.



The dorsal fin is a broad triangle consisting of 13 rays with very long proximal joints, often half as high as the total height of the fin itself (Pl. 8, fig. 2). The number of radials is probably the same as the number of fin-rays, but only an incomplete series of radials is known (2799B).

The pelvic fins lie closer to the pectorals than to the anal fin. The anal stretches back almost to the caudal fin and the dorsal fin lies at, or just anterior to, the level of the origin of the anal fin.

*Axial Skeleton.* In 2126AB (Pl. 8, fig. 2) and 2797AB (Pl. 7, fig. 2) there are true centra which are not present in 2799ABC, or 2798. They are perfect cylinders, the diameter being twice the thickness, and the perforation for the notochord occupying a little more than half of that diameter. 50 centra are present in 2797A, but one or two more are probably obscured by opercular and cranial elements. Exceedingly slender neural spines are present in the anterior region and stronger supraneural elements are present dorsally (Pl. 8, fig. 1). These latter bones disappear at the level of the dorsal fin. Dorsal intermuscular bones (epineurals) occur anteriorly. Posteriorly there is a series of fused neural arches and spines, one attached to the anterior portion of each centrum. Ventrally there is a well-formed series of long, gently curved, slender ribs which extend posteriorly as far as the origin of the anal fin and reach almost to the ventral margin of the body. They are succeeded posteriorly by a series of fused haemal arches and spines, one to each centrum. The caudal region represents a development of the type known, for example, in *Wadeichthys* and *Archaeomaene*. Although the only reasonably preserved caudal structure is that of 2799C (text-fig. 21), a little may be made of this area in 2797A. In the latter the first 2 hypurals are carried



TEXT-FIG. 21. *Koonwarria manifrons*, MUZ 2799C, caudal skeleton,  $\times 10$ .

on a single centrum which is longer than its anterior neighbour. This larger centrum may be regarded as the first ural centrum. In 2799C the first hypural ( $hy_1$ ) is larger than the second, and bears an anteriorly directed process proximally. Hypural 2 ( $hy_2$ ) is narrow and there is a considerable space between it and hypural 3 ( $hy_3$ ). The latter articulates with ural centrum 2 and is a curved structure, somewhat similar to the corresponding bone in *Elops* (Nybelin 1963) but rather larger. Beyond this there is a smaller hypural ( $hy_4$ ) which is succeeded by a bone which may be a fifth hypural ( $?hy_5$ ). The dorsal caudal skeleton is only partly preserved but the remains of the uroneurals ( $ur.$ ) may be seen as elongate elements lying parallel to each other along the posterior centra of the caudal axis in 'en echelon' fashion. As 2799C is a juvenile there is no centrum ossification, but centra are visible in the holotype.

*Squamation.* The scales are cycloid and without enamel (Pl. 8, figs. 3–5). There is not enough well-preserved material to count the number of oblique rows accurately but from 2797A this is estimated as being 52. An estimated (from 2797A, posterior trunk) 15 longitudinal rows of scales are present. The squamation is clearly visible in the axial region above the pelvic fin of 2798, above the anal fin of 2126A, generally on 2797AB, and faint indications are present on the anterior part of the notochordal canal of 2799B.

Isolated *Koonwarria* scales are fairly common and exhibit a wide size range. They are oval to rounded-rectangular, with the basal region much larger than the apical. Fanning out anteriorly are the folded basal radii which give the anterior margin of the scale a crenellated appearance. These usually number between 5 and 8, but there are occasionally more. The large basal region is covered with fine circuli, broken by the folds of the radii. The laterobasal angle is well rounded and is about  $100^\circ$ . The exposed apical region in a perfect scale takes the form of a short tongue extending posteriorly from the nucleus. It is completely free of circuli and radii, but may have exceedingly faint radial markings in a few cases. This area is, in 1 or 2 specimens, patterned with dark stippling, but no marginal spines characteristic of ctenoid scales have been observed.

I consider Pl. 8, fig. 4 to represent a slightly aberrant example of a *Koonwarria* scale, perhaps pathological. It is not greatly different from the typical scale shown in Pl. 8, fig. 5.

*Measurements of Holotype.* MUZ 2797AB

	mm
Body length (from rear of opercular)	176
Head length	73
Total length (incl. tail)	294
Body depth (max.) (approx. correction)	90
Head depth (max.) (approx. correction)	60
Depth of caudal pedicle	35
Length of anal fin base	54

*Remarks.* This new material bears a certain overall resemblance to the Upper Jurassic genera *Thrissops* (and its close relatives) and *Mesochlupea* (see Gaudant 1968). The likeness is due basically to the shape of the body and length of the anal fin in all 3 genera. When considered in detail, however, it is evident that there is no close relationship between *Koonwarria* and *Thrissops* or *Mesochlupea*. The skull anatomy, sensory canal patterns, fin positions, and fin-ray counts are very different in *Koonwarria* and *Mesochlupea*; while the *Thrissops* group differs from *Koonwarria* in fin positions, fin-ray counts, presence of well-developed teeth, sensory canal pathways, and shape of the preopercular.

It seems that the resemblances between these genera are superficial and due to convergence, which is to be expected in their evolution from the Pholidophoriformes. There is, however, a considerable weight of evidence for the derivation of *Koonwarria* from archaeomaenids similar to *Archaeomaene* and *Madariscus*. Nevertheless, although the basic archaeomaenid pattern is retained in *Koonwarria* (text-figs. 33, 37) it does differ from the pattern in the following ways.

1. The development of a compact caudal skeleton with greatly differentiated hypurals and elongate uroneurals.

2. The separation of the nasals by the frontals and the reduction of the former.
3. Cycloid scales which have lost all vestiges of enamel.
4. The presence of well-developed centra in the adult.
5. The absence of preopercular pit-lines and the reduction of parietal pit-lines.
6. The absence of fulcra.
7. The presence of epineural intermuscular bones.
8. The different shape of the preopercular.
9. The absence of keeled scales on dorsal and ventral body-margins.
10. The small size of the parietals.
11. The absence of teeth (or their extreme reduction).
12. The obliquity of the opercular/subopercular suture.
13. The different shape and greater extent of the anal fin.
14. The larger number of lepidotrichia in all fins.
15. The closer proximity of the pectoral and pelvic fins.

It is evident from this list that *Koonwarria* may be entirely separated from the rest of the archaeomaenids. In particular, items 1 to 7 are features which have been regarded by many authors as appertaining to teleostean fish. With the exception of the caudal skeleton most of the features listed are not reliable indicators of evolutionary grade, being too widespread, but Patterson (1968) gave the following definition of a teleost:

'Actinopterygian fishes in which the vertebral centra are perichordally ossified, the lower lobe of the caudal fin is primitively supported by two hypurals articulating with a single centrum, and in which the ural neural arches are modified into elongate uroneurals, the anterior uroneurals extending forwards on to the pre-ural centra.'

By this definition it is evident that *Koonwarria* may be regarded as having reached the teleostean grade of organization. Possibly the only obvious 'primitive' feature of *Koonwarria* is the presence of parietal pit-lines, cf. *Thrissops formosus* Saint-Seine 1949 (*Allothrissops salmoneus*, Nybelin 1964), although these are much reduced. There is no real case for the retention of *Koonwarria* within the Archaeomaenidae (in the redefined sense) except on the basis of ancestry. It is a somewhat similar problem to that encountered in the pholidophorid-leptolepid evolutionary line. While it is apparent that the younger group in each case is probably derived from the older, the problem is where to draw the dividing line (Schaeffer 1965). In this case it is apparent that the advanced characters outweigh the primitive ones and that *Koonwarria* should be regarded as a teleost.

As *Koonwarria* does not belong with the archaeomaenids it is necessary to create a new taxon to accommodate it. I propose, therefore, the family name *Koonwarriidae*, to be placed in the Order Clupeiformes. It seems likely that the archaeomaenids and koonwarriids inhabiting the fresh waters of the 'south-eastern Australian lake' in the Lower Cretaceous were extinguished by marine transgressions during the Middle and Upper Cretaceous. This is by no means certain, and archaeomaenids and koonwarriids may well have survived into the late Mesozoic or into the Cainozoic. Should teleosts be discovered in Australian mid-upper Cretaceous freshwater sedi-

ments, these should be considered in the light of possible koonwarriid and, therefore, archaeomaenid ancestry. With regard to this statement, it is necessary to consider the phyletic aspects of *Koonwarria*.

Patterson (1967) has stated that there is no evidence that the teleosts are not descended from *Pholidophorus* or even a particular species of that genus. It seems that *Koonwarria* represents another lineage achieving the teleost grade of organization, but it is nevertheless close to the family Pholidophoridae (Nybelin 1966) in its archaeomaenid ancestry (Gardiner 1960). The exact relationship between the Pholidophoridae and the Archaeomaenidae is unknown, but from the study of *Wadeichthys* it is likely that the two families have common ancestry in the parasemionotids. Exactly where in geological time the divergence between pholidophorids and archaeomaenids occurred is as yet unknown but the Upper Triassic is a reasonable supposition. Although the Koonwarriidae are derived from the Archaeomaenidae, the exact lineage of *Koonwarria* from within the Archaeomaenidae may only be solved by the finding of further freshwater Jurassic and Lower Cretaceous forms in Australia.

In conclusion, the finding of *Koonwarria* does not add to the evidence for major polyphyly of the teleosts, but indicates another lineage crossing the halecostome-teleost boundary. Patterson (1967) stated: 'It is my opinion that this crossing was on a narrow front, the most likely candidates being the leptolepids, the lycopterids and the elopids.'

I believe that the family Koonwarriidae nov. may be added to those 3 families.

#### Order CLUPEIFORMES

#### Family LEPTOLEPIDIDAE

*Diagnosis.* Woodward 1895, p. 500.

*Historical Summary.* The first figures of *Leptolepis* were published by Knorr in 1755, but it was not until 1832 that Agassiz gave the name *Leptolepis*, followed in 1833 by the erection of many species within the genus. Most nineteenth-century work was summed up by Woodward in 1895. Woodward (1895a) defined 3 species, *L. talbragarensis*, *L. gregarius*, and *L. lowei*, from the ?Jurassic of Talbragar, N.S.W., Australia, and in 1900 Hall described a further Australian form, *L. crassicauda*, from the Jurassic (now thought to be Lower Cretaceous) of Casterton, western Victoria (Pl. 9, fig. 3).

*L. nathorsti* was described by Woodward in 1900 from dissociated skull fragments in the Jurassic of Spitzbergen, and in 1903 Sauvage noted *L. voithi* from the Upper Jurassic (Virgulian–Upper Kimmeridgian) of Lerida, Spain. Woodward (1907a) erected *L. valdensis* from the Lower Cretaceous Weald clay of Sussex, England, and in 1911 *L. formosus*, *L. brevis*, and *L. attenuatus* were defined by Traquair from beds of the same age at Bernissart, Belgium. Bassani and d'Erasmus (1912) noted *L. brodiei* Agassiz and *L. voithi* Agassiz from the Cretaceous of Castellamare, Italy; and d'Erasmus (1915) recorded the same species at Pietraroia, Italy.

Woodward (1917) described *L. brodiei* from the English Upper Jurassic (Purbeck), and in 1923 Gregory reported *L. (?) euspondylus* from the Jurassic of western Cuba.

Wade (1930) noted the Australian forms, and in 1934 d'Erasmus mentioned part of a skull of *Leptolepis* from the Neocomian (Lower Cretaceous) of Patagonia.

*L. congolensis* from the Cretaceous of Coccobeach, French Gabon, was described by Arambourg and Schneegans in 1935, who found that the associated fauna could be correlated with a fauna of Cretaceous age from Bata, Spanish Guinea. They noted (see also Arambourg 1935) that species of *Leptolepis* fell into two groups, those of the Cretaceous being closer to the typical 'teleost' condition. Arambourg stated in 1935: 'Ces poissons constituent donc, avec *Dastilbe* et *Parachanos*, un groupe de transition qui établit la continuité entre les formes téléostéennes terminales d'un type d'organisation depuis longtemps orienté dans le sens de divers modes clupéiformes.' Also in 1935(a) Arambourg redefined and figured the species previously known as *L. bronni* Agassiz as *L. coryphaenoides* Bronn, and referred to synonymy *L. constrictus*, *L. pronus*, *L. pachystetus*, and *L. affinis*, following Woodward (1895).

The first really detailed skeletal study of *Leptolepis* was carried out by Rayner (1937) on *L. coryphaenoides* (*L. bronni*), with particular stress laid on skull anatomy. Also mentioned was a ?*Leptolepis* from the Triassic of Seefeld, Austria, in the collection of Professor D. M. S. Watson. In 1938 d'Erasmus described a leptolepid otolith from the Brazilian Cretaceous and also indicated that *Haplospondylus clupeoides* Cabrera (1927) from the Lower Cretaceous of Patagonia is related to or synonymous with *Leptolepis* (see David 1941). Dolgopol de Saez noted *L. australis* from the Tithonian (Upper Jurassic) of Argentina in 1939 and in 1940 described *L. patagonicus* and *L. argentinus* which are of similar age. Boni (1940) described *L. chiesai* from the Cenomanian (Upper Cretaceous) of Gebel Garian, Libya.

Wade (1941) grouped Woodward's (1895a) Australian species together as *L. talbragarensis*, on the basis of cranial structure. David (1941) described *L. nevadensis* and used its relationships to European and African leptolepids to date the formation whence it came as Lower Cretaceous or possibly younger. These relationships were based mainly on tail structure. In 1941 and 1942 Takai described *L. longicephalus* from the M.-U. Cretaceous Sungari series of Manchoukuo, but also stated (1942) '... this species probably belongs to the Cretaceous species group represented by *L. brodiei* Agassiz' (see Arambourg 1950). Dunkle (1942) defined *L. schoewei* from the Upper Lykins formation (?U. Triassic-L. Jurassic), Colorado, U.S.A.; and White, T. E. (1942) proposed that *L. (?) euspondylus* be reclassified as the new genus *Luisichthys viñalensis*. In 1944 Takai referred *L. longicephalus* to the new genus *Sungarichthys*. D'Erasmus (1946) noted *L. neocomiensis* Bassani from Comeno, Italy, and also erected *L. checchiai*. *L. neumayri* was referred to *Leptosomus* (Myctophoidi: Lehman 1966).

Schaeffer (1947) defined *L. bahiaensis* from the Upper Cretaceous of Brazil and also gave information on other species of *Leptolepis*. Sainte-Seine (1949) described *L. sprattiformis* from the Kimmeridgian (Upper Jurassic) of Cerin, France, and referred to synonymy *L. knorri*, *L. dubia* (*dubius*), *L. latus*, *L. macrolepidotus*, and *L. clupeiformis*. Also *L. voithi* was defined to include *L. contractus*, *L. polyspondylus*, and *L. paucispondylus*, following Woodward (1895). All of these species are from the Kimmeridgian of France and Bavaria. Dolgopol de Saez (1949) described *L. leanzai* from the Upper Cretaceous of Argentina.

Arambourg (1950) erected the genus *Clupavus* (Clupeoidei: Arambourg and Bertin 1958) for *L. brodiei* and placed within the genus most of the species from the L. Cretaceous, including the following: *L. formosus* Traquair, *L. neocomiensis*, *L. neumayri* Bassani, and *L. congolensis* Arambourg and Schneegans.

Dunkle and Maldonado-Koerdell (1953) described *L. tamanensis* from the Lower Cretaceous of San Luis Potosi, Mexico, and also stated that *L. schoewei* is from the Todilto limestone (Oxfordian–U. Jurassic) of New Mexico. Arambourg (1954) described *Clupavus* cf. *neocomiensis* (Bassani) 1882 from the Upper Cretaceous (Lower Cenomanian) of Jebel Tselfat, Morocco, and included part of *L. brodiei* (as understood by Woodward 1895) within the synonymy. Arambourg stated ‘. . . les auteurs ont continué à attribuer au genre *Leptolepis* divers petits poissons clupéiformes des formations crétacées plus ou moins voisins, en apparence de *L. Brodiei*!’. [Footnote]: ‘<sup>1</sup> Ce sont: du Purbeckien *L. formosus* Traq., *L. brevis* Traq., *L. attenuatus* Traq., du Wealdien, *L. valdensis* Woodward; du Crétacé inférieur ou moyen, *L. pygmaeus* Costa, *L. neumayri* Bass. et d’Erasmus, *L. congolensis* Aramb. et Schneeg., *L. chechchai* d’Erasmus.’ *L. chiesai* Boni (1940) was referred to the genus *Parachanos*.

Liu (1957) noted a leptolepid from Eastern Asia and provisionally named it as *Leptolepis* sp., the provenance of the specimen being unknown.

Santos (1958, 1960) described *L. diasii* from the Cretaceous of the Serra do Araripe, Brazil; and Gardiner (1960) defined *L. africana* from a bore core in the ?Triassic of Mandawa, Tanzania.

Casier (1961) monographed the ‘Eo-Cretaceous’ fish fauna of the Congo, *Leptolepis* and *Clupavus* being noted as occurring together. 2 new species of the latter were described, *C. yamangiensis* and *C. longicaudatus*; as well as *Leptolepis* (?) *minor*. Ferreira (1961) noted *Leptolepis* aff. *sprattiformis* and *Clupavus* aff. *neocomiensis* from the Cretaceous of Portugal. These genera occur together in the Turonian at Alcantara, *L.* aff. *sprattiformis* also being represented in sediments of Cenomanian age.

Nybelin (1961) described *L. dubia* from the Upper Jurassic of Eichstätt, Germany, and in 1962 redefined the species *L. bronni* as 2 species, *L. coryphaenoides* and *L. normandica*, based on differences in the skull and sensory canal pattern. Nybelin (1963) described several actinopterygian tail skeletons, including those of *L. dubia*, *L. coryphaenoides*, and *L. normandica*, introducing a new form of terminology for the caudal elements.

In 1963 Griffith and Patterson stated ‘. . . The Middle Triassic specimen mentioned by Rayner (1937:46) is indeed a leptolepid, . . . the age of *Leptolepis africana* Gardiner (1960:314) is definitely Upper Triassic.’ (Lehman (1966) summarized the sub-order Leptolepioidei. *L. nevadensis* (David 1941) was included in *Clupavus* and it was stated that in all probability the species of *Leptolepis* from the Lias and those from the Upper Jurassic belong to different genera.

Patterson (1967), in a discussion of teleost phylogeny, debated the supposed *Leptolepis*–*Clupavus*–Clupeoidei lineage and concluded that *Clupavus* did not give rise to the teleosts. Wenz (1967) described *L. coryphaenoides* in detail and referred *L. normandica* to synonymy. Gardiner (1967a) discussed the evolution of the actinopterygian preopercular and included a section on the Leptolepiformes. He stated that: ‘The Leptolepididae are known from the Middle Triassic (Ladinian) . . .’.

Arambourg (1968) proposed that the type species of *Clupavus* should be the new species *C. maroccanus*, from the Cretaceous of Jebel Tselfat, Morocco, which he had earlier (1954) described as *C. cf. neocomiensis*. The latter species, according to Arambourg (1954), had been synonymous with *C. brodiei*.

Patterson (1968) figured the caudal regions of *L. coryphaenoides* and *L. dubia* and discussed the evolution and terminology of the teleost caudal skeleton. A new definition of the Teleostei was given.

Leptolepid otoliths have been described by a number of authors including Frost (1924, 1926), d'Erasmus (1938), Martin and Weiler (1954, 1957), Schröder (1956), Stinton and Torrens (1968).

Most authors have described such otoliths as *Otolithus (Leptolepidarum)* spp., but Stinton and Torrens (1968) have named 3 otolith species under the name *Leptolepis*, these being *L. tenuirostris*, *L. densus*, and *L. roddenensis*, all from the Bathonian, Middle Jurassic, of southern England. As no associated skeletal material is known, it is probable that these 3 species will be referred to other species known from skeletal remains, at some future date.

With reference to the occurrences of *Leptolepis* in Mexico, Dunkle (pers. comm.) has stated: 'From personal experience in most of these noted sites, I can vouch for the fragmentary nature of the majority of the remains and am inclined to ignore their published taxonomic assignments.'

#### Genus. LEPTOLEPIS Agassiz 1832

*Synonymy.* See Gardiner (1960), d'Erasmus (1915), and Lehman (1966).

*Diagnosis.* Woodward 1895, p. 501.

*Type Species.* *Leptolepis coryphaenoides* (Bronn).

#### *Leptolepis koonwarri* sp. nov.

Plates 9, figs. 1, 2, 10–12; 15, figs. 1, 3; 16, figs. 1, 13; 17; 18, figs. 1–3; text-figs. 22–32, 35

*Diagnosis.* Typically a moderate-sized species, but reaching an observed maximum length of 145 mm. Length of head contained 5 times in body length; preopercular with 4 large branches of sensory canal; postorbital absent. No teeth or maxillary serrations; vertebrae pierced by well-developed but constricted notochordal canal; intermuscular bones present anteriorly. 8 unfused hypurals; dorsal fin arises opposite or very slightly anterior to level of pelvic fins; anal fin situated close to caudal fin. Scales cycloid, exposed portion of scale may have radiating grooves.

*Holotype.* MUGD 3649 (Pl. 9, fig. 1).

*Paratypes.* MUZ 2579, 3029–3034, 3098–3099, 3103–3107, 3111–3118. MUGD 3634–3643, 3652–3653. P.24670, 24678, 26129.

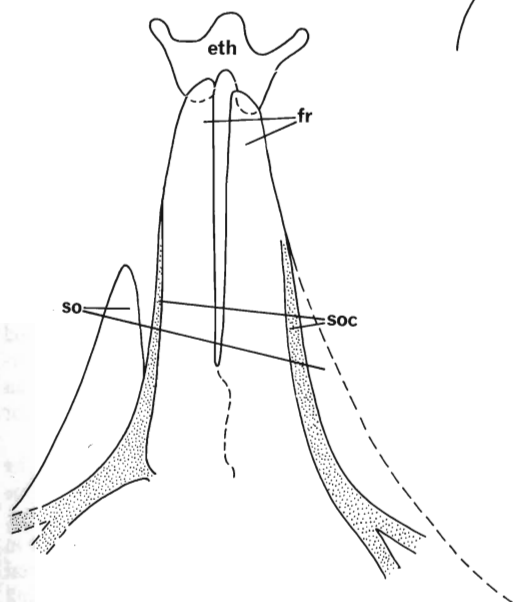
*Material.* A large number of specimens in the following collections: MUGD; MUZ; NMV; MDV; PMD.

*Horizon.* Koonwarra fish-bed, L. Cretaceous.

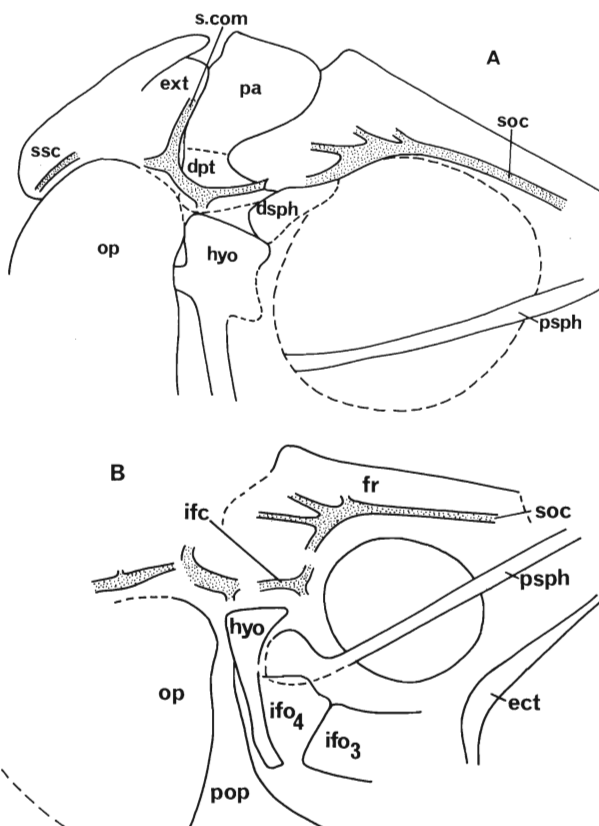
*Locality.* Koonwarra, Victoria, Australia.

*Origin of Name.* The specific name originates from Koonwarra, the type-locality. The place-name ending 'ensis' has not been used as Koonwarra is an aboriginal word meaning 'place of swans', only secondarily used as a place-name.

*Description.* The skull is preserved in a number of specimens but in many cases oxidation and seepage after fossilization have destroyed the outlines and composition of the individual bones. The premaxilla (pmx.) (text-fig. 35) is a small, toothless, lenticular element, which fits into a concave facet on the anterior ventral margin of the maxilla. The shape of the nasal (na.) is not well known but each one lies alongside a frontal, abutting against the ethmoid anteriorly and the supraorbitals posteriorly. The ethmoid (eth.) of *L. koonwarri* (text-fig. 22), is seen from above in MUGD 3643 and is visible in MUZ 3105 AB. In 3636A it may be seen in isolation. In MUGD 3643 the ethmoid (mesethmoid?) (rostral—Wenz 1967) resembles that of *L. coryphaenoides* (Rayner 1937, Wenz 1967). Arambourg (1954) described the mesethmoid of *Chupavus neocomiensis* as '... courte, robuste ...', and this makes up most of the dorsal region of the snout in that species, the frontals terminating at the anterior rim of the orbit. The ethmoid of *L. koonwarri* is very much smaller than in *C. neocomiensis* as the frontals extend further anteriorly. The frontal (fr.) is narrow anteriorly between the nasals and expands posteriorly, being of maximum width behind the orbit. The supraorbitals (so<sub>1</sub> + so<sub>2</sub>) are long and strap-like. The anterior of the two is expanded posteriorly (MUGD 3643, text-fig. 22). The dermosphenotic (dsph.) is preserved in a few specimens (text-figs. 23A, 24AB, 25AB), and may have been as large as in *L. dubia* (Patterson 1967, fig. 4). The posterior region of the skull roof

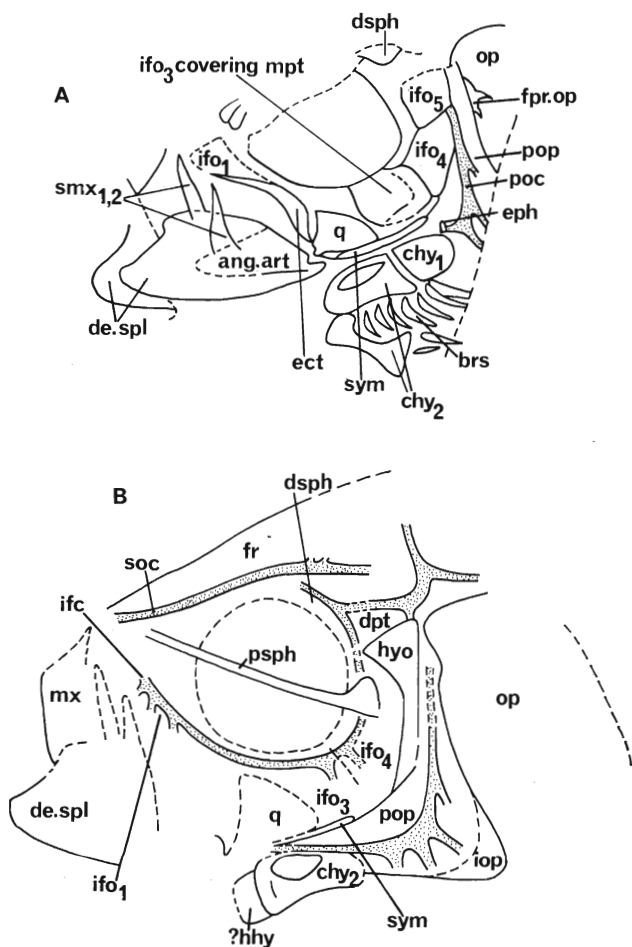


TEXT-FIG. 22. *Leptolepis koonwarri*, MUGD 3641B, dorsal view of anterior skull roof,  $\times 7$ .



TEXT-FIG. 23. *Leptolepis koonwarri*. A, MUZ 3115, posterior skull roof,  $\times 8$ . B, MUZ 3033, posterior skull roof and orbital area,  $\times 3.5$ .



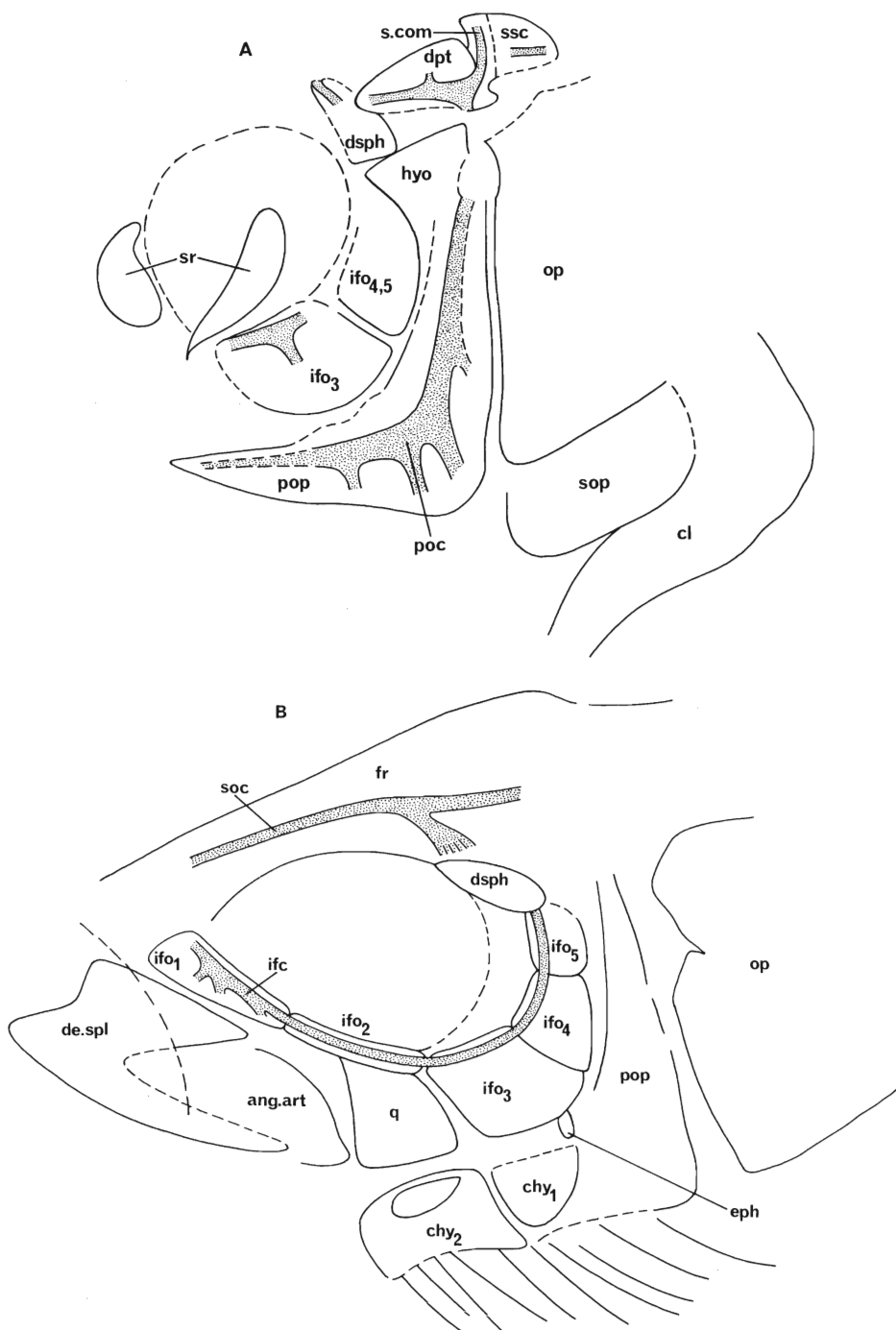


TEXT-FIG. 24. *Leptolepis koonwarri*. A, MUZ 3642B, cheek, ceratohyal and palatal elements,  $\times 4$ . B, MUZ 3099B, lateral view of skull,  $\times 4$ .

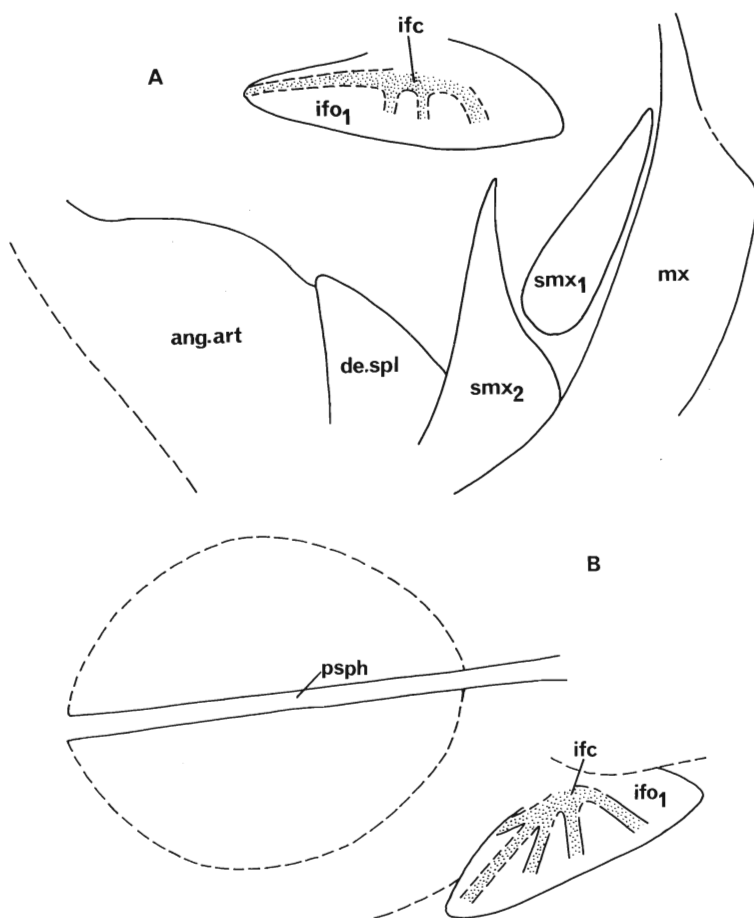
(text-figs. 23A, 25A, 27AB) is very poorly preserved in the available material, the bones being crushed and distorted. The general pattern, however, seems to resemble *L. dubia* and *Allothrissops mesogaster* (Patterson 1967, figs. 2, 4) particularly in that the postero-lateral margin of the frontal is much narrower than in, for example, *L. sprattiformis* (Saint-Seine 1949, fig. 99). There is no resemblance to the elevated posterior skull roof present in *L. africana* (Gardiner 1960, fig. 48).

The parietal (pa.) is slightly broader than long, with its lateral apex truncated as it abuts against the postero-mesial margin of the dermopterotic (text-fig. 23A). The dermopterotic (dpt.) resembles that bone in *L. coryphaenoides* (Nybelin 1962, Wenz 1967), being nearly twice as long as it is broad (text-figs. 23A, 25A). The extrascapular (ext.) is similar to that of *L. coryphaenoides* but may have been slightly larger in relation to the size of the skull (MUGD 3649). The sutures between frontal, dermopterotic, and parietal may be difficult to see, giving the false impression that the frontal lies against the extrascapular. (Skull reconstruction, text-fig. 35.)

**Cheek Region.** The maxilla (mx.) is a long arcuate bone and bears on its antero-ventral margin a long, concave facet to accept the small, toothless premaxilla. The maxilla possesses neither teeth nor serrations.



TEXT-FIG. 25. *Leptolepis koonwarri*. A, MUGD 3652B, posterior cheek region,  $\times 6$ . B, MUGD 3634, lateral view of skull,  $\times 7$ .



TEXT-FIG. 26. *Leptolepis koonwarri*. A, MUZ 3117, displaced jaws and lachrymal,  $\times 9$ . B, MUZ 3111, lachrymal,  $\times 7$ .

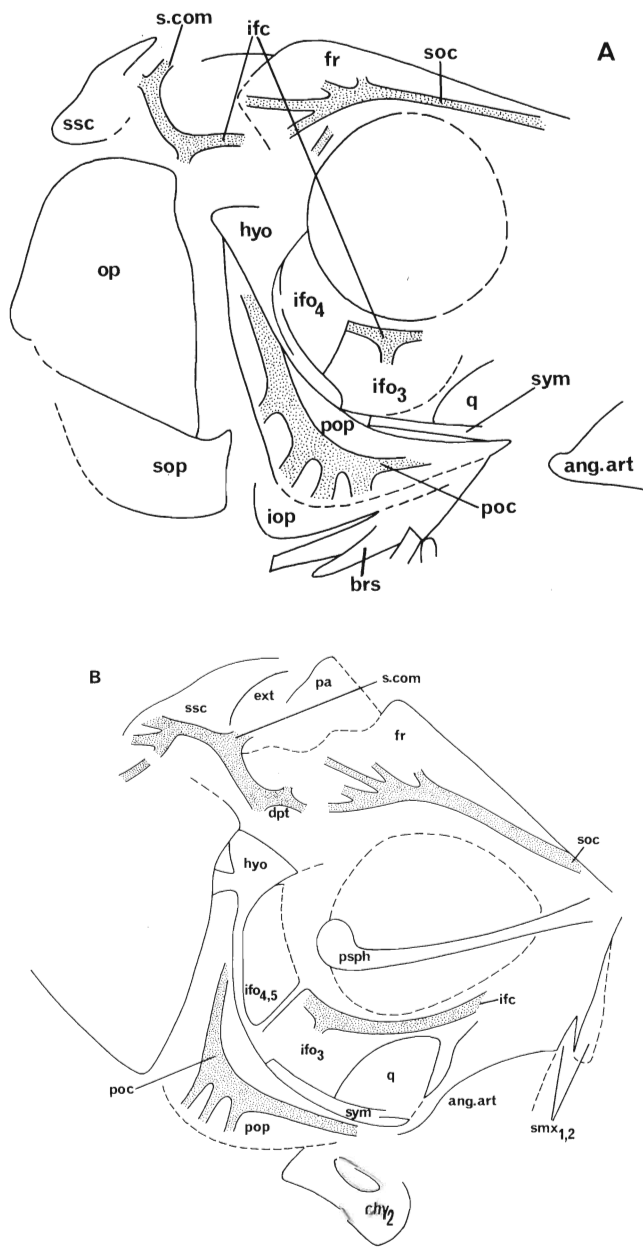
2 supramaxillae (smx. 1+2) are present, the posterior one having a fine, anterior process which overlies the dorsal margin of the anterior, lanceolate supramaxilla (text-fig. 26A; Pl. 10, figs. 1, 2).

The antorbital is not clearly preserved in any specimen.

The first member of the infraorbital series, the lachrymal (ifo<sub>1</sub>) (text-figs. 24AB, 25B, 26AB), is similar in shape to the same element in *L. sprattiformis* (Saint-Seine 1949, fig. 99), and relatively smaller than that of *Clupavus neocomiensis* (Arambourg 1954, fig. 14). It is often obscured by the anterior limb of the ectopterygoid being crushed against it. Infraorbital 2 (ifo<sub>2</sub>) is a narrow, rectangular bone which lies directly beneath the orbit. The third infraorbital (ifo<sub>3</sub>) is the largest, meeting the second infraorbital with a small anterior process and infraorbital 4 (ifo<sub>4</sub>) along an oblique suture (text-figs. 23A, 24A, 25AB). The fourth infraorbital is smaller than the third, but is curved in similar fashion and articulates with the fifth infraorbital (ifo<sub>5</sub>) (text-figs. 24A, 25B). The latter lies against the dermosphenotic.

The infraorbital series is known from a number of specimens, including: MUGD 3634, 3636AB, 3640AB, 3642AB, 3652AB, 3653AB; MUZ 3030AB, 3031, 3032AB, 3099AB, 3106; and P.24670b.

The postorbital ('suborbital' of Rayner 1937) is absent, as in *L. dubia* (Patterson 1967, fig. 4). The opercular (op.) has the shape of a tall triangle with a well-rounded apex. The ventral margin is slightly convex and overlies the smaller subopercular with an oblique suture. The subopercular (sop.) possesses a short vertical process which lies along the anterior rim of the opercular (text-fig. 27A). The interopercular



TEXT-FIG. 27. *Leptolepis koonwarri*. A, MUZ 3116A, cheek region,  $\times 5$ . B, MUZ 3640B, cheek region,  $\times 6$ .

(iop.) lies postero-ventrally to the preopercular and is overlapped by it, the 2 bones very often falsely appearing to be 1 element (text-figs. 24B, 27A). The preopercular (pop.) (text-figs. 24A, 25A, 27AB) is boomerang-shaped and is often almost completely exposed to the extremities of both gently tapered limbs. There is a good-sized flange of bone in advance of the angle of the preopercular canal, but its margin remains slightly concave or straight (Pl. 10, fig. 4). No convexity of this flange is visible in any specimen (see Gardiner 1967).

*Lower Jaw.* This is not generally completely visible as it is overlain by the upper jaw. However, in a few specimens disarticulation has occurred, both dentalo-splénial and angulo-articular elements being separately preserved (Pl. 10, figs. 1, 2, 3). They are very similar to those of *L. coryphaenoides* (Rayner 1937, fig. 4A; Wenz 1967, fig. 100) and *L. sprattiformis* (Saint-Seine 1949, fig. 100a). The length of the coronoid process resembles the former, as does the deep concavity on the upper anterior margin of that process. The posterior extremity of the coronoid process terminates in a point, much as in *L. sprattiformis* and in common with that species the dentalo-splénial is toothless.

The angulo-articular (ang. art.) (Pl. 10, figs. 1, 2, 3) is a more slender bone than in either of the species named, its convex dorsal margin being a shallow curve, unlike the steep convexities of that element in *L. sprattiformis*. Posteriorly it bears a deep facet for articulation with the quadrate (text-fig. 24A; Pl. 10, fig. 4) (MUGD 3642AB). The ventral margin of the angulo-articular is straight.

The gular plate is visible in only a few specimens (e.g. MUZ 3111) and is slender, tapering to a sharp point anteriorly. It is very thin, appearing almost membranous.

*Sensory Canal System.* The description is based largely on the following specimens: MUZ 3030B, 3033, 3099AB, 3107AB, 3111, 3113AB, 3114A, and MUGD 3634A.

Due to imperfect preservation of the nasal bone, the canal is not known in that element. The supra-orbital sensory canal (soc.) (text-figs. 22–24AB, 25B, 27AB) runs longitudinally through the lateral region of the frontal, turning laterally to run parallel with the orbit (e.g. MUZ 3033) for a short distance. On this curve 3 tubules are given off, the first two postero-mesially, and the third and longest posteriorly (text-figs. 23, 27A). In MUZ 3116 (text-fig. 22A) 4 tubules are emitted in this position. The termination of the frontal canal is visible in MUGD 3634A, represented by a fanning-out and splitting-up of the canal into very small, short branches (text-fig. 25B). This may have been partly covered in life by the dermosphenotic (cf. *L. dubia*, Patterson 1967, fig. 4).

The ethmoid commissure is unknown and the antorbital is not well preserved in any specimen. In the lachrymal (ifo<sub>1</sub>) (text-figs. 24B, 25B, 26AB), however, the infraorbital sensory canal is strongly developed and may extend mesially on to the antorbital (3030A). The canal runs longitudinally fairly close to the dorsal border of the lachrymal, giving off 3 or 4 long branches at fairly regular intervals (MUZ 3030AB, MUGD 3634, MUZ 3111).

Infraorbital 2 shows an unbranched longitudinal canal (text-figs. 18B, 19A). The third infraorbital contains one tubule only, as does the fourth (cf. *Allothrissops*, Patterson 1967, fig. 2). The condition in infraorbital 5 is not known (text-figs. 24B, 25A, 27AB).

The canal pathway on the dermosphenotic is visible in MUZ 3099B (text-fig. 24B) and less clearly on MUZ 3033 (text-fig. 23B). Parallel with and close to the edge of the orbit the canal turns at right-angles (MUZ 3099) and runs posteriorly at a slight upward angle on to the dermopterotic. In MUZ 3099B part of the outline of the dermosphenotic is visible, together with the anterior portion of the canal which tapers towards the frontal much as in *Allothrissops*, *L. dubia* and *Clupavus* (Patterson 1967), and *L. normandica* Nybelin (1962) (*L. coryphaenoides*, Wenz 1967). The most anterior portion of the canal may lie on the frontal as in *L. normandica* (loc. cit.). On the probable posterolateral region of the dermopterotic the main canal exhibits a T-, or shallowly forked Y-junction, the vertical stem representing the origin of the canal to the dorsal limb of the preopercular. This is visible in a number of specimens (text-figs. 23A, 24B, 25A, 27AB). Minor tubules are emitted mesially between the dermosphenotic and the preopercular canal junction on the dermopterotic (text-fig. 25A) but are generally very poorly preserved.

*Cephalic Division of Main Lateral Line.* The supratemporal commissure (s. com.) (text-figs. 23AB, 24B, 25A, 27AB) is visible in MUGD 3652A, 3640B; and also in MUZ 3033, 3099, and 3105A. It runs mesially after the canal enters the extrascapular from the dermopterotic. The branches of the supratemporal commissure are not well known. In MUZ 3033, 3099B, 3115, and 3116A (text-figs. 23AB, 24AB, 27B) the long posterior arm of the main canal to the suprascapular is visible, situated at the upward curve of the commissure, a little lower than in *L. coryphaenoides* (Nybelin 1962).

The preopercular sensory canal (poc.) (text-figs. 24B, 25A, 27AB; Pl. 10, fig. 4) runs fairly close to the anterior margin of the bone and gives off 4 well-developed tubules. One of these is situated about half-way along the dorsal limb, and the other three are evenly spaced about the angle of the bone. It is often only these 3 branches that are visible, the second and third being particularly robust. All extend to the posterior margin of the element (e.g. MUGD 3640B). On one preopercular of MUGD 3653A, there are minute

infillings on the anterior margin of the canal. It seems that they are actually within the canal itself, but this is not certain (Pl. 10, fig. 4).

The mandibular sensory canal (mdc.) (Pl. 10, fig. 3) is partially and poorly preserved in several specimens, but the exact number of apertures is not known. In MUZ 3031 3 tubuli are seen, regularly spaced along the anterior half of the jaw. No tubuli are known from the posterior part of this canal.

*Lateral Line.* This canal is visible on the suprascapular, but is not clearly preserved within the pectoral region of any specimen. In MUZ 3116A (text-fig. 27B), however, 3 small, imperfectly preserved tubules are visible, one of which represents the main canal passing through to the supracleithrum. The supracleithral canal is poorly known. The lateral line is preserved in a number of individuals and every scale of the line is perforated by a single pore. As the line runs parallel with the vertebral column it is often obscured by compression against the latter.

*Hyobranchial System.* The hyomandibular (hyo.) (text-fig. 28A) is partly exposed in a number of specimens, due to breakage of the (presumably) very thin and fragile infraorbitals. The head of the hyomandibular and part of the vertical shaft are often visible, but in the disarticulated skull remains of MUGD 3636AB, an isolated hyomandibular is clearly visible (text-fig. 28A). It is a slender element with an expanded triangular head which bears small vertical rugae. Ventral to the head there is a well-developed posterior processus opercularis (pr. op.) and opposite this is a bulge in the anterior margin. 2 flanges of bone are present, one linking the processus opercularis with the postero-dorsal corner of the head of the hyomandibular, and the other is placed anteriorly, protruding antero-ventrally much as in *L. sprattiformis* (Saint-Seine, 1949). This general pattern differs from that of *L. coryphaenoides* (Wenz 1967, figs. 103–104) in that the shaft is much slimmer and in the absence of a preopercular process at the base of the shaft. The thin vertical shaft is slightly curved and expands gently ventrally. Part of the pathway of nerve VII is visible in the dorsal part of this shaft (hyo. VII).

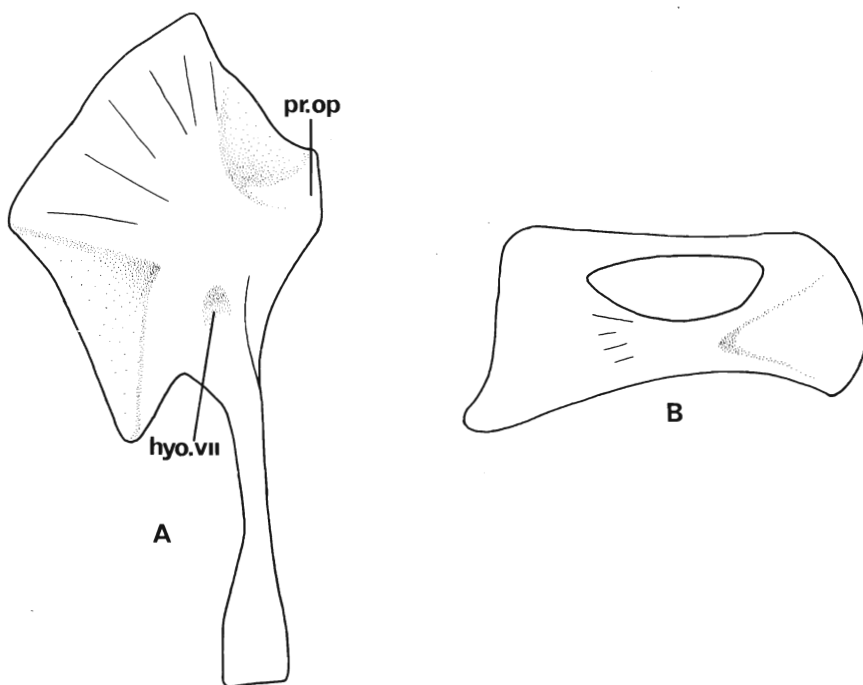
The symplectic (sym.) is visible in several specimens (text-figs. 24AB, 27AB) and is an elongate bone, curved in a shallow arc. It is tapered at its insertion into a groove close to the ventral margin of the quadrate. Its posterior termination is abrupt, having a squared-off appearance. The ceratohyal bones (chy. 1–2) (text-figs. 24AB, 25B, 27B, 28B) are almost identical with those of *L. coryphaenoides* (Rayner 1937), but the suture between proximal and distal elements is almost straight and oblique. The dorsal margin of the proximal one (chy. 1) is straight and lacks the concavity in front of the epihyal possessed by *L. coryphaenoides*. The postero-ventral region is finely tuberculated. The distal ceratohyal (chy. 2) is broader proximally than distally, and is of the hourglass-shape previously described in *Leptolepis*, with a thin connecting-rod of bone joining the posterior and anterior tips on the dorsal margin (Pl. 10, fig. 1) (Woodward 1900, Rayner 1937, Saint-Seine 1949). A similar condition exists in the family Protelopidae, e.g. *Eoprotelops* (Saint-Seine 1949). MUGD 3642AB shows the small, lozenge-shaped epihyal (eph.) and MUZ 3099B exhibits a poorly preserved hypohyal (hhy.) which is larger than the epihyal but of similar shape. The course of the hyoid artery is not clearly seen.

There are 10 branchiostegal rays (brs.), of which the anterior 6 are fairly small and the rays increase in size passing posteriorly. These 6 rays each curve to a point, and are sabre-shaped. The seventh is straighter and pointed at its distal extremity, but the last 3 are longer and strap-like in form.

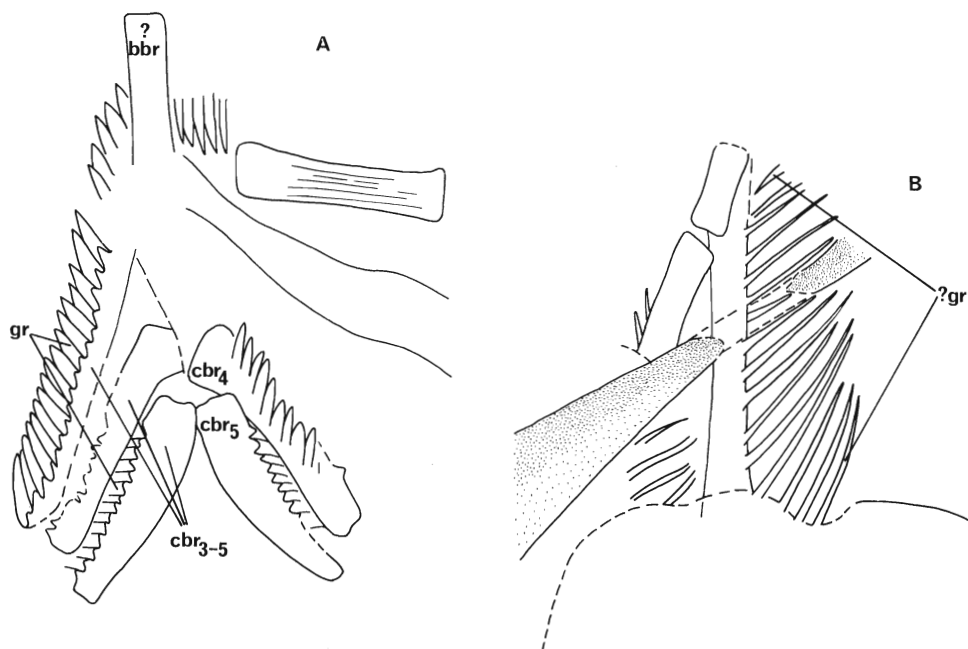
Parts of the internal gill region are preserved in 3 specimens only: MUZ 3030AB (text-fig. 29A), MUZ 3031 (text-fig. 29B; Pl. 17, fig. 2), and P.26129 (Pl. 12, fig. 1). The first and last specimens are among the largest individuals in the collection, whilst MUZ 3031 represents the incomplete remains of two fairly small fish.

In MUZ 3030AB the skull has apparently been displaced laterally on a bedding plane after preservation (Pl. 11, fig. 2), leaving part of 3 pairs of gill-arches embedded in the matrix. The exposed portion consists of 3 pairs of ceratobranchials (cbr.). On one side these lie nearly parallel and on the other the third of the ceratobranchials has been moved from its original position. One-half of the third arch preserved bears a series of close-set gill-rakers (gr.), about 18 per centimetre. The rakers are robust, lanceolate elements about 4 times as long as they are broad, and set at an angle of 45° to the gill-arch. Their points of insertion give that margin of the ceratobranchial a toothed or serrated appearance (cf. *Sardinops*, Phillips 1942). Gill-rakers or their insertions may be clearly seen on all the arches present. No gill-filaments are known in this specimen.

The last pair of ceratobranchials is convex mesially and the elements meet briefly posteriorly. The next pair is expanded proximally, and is almost straight-edged distally. The third ceratobranchials are much



TEXT-FIG. 28. *Leptolepis koonwarri*. A, MUGD 3636A, hyomandibular,  $\times 19$ . B, P.26129A, second ceratohyal,  $\times 4$ .



TEXT-FIG. 29. *Leptolepis koonwarri*. A, MUZ 3030A, part of gill-arch region,  $\times 4$ . (See also Pl. 11, fig. 2.) B, MUZ 3031, part of gill-arch region,  $\times 16$ .

longer and are linear. The ceratobranchials abut against the basibranchial series in oblique fashion, much as in *Sardinops caerulea* (Phillips 1942) although the size relationship of the elements is different. From comparison with Ridewood (1904a, b), Phillips (1942), and Nelson (1967) it is evident that the third, fourth, and fifth ceratobranchial pairs have been preserved. There is no apparent posterior protrusion of the fourth basibranchial between the final pair of ceratobranchials, a condition comparable to that of *Chirocentrodon* (Clupeidae) (Nelson 1967) and *Albula* (Ridewood 1904a).

P.26129AB reveals part of the gill-arches of the right side, 2 of which are composed of 2 articulating elements which meet along straight sutures. The relationships are such as to indicate that these structures are the first and second gill-arches, each consisting of a ceratobranchial distally and a hypobranchial (hybr.) proximally. In P.26129AB, the first gill-arch is preserved close to the ceratohyals, almost in its original position. Although the ceratobranchials have their distal regions broken away, the size relationship of cerato- to hypobranchial appears to be closely similar to that of *Sardinops caerulea* (Phillips 1942). The shape of the attached gill-rakers is difficult to ascertain exactly, but on the ceratobranchial element of the second arch (P.26129B) some gill-raker structure is visible. The articulatory base is wide, but is narrowed almost immediately by a fairly deep triangular notch on the posterior margin, and a shallow one on the anterior. The latter margin may be shallowly concave, compared with the slight convexity of the posterior edge. Each raker, therefore, resembles a slightly curved dagger, drawn in at the hilt. When the gill-rakers are arranged naturally, they overlap considerably and little of their actual shape may be seen.

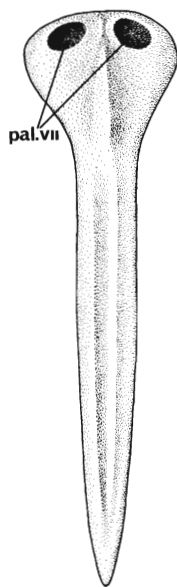
In MUZ 3031 it is not certain which part of the hyobranchial region is preserved. Portions of two arches are preserved and these bear more slender structures. The notches mentioned for P.26129AB are not seen. There is also a considerable difference in the number of structures per unit length, MUZ 3031 having (by extrapolation) 50 per centimetre length of arch, about 3 times the number in P.26129AB or MUZ 3030AB. This disparity may be due to a different gill-arch region being preserved, be related to size, or indicate a species difference. The last-named is considered unlikely as other anatomical differences have not been observed. Phillips (1942, p. 492) noted that 'The gill-raker count of the first gill-arch of *Sardinops caerulea* varies with size of fish . . . younger fish having a smaller count than do the older ones.' If size is used as an explanation, then the reverse of the above statement has occurred. It is also possible that these structures represent gill-filaments rather than rakers, but this is uncertain.

Gill-filaments (gf.) are visible in P.26129 (Pl. 10, fig. 1) as faint grey strands, exceeding the rakers in length. They run out from the cerato-hypobranchials in a shallow arc, reach a maximum length of about 7 mm, and number about 20 per centimetre.

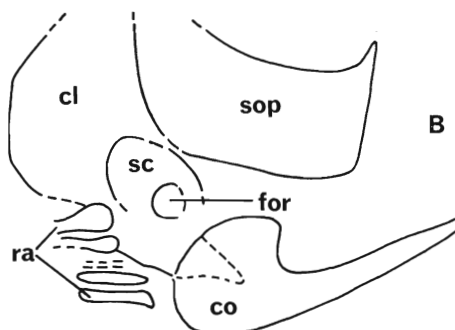
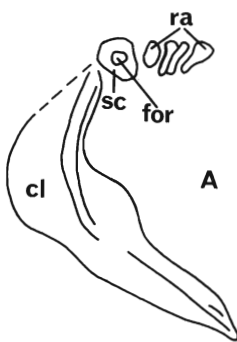
*Palate.* The quadrate (q.) is of the usual triangular shape. At its antero-ventral apex it bears a small, but well-marked process which fits into a curved notch on the posterior extremity of the angulo-articular (text-fig. 24A; Pl. 10, fig. 4). Ventrally it exhibits a groove for the symplectic (text-figs. 24AB, 27A) and posteriorly it bears rugae which radiate fanwise. These rugae may be represented in some specimens by minute tubercles (Pl. 10, fig. 2). Lying against its nearly vertical anterior margin is the ectopterygoid (ect.) (text-figs. 23B, 24A; Pl. 10, fig. 4). This is a boomerang-shaped bone, with the horizontal limb longer than the vertical. The horizontal arm extends anteriorly and is often compressed against the lachrymal in the fossil state. The entopterygoid (ent.) is only visible to any degree in the large individual P.26129B, B<sub>1</sub> (Pl. 10, fig. 2). It somewhat resembles that element in *L. coryphaenoides* (Rayner 1937) and *Notelops brama* (Dunkle 1940), but has an even more marked resemblance to the entopterygoid of the living *Sardinops caerulea* (Phillips 1942). It is wide and concave dorsally where it forms part of the orbit floor. It is formed in both vertical and horizontal planes, the latter being the larger. The entopterygoid tapers anteriorly along the dorsal margin of the ectopterygoid, giving a lanceolate appearance. The dorsal rim of the horizontal flange is not straight as in *L. coryphaenoides* but slightly sinuous as in *Sardinops caerulea*. The part of the bone forming the orbital floor is interesting in that it possesses several parallel rows of minute tubercles. These rows are inclined antero-dorsally and may represent the vestiges of small teeth. The metapterygoid (mpt.) is never seen clearly, due to the third infraorbital being compressed against it (text-fig. 24A; Pl. 10, fig. 2) and so its exact shape is not known. It is sometimes partly exposed along the antero-ventral margin of that element, and this portion is tuberculate. These tubercles are visible in P.26129AB and MUGD 3642B.

Examination of P.26129B, B<sub>1</sub> reveals that the outline of the metapterygoid, although uncertain, seems to resemble that of *L. coryphaenoides* (Rayner 1937, Wenz 1967). The suture between metapterygoid/entopterygoid and quadrate is somewhat sinuous (Pl. 10, fig. 2). In 3030B the palatine (pal.) is partly visible,





TEXT-FIG. 30. *Leptolepis koonwarri*, MUGD 3636A, ventral view of vomer,  $\times 24$ .



TEXT-FIG. 31. *Leptolepis koonwarri*. A, MUZ 3098B, distorted pectoral girdle,  $\times 4$ . B, MUGD 3653A, distorted pectoral girdle,  $\times 5$ . (See also Pl. 10, fig. 4.)

and although not particularly well preserved, shows a pronounced maxillary process which seems to articulate on to the antero-dorsal tip of the maxilla. In 3030B and 3113A there are impressions of what may have been exceedingly small palatine teeth.

**Neurocranium.** In many specimens the parasphenoid (psph.) is visible in lateral view through the orbit. Its structure is not known, but sometimes the ascending process is visible where the bone crosses the posterior margin of the orbit (text-figs. 23B, 24B, 27B). No other details of the neurocranium are known apart from the vomer (v.) (text-fig. 30). The vomer is a median sliver of bone, expanded at its anterior extremity which adjoins the ventral margin of the ethmoid. 2 ventral foramina in this region allow passage of the palatine section of the seventh nerve (facialis, pal. VII) (cf. *Chirocentrus dorab*, Bardack 1965). Posteriorly it tapers to a sharp point and articulates with the parasphenoid. Although in close association with the ethmoid it does not fuse with it and is found separately in some specimens, e.g. MUZ 3105B, MUGD 3636A. This vomer is closely similar in shape to that of the living *Sardinops caerulea* (Phillips 1942).

**Pectoral Girdle and Fins.** The suprascapular (ssc.) is a curved element with an antero-dorsal process toward the extrascapular (text-figs. 23A, 27AB). The supracleithrum (scl.) is an elongate, approximately elliptical element which overlaps the dorsal margin of the cleithrum. The cleithrum (cl.) is visible to some extent in a large number of specimens, but is best seen in MUGD 3641, 3643B (Pl. 12, fig. 5). This bone resembles that of *L. coryphaenoides* (Rayner 1937), but the lower limb of the cleithrum of *L. koonwarri* is longer and its shape and curvature slightly different. The concavity on the ventral margin of that limb is placed further forward than in the former species and the anterior margins are curved, as in *L. sprattiformis* (Saint-Seine 1949). The cleithrum bears a long, curved facet on its postero-dorsal margin for the post-cleithrum (pcl.). This gives the dorsal region of the cleithrum a finely pointed shape. Below this facet the cleithrum expands posteriorly, as in *L. coryphaenoides*. The coracoid, scapular, and cleithrum are clearly visible in MUGD 3643B (Pl. 12, fig. 5). The coracoid (cor.) has an almost discoidal posterior expansion which would have been overlapped by the lower limb of the cleithrum, and from this a slender, tapering process runs anteriorly. This resembles the condition in *L. sprattiformis* (Saint-Seine 1949) and *Thrissops formosus* (Saint-Seine 1949), the latter reclassified as *Allothrissops salmoneus* (Blainville) by Nybelin (1964).

In MUGD 3653AB (text-fig. 31B) the relationship of the cleithrum, coracoid, and scapular is again

visible. The scapular articulates with but is not fused to the postero-dorsal region of the coracoid and has a broad dorsal flange. The exact shape of this specimen is difficult to interpret particularly as the cleithrum cuts off the anterior region from view. MUZ 3098AB (text-fig. 31B) consists of an isolated cleithrum, scapular, and 4 radials, and a definite fenestra is visible in the partly exposed scapular, giving an annular appearance. In MUGD 3653AB 5 pectoral fin radials are present, 2 of which appear to insert on to the posterior margin of the coracoid as in *L. sprattiformis*, and the other 3 on to the scapular, which seems to be slightly excavated at the points of articulation. Similar articulatory facets were illustrated by Wenz (1967) for *L. coryphaenoides*. 2 of the latter radials are enlarged and club-shaped at that point. The pectoral fins each have 9–10 lepidotrichia which dichotomize distally (e.g. MUGD 3637).

**Pelvic Girdle and Fins.** The girdle is represented by a pair of elongate, rod-shaped bones, expanded at their articulation with the fin-rays. The pelvic fins are triangular, possess 7 lepidotrichia which begin the first of 2 bifurcations quite close to the body and are situated about mid-way between pectoral and anal fins.

**Unpaired Fins.** The dorsal fin contains 13 lepidotrichia supported by the same number of radials. The fin origin is situated opposite, or very slightly in advance of the level of the pelvic fins, but the pelvic girdle is anterior to this level. The small, triangular anal fin is placed closer to the caudal fin than the pelvic fins and has 9 lepidotrichia, of which the last 8 bifurcate. These rays are supported by an equal number of slender radials, which reach the level of the haemal spines. The caudal structure is homo-heterocercal and quite deeply cleft, each fin lobe having a slightly convex posterior margin.

**Axial Skeleton.** The vertebral column consists of 45–50 vertebrae, the exact number being difficult to determine as anterior vertebrae are often obscured by the opercular and posterior skull bones. Infillings of the notochordal canal (Pl. 12, fig. 3) in MUZ 3104A and MUGD 3638A reveal it to have been well developed, although constricted, occupying about half the diameter of the vertebra.

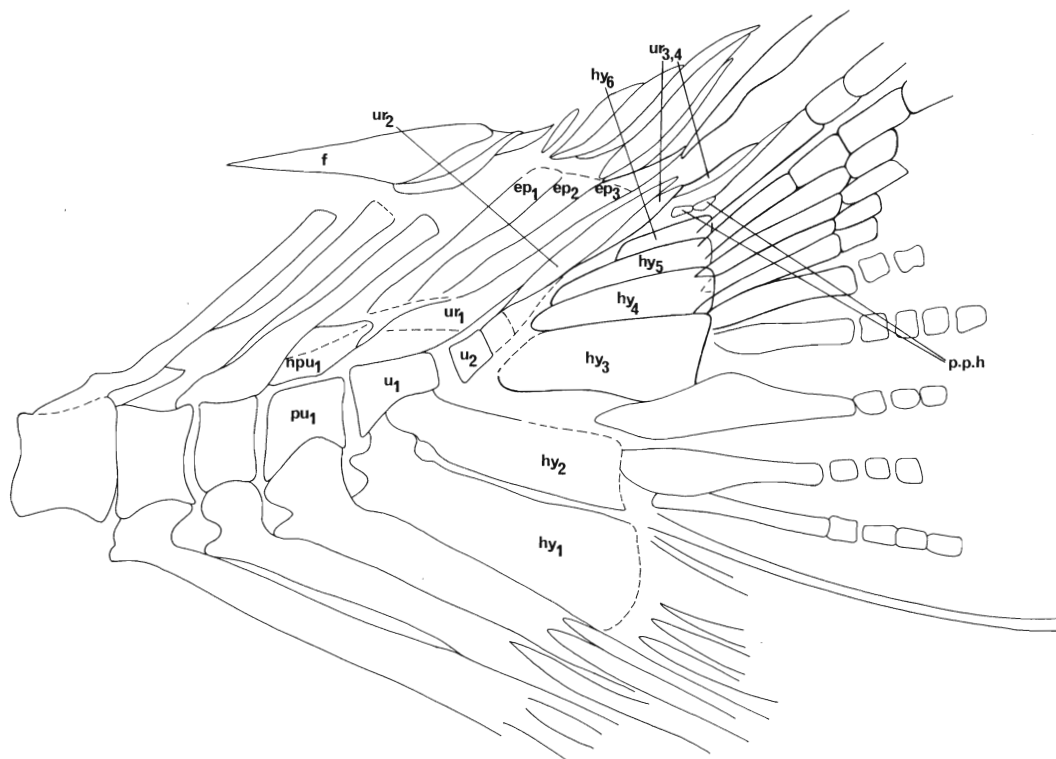
Anteriorly the neural spines are very slender and each half remains separate from its partner, but not from the arch. In the most anterior region of the body supraneural elements are present.

Delicate intermuscular bones lie across the neural spines, as far back as the termination of the dorsal fin radials. Beyond this point the neurals become stronger, their dorsal region being curved toward the posterior. This curvature lessens progressively until the last few neurals are straight, blade-like bones. The ribs are slender and well formed, curving almost to the ventral margin of the body, the series terminating at the level of the proximal tip of the first anal fin radial. Posteriorly the haemal spines come to lie at progressively shallower angles to the vertebrae, until the hypurals are reached (Pl. 11, fig. 1).

The caudal region is regarded by many authors as being of considerable diagnostic importance (see Patterson 1968) and is considered here in detail (text-fig. 32; Pl. 11, fig. 1). The first ural centrum ( $u_1$ ) carries 2 hypurals which support the lower lobe of the caudal fin (10 lepidotrichia). The first of the hypurals ( $hy_1$ ) is the larger, and near its articulation with the centrum, possesses a flange which projects anteriorly. The second hypural ( $hy_2$ ) closely resembles its counterpart in *L. coryphaenoides* (Nybelin 1963) and is narrower than hypural 1. Hypural 3 ( $hy_3$ ) is situated on the second ural centrum ( $u_2$ ) and is similar in shape to that of *L. normandica* (Nybelin 1963; *L. coryphaenoides* of Wenz 1967). Also attached to this elongate centrum are 3 smaller hypurals which decrease in size posteriorly ( $hy_{4-6}$ ).

Lying immediately above the posterior dorsal margin of hypural 6 are 2 small lenticular bones which I consider to be identical with elements in the caudal regions of *Leptolepis dubia*, *Pholidophorus bechei*, and *Pholidolepis dorsetensis*, described as hypural postero-dorsal processes (p.p.h.) by Patterson (1968). The total number of hypurals in the tail of *L. koonwarri* seems, therefore, to be at least 8, but there is always the possibility that 1 or 2 more small, distal hypurals may be hidden by the disturbed lepidotrichia or other caudal elements. The hypurals of the dorsal lobe support a further 10 fin-rays, making a total of 20 rays in the caudal fin, plus a series of unbranched rays beginning with a single fulcral scale, there being 9 in each dorsal and ventral series. The first pre-ural centrum ( $pu_1$ ) bears a robust, short neural process (ANP 1 of Monod 1967; npu, of Patterson 1968). Postero-dorsally there are 3 epurals ( $ep_{1-3}$ ), arranged much as in *Elops saurus* (Nybelin 1963). Overlying the dorsal margin of the last vertebrae are the uro-neural elements (ur.), which lie 'en echelon' along the homo-heterocercal axis of the tail. In MUZ 3103 and MUGD 3640AB (text-fig. 32), uroneural 1 ( $ur_1$ ) extends anteriorly on to the first pre-ural centrum at least. 6 uroneurals are known in MUGD 3640AB and 4 or 5 in MUZ 3103. More may have been present as the relevant region of 3103 is possibly incomplete.

The lepidotrichia of the caudal fin are jointed and divide distally with the exception of the outermost



TEXT-FIG. 32. *Leptolepis koonwarri*, MUGD 3640A, caudal skeleton,  $\times 3.5$ . (See also Pl. 11, fig. 1.)

principal ray in each caudal lobe which is unbranched. One particular ray is specially adapted for articulation with the ventro-distal margin of hypural 3 by being particularly forked proximally (cf. Nybelin 1963).

*Squamation* (Pl. 12, figs. 2, 4, 6). The scales are cycloid and semicircular in plan view. The basal region of attachment is totally covered by fine circuli, which possess a fairly sharp latero-basal angle and sinuous anterior margins. Radiating fanwise posteriorly from the nucleus into the apical region of the scale are smooth but sometimes irregular grooves, most commonly represented by raised ridges of matrix after destruction of the actual scale. However, 1 or 2 specimens display these grooves on well-preserved scales. The grooves display considerable variations in number, size, and disposition and are sometimes completely absent, but in all cases the apical region is perfectly smooth. There are 11 longitudinal rows of scales (Pl. 9, fig. 2), the fifth (numbering from the dorsal side) bearing the lateral line.

*Measurements of Holotype*. MUGD 3649.

	mm
Body length (excl. head)	46
Head length	17
Total length (incl. tail)	78
Body depth (max.)	16
Head depth (max.)	14
Depth of caudal pedicle	8

*The affinities of Leptolepis koonwarri*. It is apparent that the leptolepids from Talbragar and Koonwarra are closely related, differing in only a few characters.

As described in the historical summary of *Leptolepis*, Arambourg (1950, 1954,

1968) has placed most of the species of *Leptolepis* from the uppermost Jurassic (Purbeck) and Lower Cretaceous within the genus *Clupavus* Arambourg (1950). This lumping of the 2 genera (in part), on the premiss that geological age equals degree of advancement, has led to a great deal of confusion. An example of this confusion was apparent when Wenz (1967) stated that it is impossible to separate the genera *Clupavus* and *Leptolepis*. Patterson (1967) has partly unravelled the tangle by describing and figuring a new (as yet unnamed) species of *Clupavus* from the Cenomanian of Lebanon which ensures that the genus is now clearly recognizable, but the situation still requires further clarification as the suspicion remains that too many species have been 'lumped' within *Clupavus*, as was previously the case with *Leptolepis*.

Examination of *L. koonwarri* and *L. talbragarensis* shows that in shape, proportions, and arrangement of fins, these species are similar to *Clupavus brodiei* and *C. formosus* (Traquair 1911). The paucity of preopercular branch canals resembles *C. brodiei* (which also has a 'leptolepid' caudal skeleton) and *Leptolepis nathorsti* from the Jurassic of Spitzbergen (Woodward 1900). I have no information on the presence or absence of a post-orbital in *C. brodiei* and *C. formosus*, but it is probable that it was absent as in the Koonwarra species. The caudal skeleton of the 2 Australian species resembles the 'complexe urophore imaginaire' described by Monod (1967), and also shows a marked similarity to the Lower Jurassic *L. coryphaenoides* (Nybelin 1963) although Wenz's (1967) interpretation of the latter species is a little different. It is unlike *L. dubia* (Patterson 1967) in that hypurals 1 and 2 are not fused proximally and differs considerably from *Clupavus* sp. nov. (Patterson 1967) which exhibits further fusion. The termination of the supraorbital canal on the frontal resembles the case in *Leptolepis dubia*.

Wenz (1967) noted a considerable variation in the number of preopercular sensory canal branches (5–23) within the species *L. coryphaenoides*, as well as some diversity of preopercular shape. Although individuals with a small number of branch canals (5–8) are rare, it is significant that all of them are of small size according to Wenz. In view of the small size of most individuals of *L. koonwarri* and *L. talbragarensis* and taking into account that most specimens of the former species are about a year old, it should be noted that I have observed no variation at all in the number of preopercular canal branches in *L. koonwarri*, in the course of examining several hundred examples of varying size. Bifurcation of branch canals is unknown in either of the Australian species.

The taxonomic position of the Koonwarra species depends upon which criteria are considered to be of the greatest evolutionary significance. The structure of the caudal region may be regarded as the most significant single item for classification purposes within the leptolepids, and indeed the best method of diagnosing the teleostean stage of organization. This idea has been voiced by a number of authors (see Patterson 1968 for references and include Arambourg 1935, 1950, 1954). In body form and fin positions the Koonwarra form is similar to *Clupavus brodiei* and also *Clupavus formosus*. The form of the skull bones, however, does not particularly resemble that genus. The preopercular canal has few branches as in *Clupavus*, but there is no large forward expansion of the preopercular for attachment of an enlarged adductor mandibulae muscle (Gardiner 1967). The notochordal canal is

well developed, but shows some constriction, and the caudal region is of the type found in *Leptolepis* from the Lias (Lower Jurassic), e.g. *L. coryphaenoides*.

It is evident, therefore, that the Koonwarra form is an example of what De Beer (1954) has called 'mosaic evolution' representing a combination of primitive and advanced characters within the one form (see Schaeffer 1956, 1965). Schaeffer (1956) stated: 'Transitional forms frequently combine primitive and advanced characters in such a way that allocation of these forms to an ancestral or a descendent category becomes more or less arbitrary.' This is precisely the problem encountered here.

It may be that the Koonwarra and Talbragar leptolepids are directly derived from Triassic ancestors which became isolated in fresh waters in the late Triassic, or more probably the early Jurassic. Possibly such a change from the marine environment of ?Tethys to landlocked freshwaters may have entailed a change in feeding habits and, therefore, changes in skull anatomy. To quote Schaeffer (1956):

... modifications in the feeding mechanism nearly always include changes in the skull, in the jaw musculature, and to some extent in the nerve supply and circulation.

There is also good reason for believing that changes may occur in different parts of the body more or less simultaneously but independently of each other. All alterations must, of course, be integrated in respect to the entire organism, but this does not necessarily involve close functional interdependence of all the complexes undergoing change at any particular time.

For example, in the case of the Koonwarra form the skull has evolved in some ways to what is generally considered to be an Upper Jurassic or Lower Cretaceous grade of structure, whereas the vertebral column and the internal structure of the caudal fin are of a 'Lower Jurassic type'.

Using the caudal region as the main criterion of classification there is no doubt that the Koonwarra and Talbragar species belong to *Leptolepis* rather than *Clupavus*. Differences in structure from Northern Hemisphere forms of similar age may be due to isolation in Southern Hemisphere freshwaters. In this context it is desirable that a detailed examination be made of the 3 species of *Leptolepis* from the Wealden of Belgium: *L. formosus*, *L. brevis*, and *L. attenuatus*, which require description, and which Arambourg (1950) referred to *Clupavus*.

Santos (1958, 1960) has described *Leptolepis diasii* from the Cretaceous of Serra do Araripe, Brazil. Although the specimens are imperfectly preserved, certain characteristics closely resemble those of *L. koonwarri*. One of these is the paucity of branch canals on the preopercular, there being 3 in *L. diasii* and 4 in *L. koonwarri*. The pattern of the infraorbital series (where preserved) is similar, and the fin positions are very similar to those of the Koonwarra form. The dorsal fin is placed slightly in advance of the level of the pelvic fins, and the anal fin is placed well back toward the caudal region, much as in *Clupavus brodiei* and *C. formosus*. The structure of the caudal region is too poorly preserved to be diagnostic. Whether these similarities represent convergence, the Brazilian and Australian forms having been derived separately from a Triassic ancestor; or whether the relationship is a closer one, will depend on the discovery and analysis of more complete material from South America.

The palatal and hyoid regions of *Leptolepis koonwarri* differ from other leptolepids in tuberculation or minor dentition of the bones of those regions. Ceratohyal, quadrate, entopterygoid, and metapterygoid elements are all rugose or tuberculate, and

it is apparent from larger and better-preserved specimens that the palatine may have carried small teeth. Teeth, however, are totally absent from the jaws, even serrations being unknown, and the condition with regard to the parasphenoid is indeterminable.

*Feeding habits.* As the dentition or tuberculation of bones in these areas is concerned with feeding mechanisms, the structure of the gill-rakers must be considered as an integral part of the system. It is evident from the structure of such rakers that *Leptolepis koonwarri* did not feed on microplankton (cf. *Sardinops*, Phillips 1942). However, tooth reduction is complete within the jaws, and greatly reduced elsewhere, so that it is unlikely to have been a predatory fish. From a consideration of these structures and also of the available food it seems most likely that *L. koonwarri* fed on aquatic insects and crustaceans.

Until recently the use of gill-arches in classification had not been exploited. Nelson used the technique with considerable success in elucidating the relationships of the subfamilies of the Clupeidae. He found that his results were in agreement with those arrived at by other methods, including analysis of 'branchiostegal rays, scute development and other osteological characters . . .' (Nelson 1967).

TABLE 2A

*L. koonwarri* and *L. talbragarensis* have the following characters in common:

1. Fin positions.
2. Large notochordal perforation of centra.
3. Absence of scale enamel.
4. Lack of postorbital.
5. Similar circumorbital arrangement.
6. Supraorbital and infraorbital sensory canals do not meet.
7. Long parietal branch of supraorbital sensory canal.
8. Few branches of preopercular sensory canal.

There are, however, a number of differences between the 2 species:

TABLE 2B

<i>L. koonwarri</i>	<i>L. talbragarensis</i>
Jaws toothless	Upper and lower jaws toothed
Parts of hyoid and palatal regions tuberculate or rugose	Hyoid and palatal regions smooth
Preopercular with 4 branches of the sensory canal	Preopercular with 7 branches of the sensory canal
Preopercular with dorsal limb vertical, and longitudinal limb horizontal	Preopercular with large obtuse anterior angle between limbs. Longitudinal limb inclined antero-ventrally
8 hypurals in caudal region	7 hypurals
Scales with posterior radial ornamentation	Scales with no such ornamentation

## THE KOONWARRA FISH FAUNA

This fauna is much more primitive than any other definitely Lower Cretaceous fish fauna and is closely comparable with that of the ?Jurassic locality of Talbragar, New South Wales. The families Coccolepididae, Archaeomaenidae, and

Leptolepididae are common to both sites, although Macrosemiidae are absent from Koonwarra, and Ceratodontidae and Koonwarriidae are missing from Talbragar.

TABLE 3

Koonwarra	Talbragar
COCCOLEPIDIDAE	
<i>Coccolepis woodwardi</i>	<i>Coccolepis australis</i>
? <i>Coccolepis</i> sp.	? <i>Coccolepis</i> sp.
	(Plus supposed 'Coelacanth' fin, see Berg 1948)
ARCHAEOMAENIDAE	
<i>Wadeichthys oxyops</i>	<i>Aetheolepis mirabilis</i>
	<i>Aphnelepis australis</i>
	<i>Madariscus robustus</i>
	<i>Archaeomaene tenuis</i>
KOONWARRIIDAE	
<i>Koonwarria manifrons</i>	absent
LEPTOLEPIDIDAE	
<i>Leptolepis koonwarri</i>	<i>Leptolepis talbragarensis</i> (which includes <i>L. gregarius</i> and <i>L. lowei</i> )
CERATODONTIDAE	
<i>Ceratodus</i> sp.	absent
MACROSEMIIDAE	
absent	<i>Uarbryichthys latus</i>

Regarding faunal resemblance between these localities, I have used 'Index 2' of Simpson (1960) as it is not greatly influenced by discrepancy in sample size.

For example:

$$\frac{C}{N_1} \times 100$$

where  $C$  = Number of taxa common to both

$N_1 = E_1 + C$ , Total taxa in first

$E_1$  = Number of taxa (at a specified level) in the first, smaller (or equal) of the 2 faunas or samples compared, but absent in the second

On the family level:

$$\frac{3}{5} \times 100 = 60$$

On the generic level:

$$\frac{2}{5} \times 100 = 40$$

N.B. 0 signifies no resemblance; 100 signifies total resemblance.

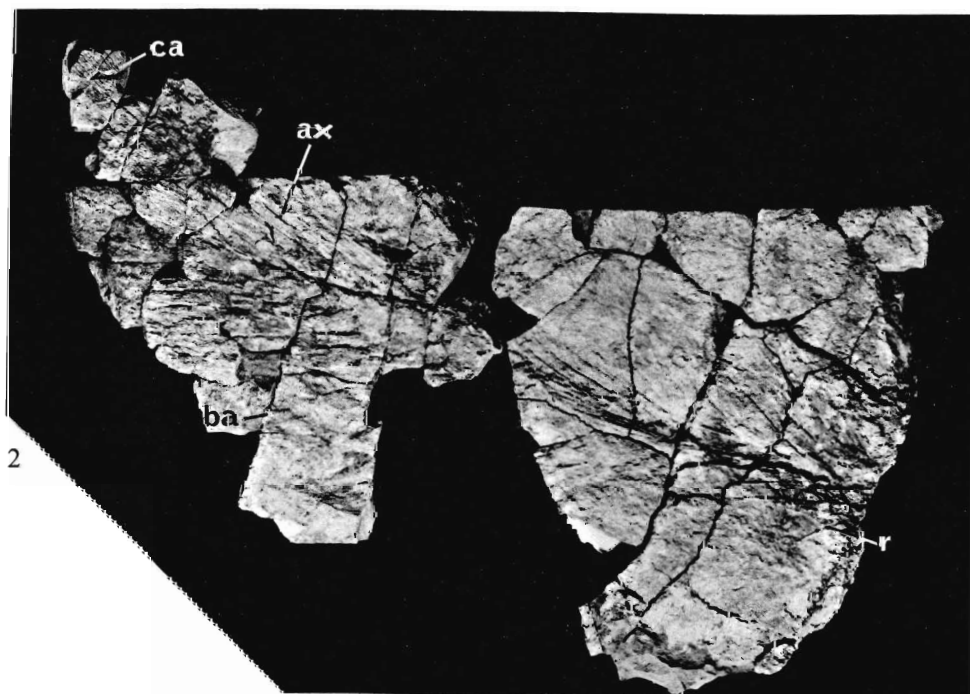
I do not consider the calculated figures to be of great use at the moment, except to indicate the decrease in faunal resemblance, particularly of the archaeomaenids, as progress into the Lower Cretaceous was made. In families common to both localities the most significant points lie with the Archaeomaenidae, Koonwarriidae, and the Leptolepididae. There are more archaeomaenid genera at Talbragar but it is difficult to know what this means. The Koonwarra fauna occupied a specialized ecological situation, and this may account for the reduction in generic number. Alternatively it may be suggested that with the passing of time the archaeomaenids

EXPLANATION OF PLATE 1

Figs. 1, 2. *Ceratodus* sp., MUZ 3343.

- 1, Axial caudal lobe, with scale imprints in the mid-line,  $\times 3$ .
- 2, Part of axial skeleton,  $\times 0.2$ .



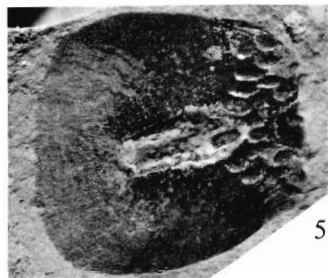
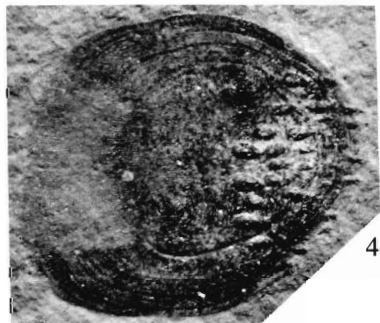
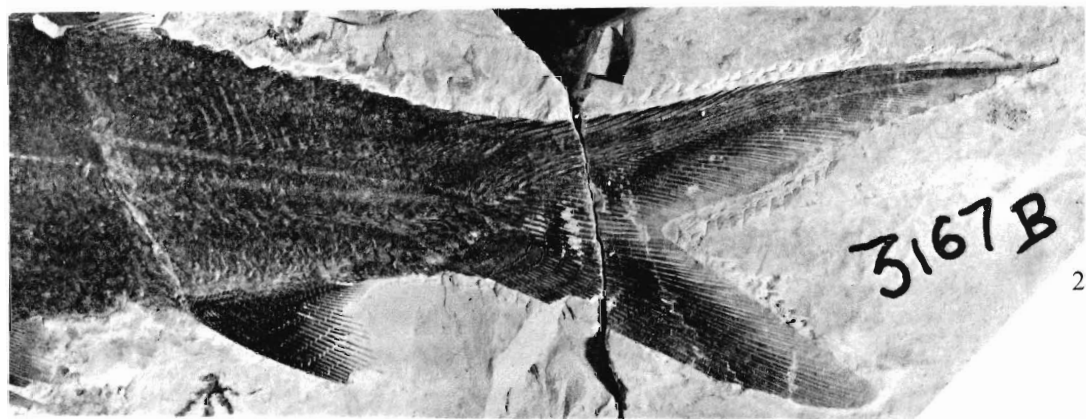
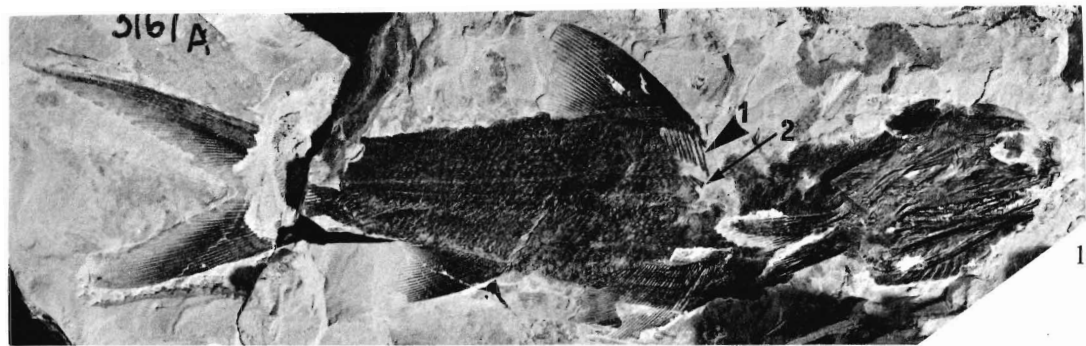


WALDMAN, Australian Cretaceous fish

EXPLANATION OF PLATE 2

Figs. 1-5. *Coccolepis woodwardi* sp. nov.

- 1, MUZ 3167A, holotype. Note dorsal fin radials (arrow 1) and paired neural spines (arrow 2),  $\times 1.1$ . (See also text-fig. 6.)
- 2, MUZ 3167B, holotype. Caudal region. Note fleshy extremity of upper dorsal lobe lacks fulcra and fin-rays.  $\times 2$ .
- 3, MUZ 3631A. Note 'hump' beneath dorsal fin.  $\times 1.7$ .
- 4, MUZ 2252. Scale,  $\times 13$ .
- 5, MUZ 1115. Lateral line scale,  $\times 11$ .



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# EXPLANATION OF PLATE 3

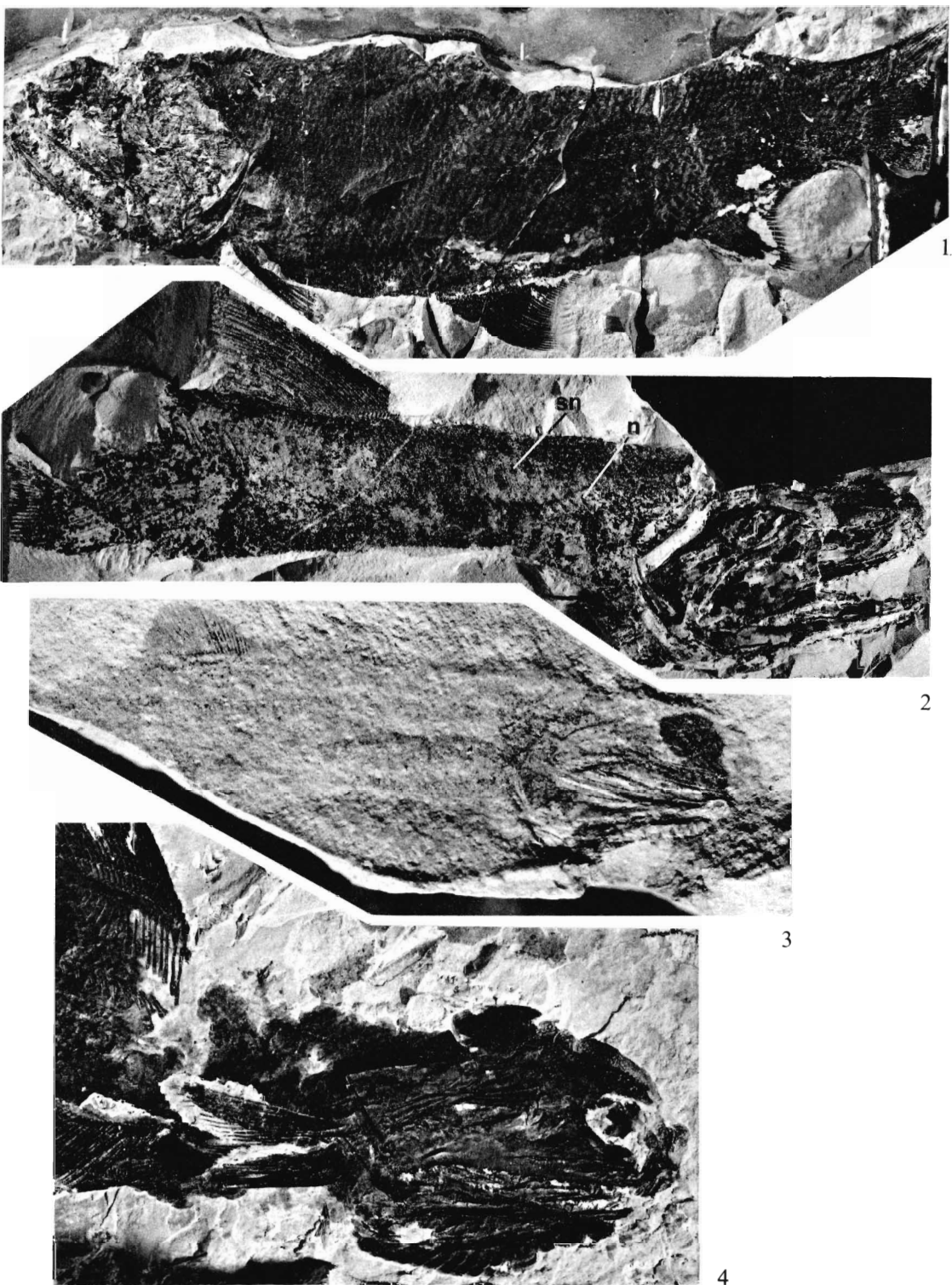
Figs. 1-4. *Coccolepis woodwardi* sp. nov.

1, MUZ 2511A. The largest complete specimen known,  $\times 0.8$ .

2, P.26062,  $\times 1.5$ .

3, P.24682. A very young fish,  $\times 6$ .

4, MUZ 3167. Skull and pectoral region,  $\times 2$ . (See also text-figs. 4, 5.)

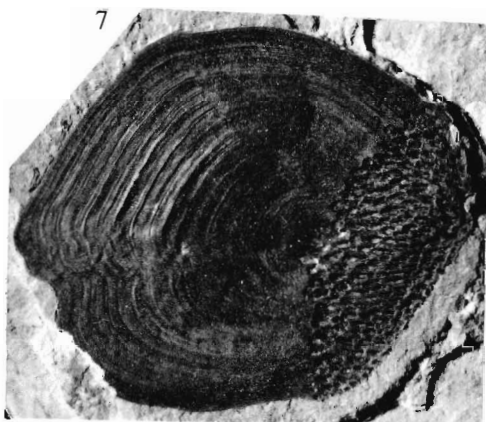
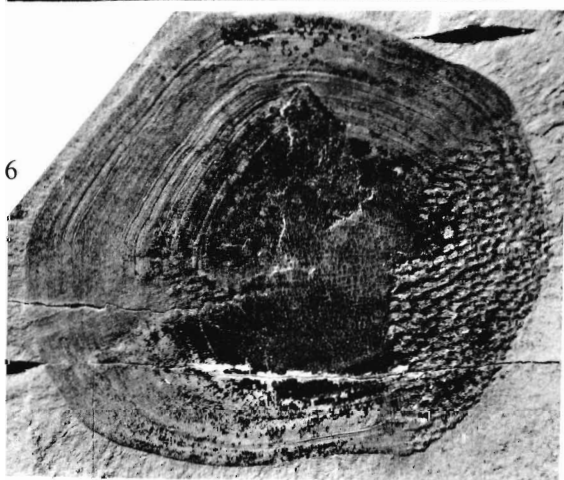
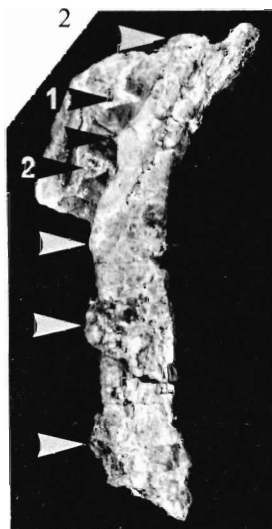
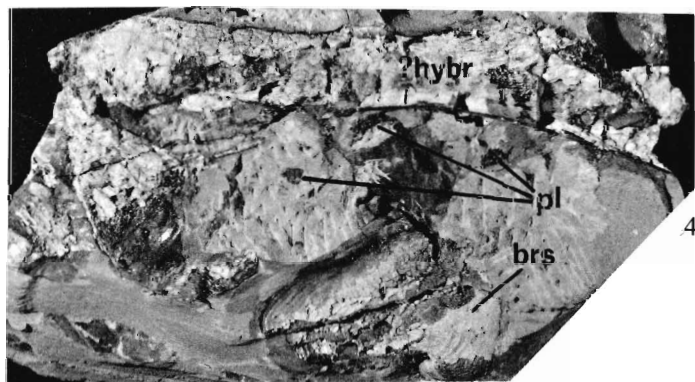


WALDMAN, Australian Cretaceous fish

#### EXPLANATION OF PLATE 4

Figs. 1-7. ?*Coccolepis* sp.

- 1, MUZ 3144E. Entopterygoid showing palatal teeth (arrowed),  $\times 1$ .
- 2, MUZ 3144A. Parts of two jaw elements,  $\times 0.6$ . The larger piece, a mandible, bears five teeth and the smaller carries two (arrows 1, 2). Positions of teeth shown by arrows.
- 3, MUZ 3144E. Coronoid showing stellate tooth impressions,  $\times 6$ .
- 4, MUZ 3144I. Remains of gill-arches,  $\times 1.2$ .
- 5, MUZ 3144A. Mandible in mesial view,  $\times 0.6$ . Teeth arrowed.
- 6, P.24680B. A large scale,  $\times 9$ .
- 7, (Author's Collection). A large scale,  $\times 8$ .



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#### EXPLANATION OF PLATE 5

Figs. 1-4. *Wadeichthys oxyops*, gen. et sp. nov.

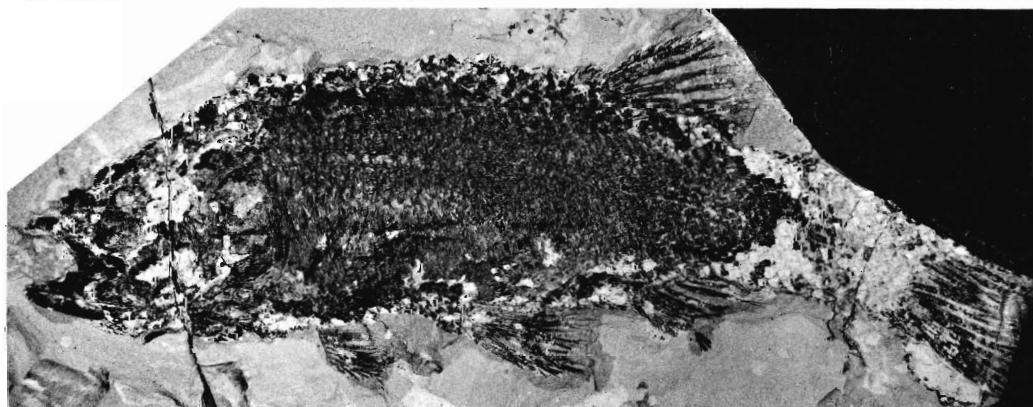
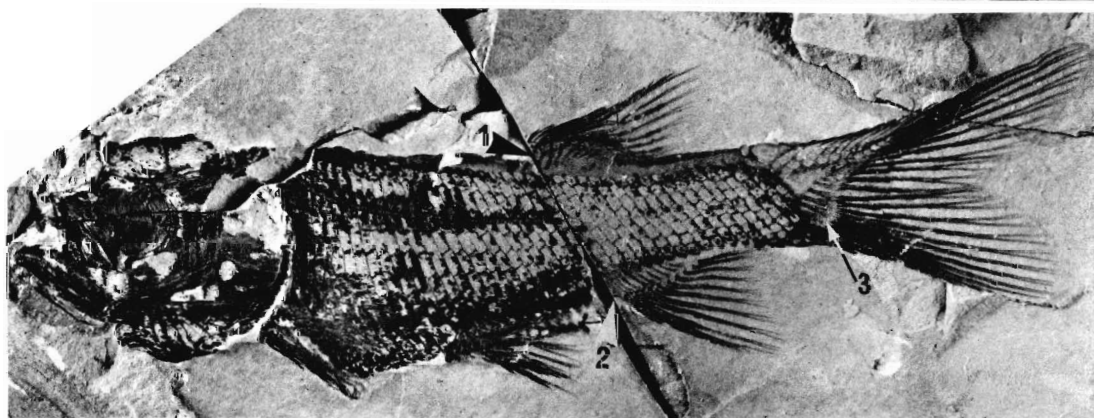
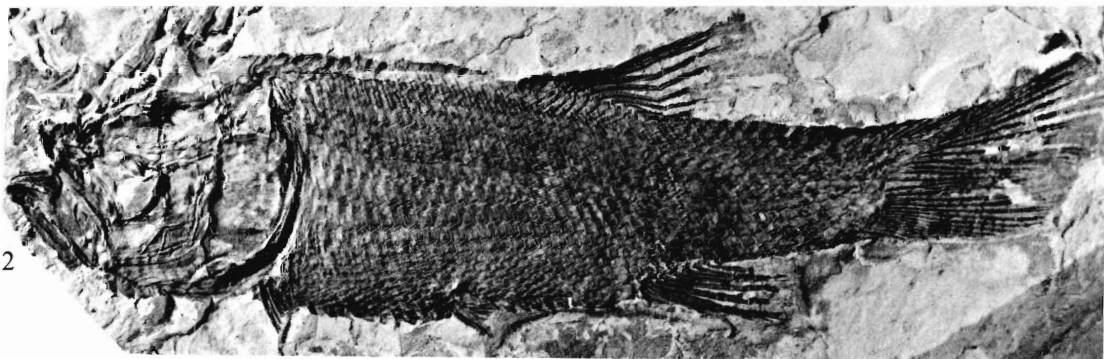
1, MUZ 3075A, holotype,  $\times 1.4$ . (See also text-figs. 7A, B.)

2, MUZ 3232A,  $\times 1.6$ . (See also text-fig. 9.)

3, MUZ 3230A,  $\times 1.5$ . To show sub-adult growth stage of scale coverage. Dorsal (1), anal (2), and caudal (3) fin supports are exposed. (See also text-fig. 13.)

4, MUZ 3626A. Adult fish with well-marked dorsal convexity,  $\times 1$ .





WALDMAN, Australian Cretaceous fish

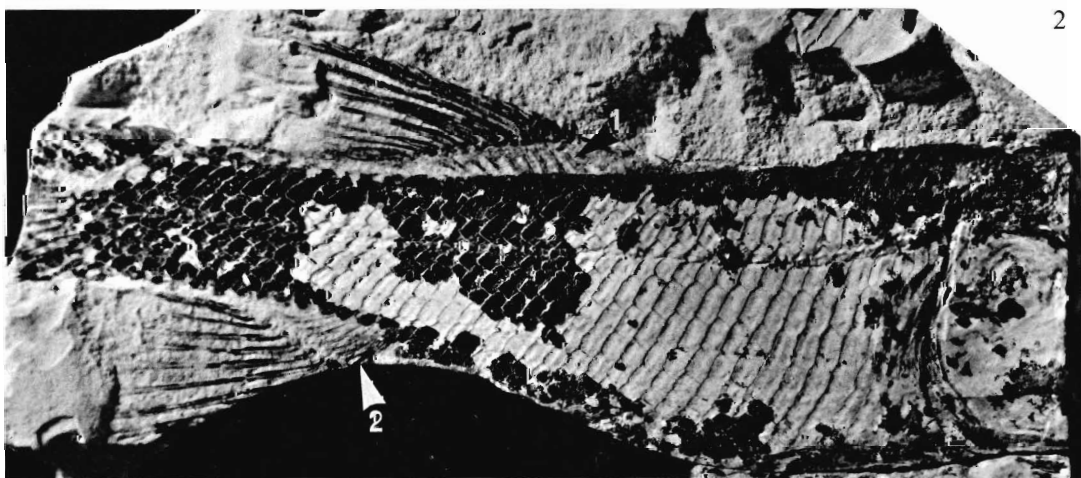
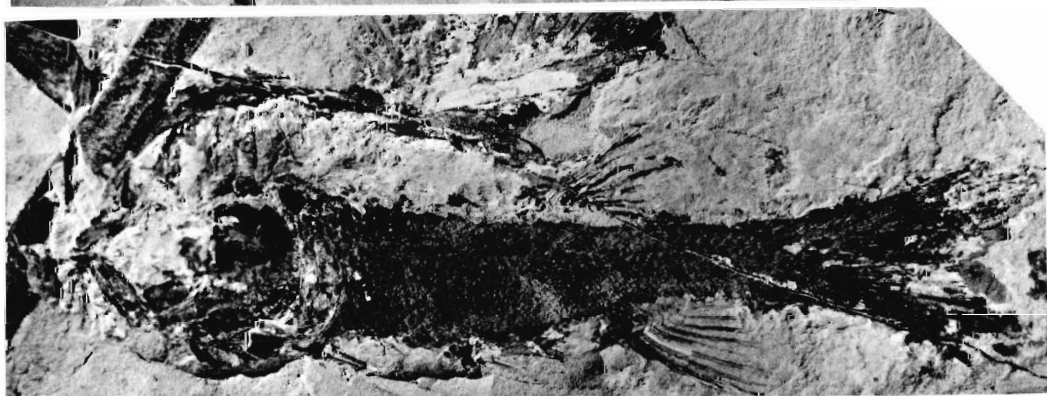
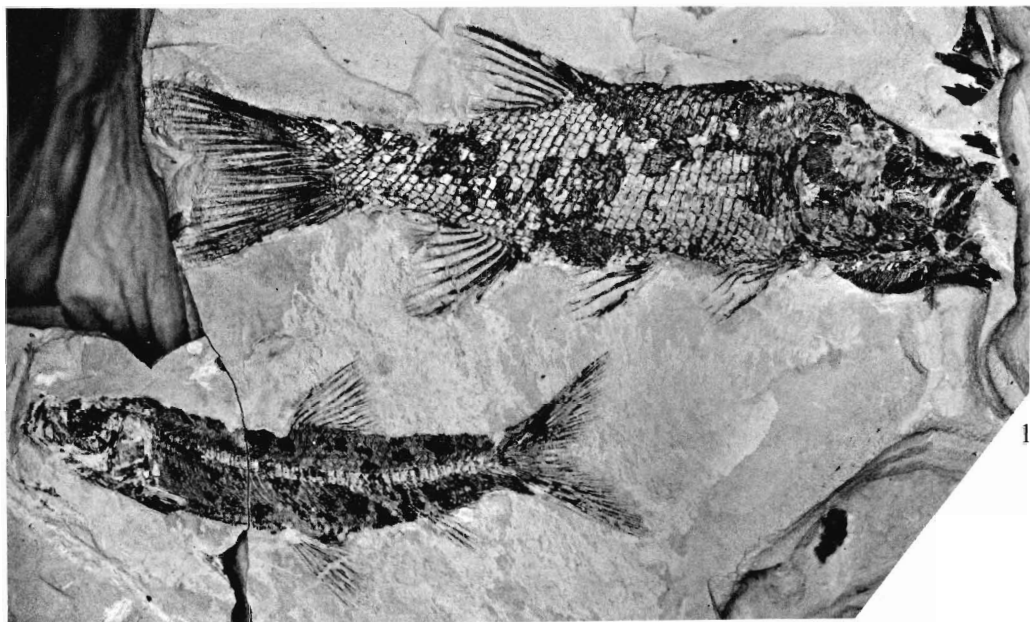
EXPLANATION OF PLATE 6

Figs. 1-3. *Wadeichthys oxyops*, gen. et sp. nov.

1, *W. oxyops*. P.24676A (top) and *Leptolepis koonwarri* preserved on the same bedding plane,  $\times 1$ .

2, MUZ 3231A. The youngest individual known,  $\times 1.5$ .

3, MUGD 3647B. Sub-adult growth stage of scale coverage. Dorsal (1) and anal, (2) fin radials exposed,  $\times 1.4$ .



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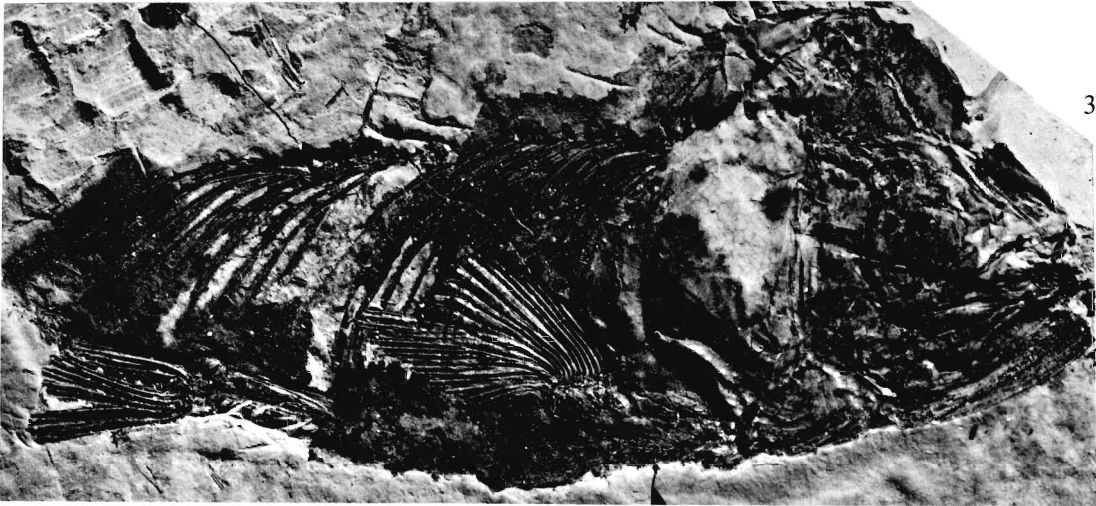
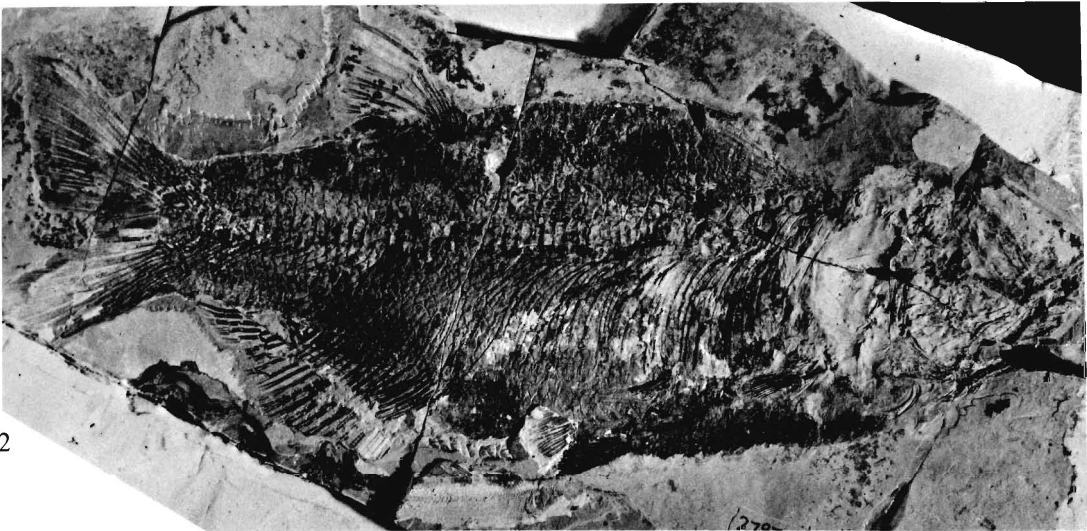
EXPLANATION OF PLATE 7

Fig. 1. *Wadeichthys oxyops*, gen. et sp. nov. MUZ 2385B. Young fish, exhibiting posterior axial skeleton,  $\times 6$ .

Figs. 2, 3. *Koonwarria manifrons*, gen. et sp. nov.

2, MUZ 2797A. Holotype. Largest specimen known,  $\times 0.5$ .

3, Young fish, centra undeveloped,  $\times 4$ .



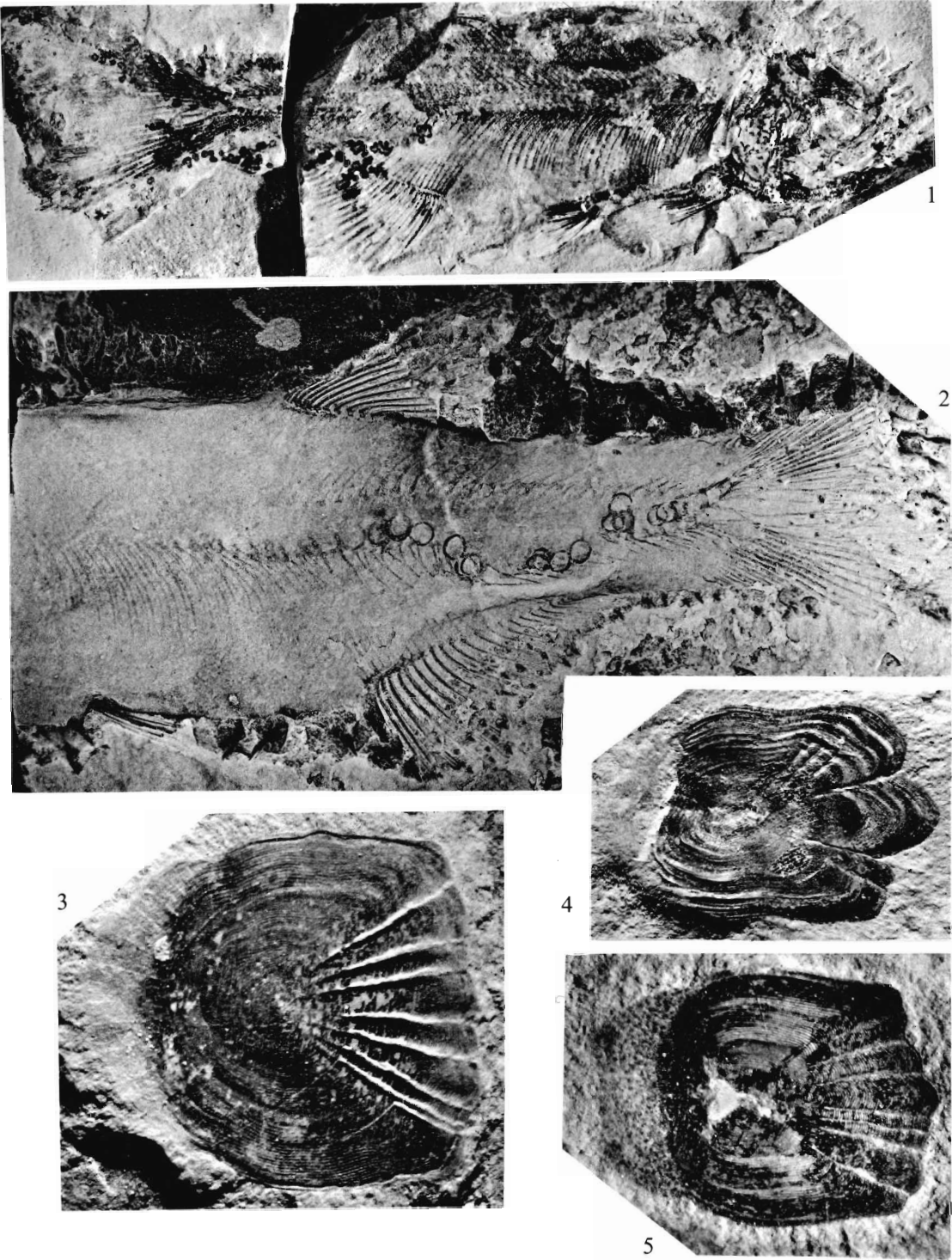
WALDMAN, Australian Cretaceous fish

EXPLANATION OF PLATE 8

Figs. 1-5. *Koonwarria manifrons*, gen. et sp. nov.

- 1, MUZ 2799B. Young fish, centra undeveloped,  $\times 1.6$ .
- 2, MUZ 2126A,  $\times 2$ . Note preservation of ring centra in posterior axial region.
- 3, MUZ 3032. Scale,  $\times 11$ .
- 4, P.24681. Possibly a pathological scale,  $\times 10$ .
- 5, MUZ 2697. Scale,  $\times 12$ .





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EXPLANATION OF PLATE 9

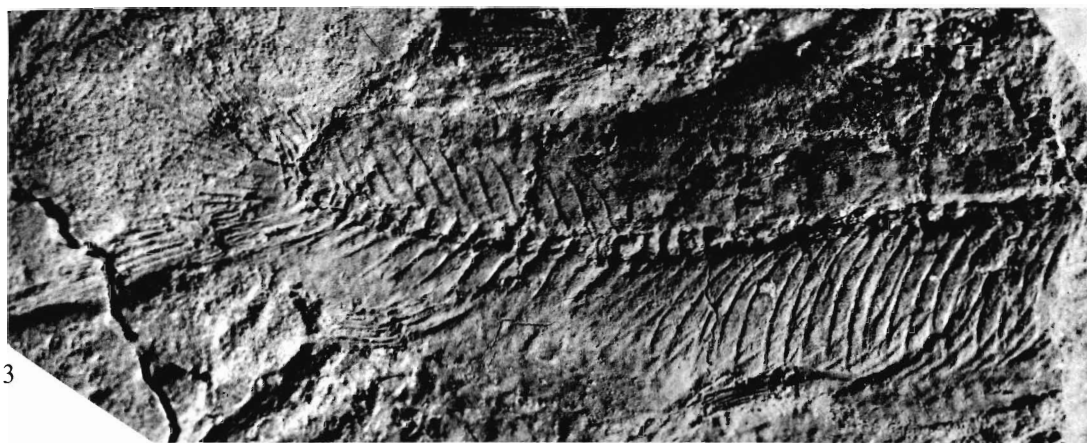
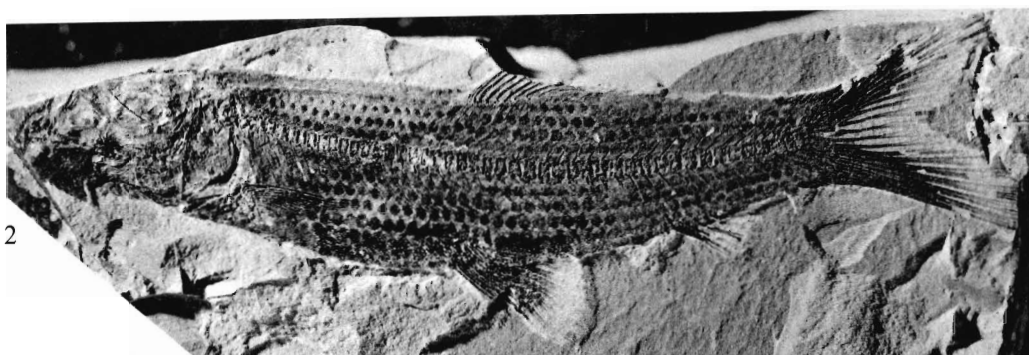
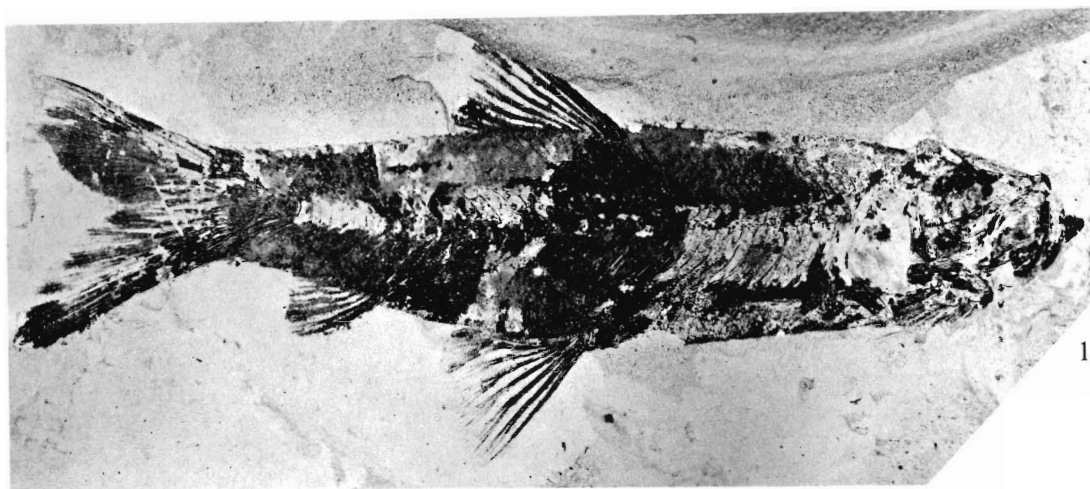
Figs. 1, 2. *Leptolepis koonwarri* sp. nov.

1, MUZ 3649, holotype,  $\times 1.8$ .

2, MUZ 3107A,  $\times 1.3$ . Note scale pattern.

Fig. 3. *Leptolepis crassicauda* Hall, holotype and sole specimen. National Museum of Victoria,  $\times 1.1$ .





WALDMAN, Australian Cretaceous fish

EXPLANATION OF PLATE 10

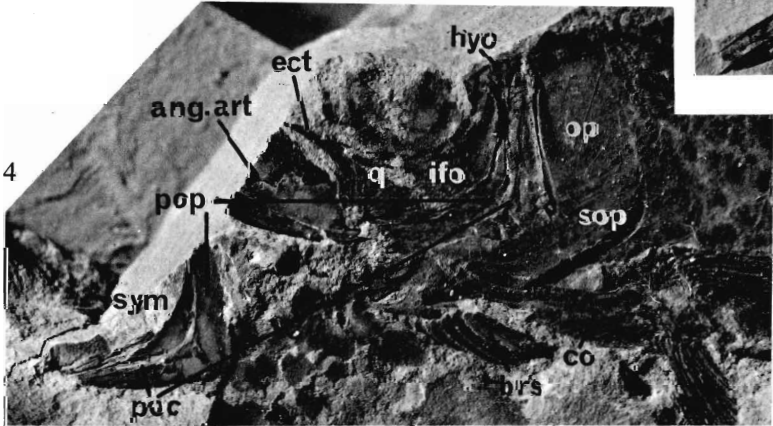
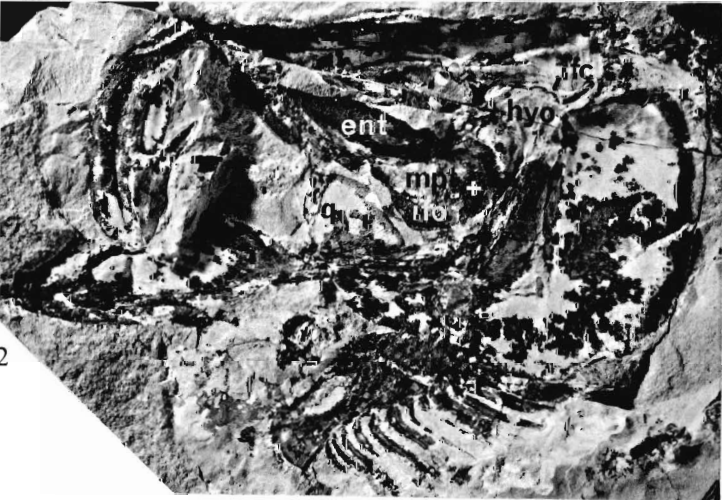
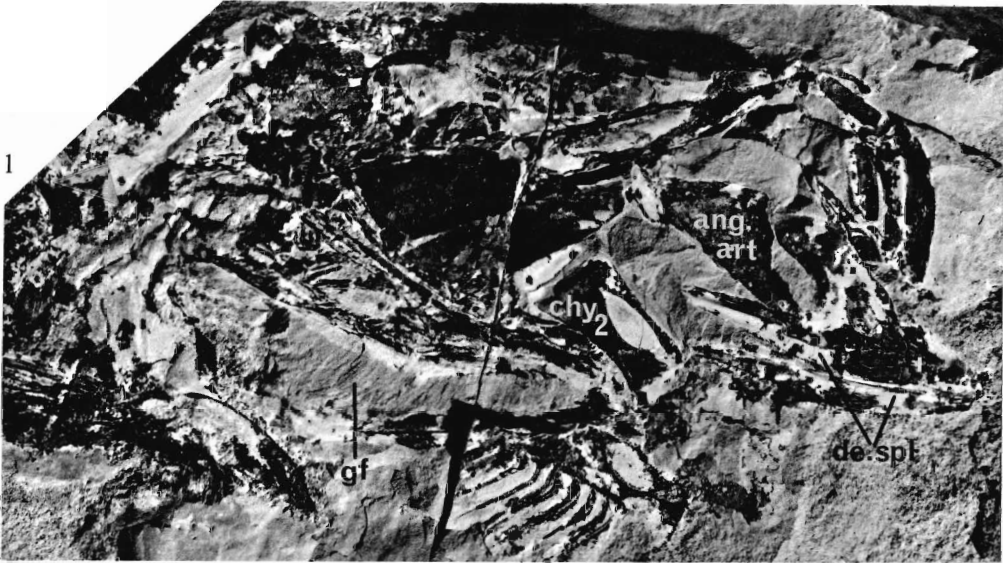
Figs. 1-4. *Leptolepis koonwarri* sp. nov.

1, P.26129A. Skull in mesial aspect,  $\times 2$ .

2, P.26129B,  $\times 1.6$ . Note tuberculate quadrate.

3, MUGD 3636B. Disarticulated lower jaws,  $\times 6$ .

4, MUZ 3653A. Partially disarticulated skull,  $\times 5$ . (See also text-fig. 31B.)



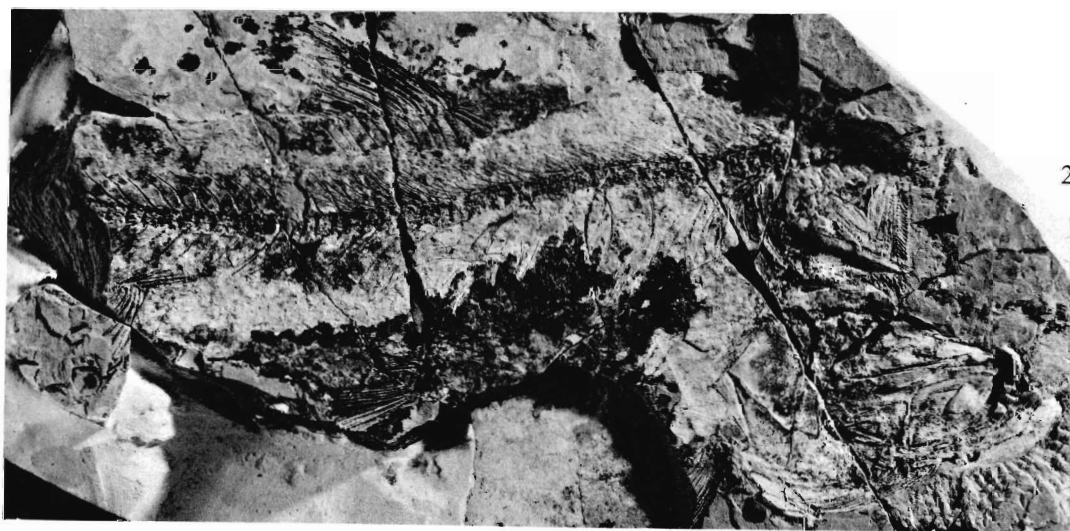
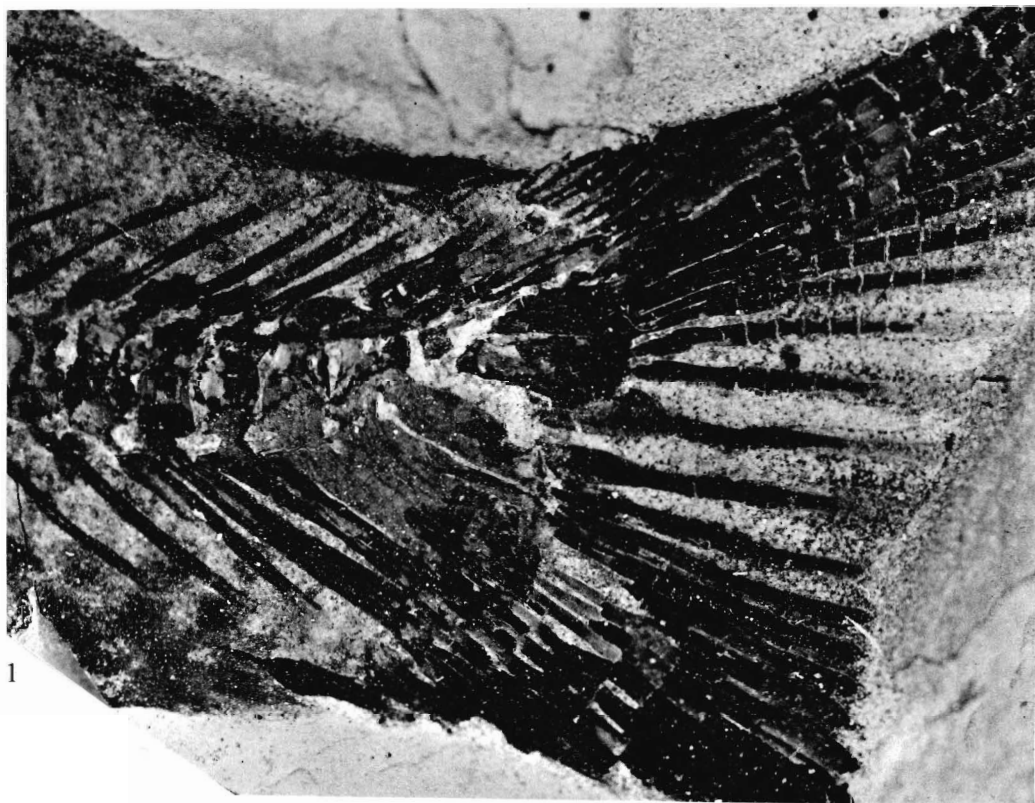
WALDMAN, Australian Cretaceous fish

EXPLANATION OF PLATE 11

Figs. 1, 2. *Leptolepis koonwarri* sp. nov.

1, MUGD 3640A. Caudal region,  $\times 8$ . (See also text-fig. 32.)

2, MUZ 3030A. Skull displaced to reveal gill-arches (arrowed),  $\times 0.7$ . (See also text-fig. 28A.)

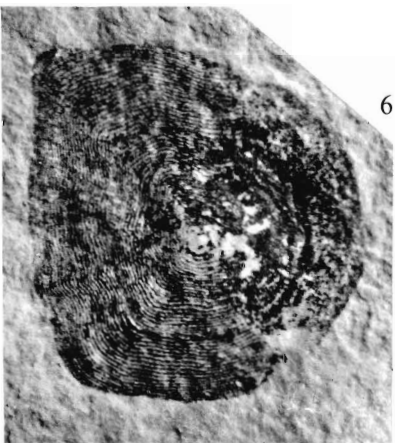
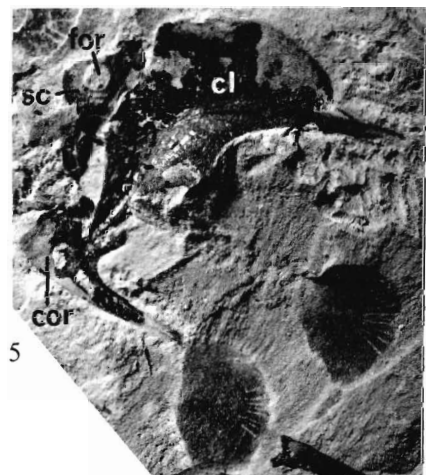
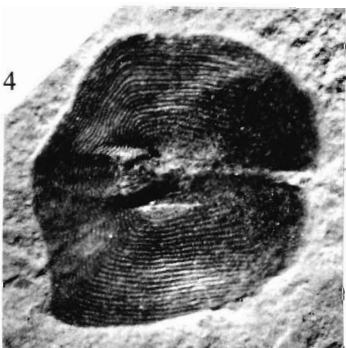
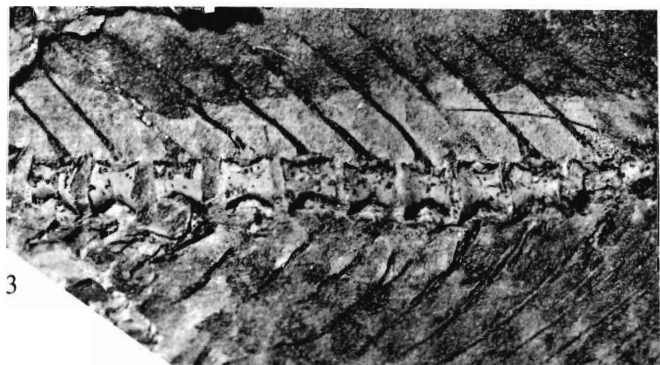
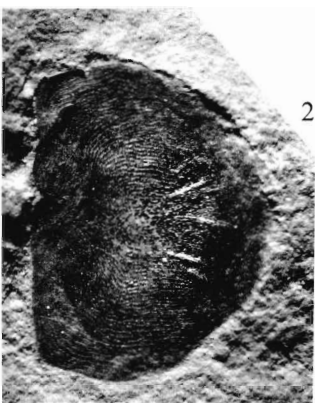
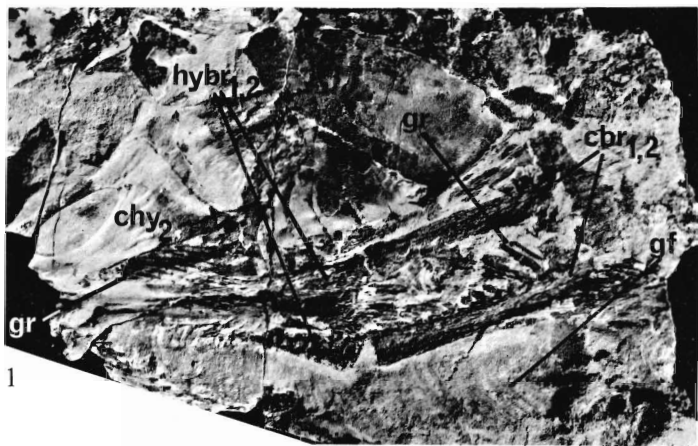


WALDMAN, Australian Cretaceous fish

# EXPLANATION OF PLATE 12

Figs. 1-6. *Leptolepis koonwarri* sp. nov.

- 1, P.26129B1. Part of 1st and 2nd gill-arches. Note gill-rakers and filaments,  $\times 4$ .
- 2, MUZ 3034. Two scales superimposed, showing radiating grooves,  $\times 8$ .
- 3, MUZ 3104A. Clay infilling of notochordal canal, surrounding vertebral bone having been destroyed by weathering,  $\times 6$ .
- 4, MUZ 3035. Lateral line scale,  $\times 21$ .
- 5, MUGD 3643B. Displaced pectoral girdle,  $\times 5$ . (See also Pl. 16, fig. 1.)
- 6, MUZ 3033. Scale,  $\times 14$ .



WALDMAN, Australian Cretaceous fish



were becoming fewer, but it should be remembered that the exact age of the Talbragar beds is unknown. During this time the archaeomaenids had also given rise to the koonwarriids. While the archaeomaenids of Talbragar exhibit a scale gradation from the rhomboid, enamelled-scale condition to the cycloid state, *Wadeichthys* retains the 'primitive' rhomboid scales with no evidence of thinning. The scales of *Koonwarria* (the type genus of the new family Koonwarriidae) are indistinguishable from those of many modern teleosts and this family is undoubtedly derived from the Archaeomaenidae.

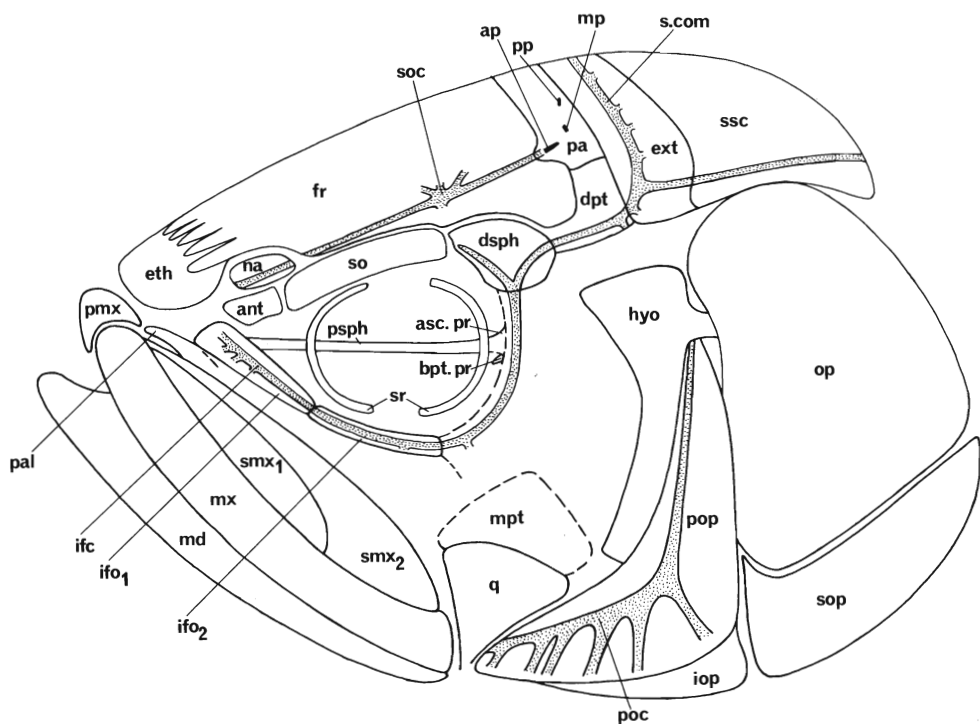
I consider it diagnostic of the younger age of the Koonwarra beds that the intermediate forms with both rhomboid and cycloid scales together (e.g. *Aetheolepis*) are absent, and that the teleost *Koonwarria* is present.

Patterson (1967) has rejected the idea of any major polyphyly in teleost origins, and the evidence provided by the archaeomaenids and koonwarriids is in accordance with his statements, in so far as the Pholidophoriformes may still be regarded as the group ancestral to the teleosts. The leptolepids are by far the most common fish at each locality, implying their great success in these environments. It is unfortunate that we know little of the ecological niche of *Koonwarria*, and cannot derive any real information from its comparative rarity at Koonwarra. This may be merely due to the region of the lake explored on the site, or be a true representation of its occurrence.

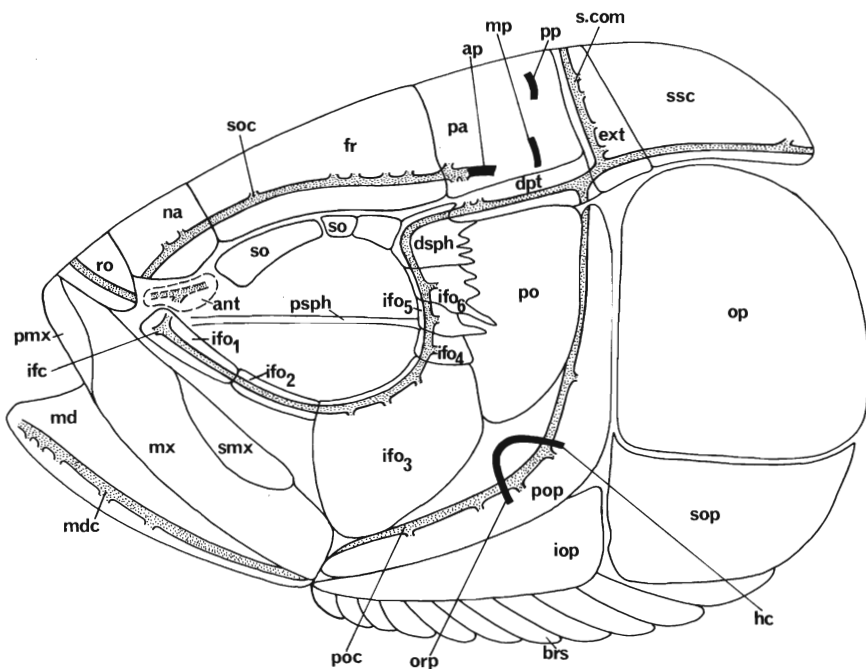
The Leptolepididae of the 2 sites show a close relationship, however, and *L. koonwarri* represents a higher level of organization than *L. talbragarensis*. This lends further weight to the hypothesis that the Koonwarra beds are younger than those of Talbragar. It is evident that a considerable amount of biotic interchange must have occurred in the 'south-eastern Australian lake' in the Jurassic-Lower Cretaceous. Apart from scattered, fragmentary finds, the two sites mentioned have yielded the only freshwater faunal assemblages of any magnitude in the mid-upper Mesozoic of Australia. It is difficult on this rather scanty evidence to propose any definite hypothesis as to the nature of the 'south-eastern lake'. Whether it was one large inland body of water, or a basin or trough containing a vast number of interconnected lakes, ponds, rivers, and streams is not known. On the available faunal evidence the latter theory appears more convincing, providing a type of 'filtration route' allowing some to pass and some not. This might explain, for example, the absence of macrosemiids from Koonwarra. A much greater weight of evidence must be built up, however, before anything definite may be said on this matter (see also Douglas 1969).

The freshwater Triassic exposures in New South Wales have yielded a large fish fauna, described by Woodward (1890a, 1908) and Wade (1935, 1939, 1940). It is difficult to derive any of the Australian Jurassic or Cretaceous forms (except *Ceratodus*) from that fauna. No leptolepids are known, for example, although these are present in the Triassic of Austria (Seefeld) and Tanzania. Pholidophorids are also unknown as the specimens referred to that family by Woodward (1890a, 1908) were incorrectly assigned (Wade 1939, 1940). Palaeoniscoids are very common. With regard to dipnoans, *Ceratodus* is known from Brookvale (Wade 1935), *Gosfordia* from Gosford (Woodward 1890a), and *Sagenodus* (*Ceratodus*, Wade 1940) from St. Peter's (Woodward 1908), all in New South Wales. The familial positions of *Gosfordia* and *Sagenodus* are doubtful, due to incomplete preservation.

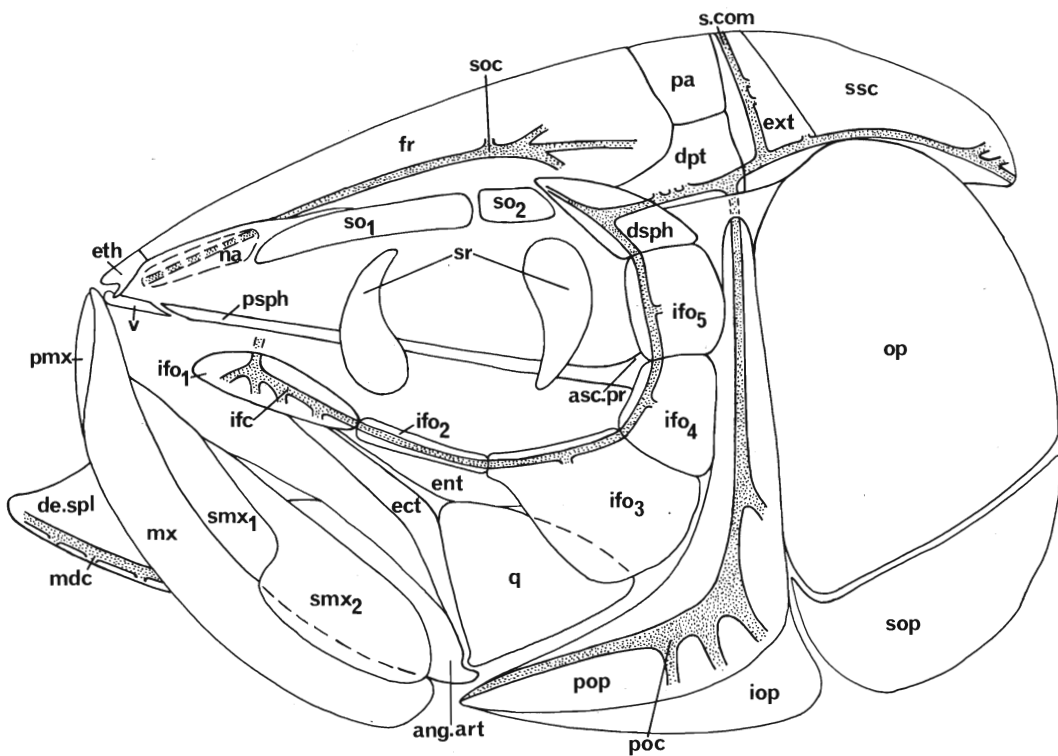




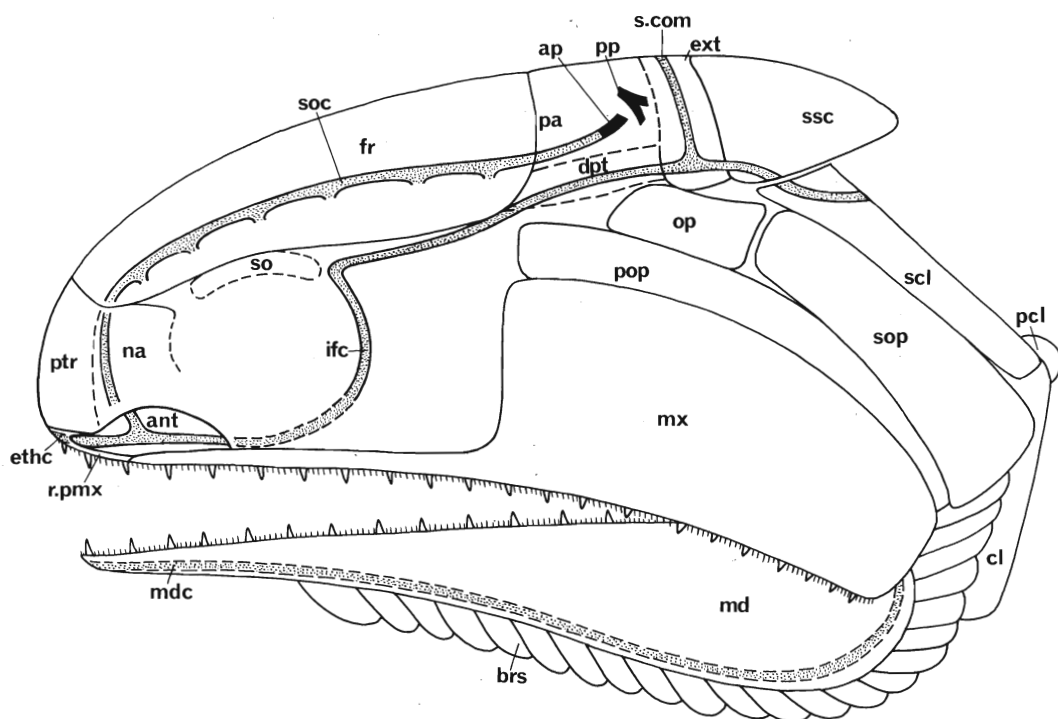
TEXT-FIG. 33. *Koonwarria manifronds*, reconstruction of skull. About twice adult size.



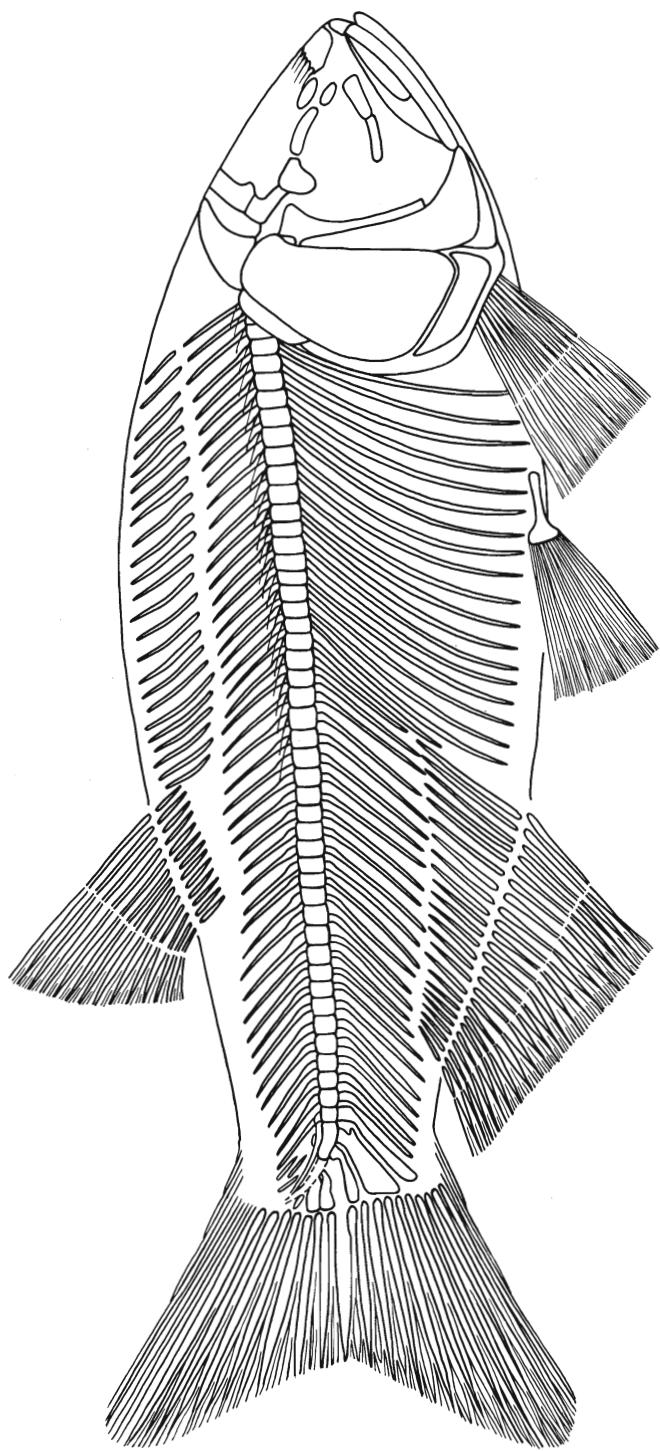
TEXT-FIG. 34. *Wadeichthys oxyops*, reconstruction of skull. About 5 × adult size.



TEXT-FIG. 35. *Leptolepis koonwarri*, reconstruction of skull. About  $4\times$  adult size.



TEXT-FIG. 36. *Coccolepis woodwardi*, reconstruction of skull. About  $2.5\times$  adult size.



TEXT-FIG. 37. *Koonwarria maniffrons*, reconstruction. About  $0.6\times$  size of largest specimen.

It seems likely that the Jurassic-Lower Cretaceous fish-fauna of the south-eastern lake represents an incursion of fish at a date later than that represented by the Triassic exposures. Jakovlev has informed me (pers. comm.) of archaeomaenid-like fish from the U.S.S.R. If these do turn out to be true archaeomaenids then the situation becomes intriguing as there are no suitable archaeomaenid-ancestors (i.e. neither parasemionotids nor primitive pholidophorids) in the Australian Triassic. The only parasemionotiform described from Australia is the Triassic *Promecosomina* (Promecosominidae) (Wade 1935, 1940) which Gardiner (1960) considered an offshoot of the parasemionotid-furid lineage. This suggests a migration route towards, rather than a radiation from Australia for the Archaeomaenidae. The occurrence of the coccolepids (see Liu 1957) shows an interesting distribution including England, continental Europe, U.S.S.R., China and possibly Korea, as well as Australia. The migration pattern of the coccolepids and primitive pholidophoroids/archaeomaenids may have been somewhat similar. It is, of course, possible that the archaeomaenids are descended from a different parasemionotoid ancestor than are the pholidophorids. *Leptolepis* is much more difficult to follow accurately, due largely to taxonomic confusion in past literature, but definite Triassic leptolepids are known from outside Australia, as previously stated.

In Eastern Asia, as far as I am aware, *Leptolepis* is replaced by *Lycoptera* and its allies as well as *Mesoclupea* (?Chirocentridae), in the extensive freshwater beds of that region. The only possible exception is the specimen tentatively called *Leptolepis* by Liu (1957). It seems likely that whatever the migration routes of *Leptolepis*, these were dissimilar in some ways from the early pholidophorids (from which they may be derived) and the coccolepids.

All three families common to Talbragar and Koonwarra appear to have arrived in Australian waters probably very early in the Jurassic and subsequently became isolated in freshwater. From their fossil record elsewhere (see individual historical summaries) these groups appear to include species tolerant of both marine and fresh waters.

#### THE INVERTEBRATE FAUNA

This fauna is to be described by E. F. Riek, Department of Entomology, C.S.I.R.O., Canberra, but a brief résumé of its general aspects may be given here.

Many orders of insects are known from Koonwarra, including the following: Ephemeroptera (Mayflies), Plecoptera (Stoneflies), Odonata (Dragonflies), Dictyoptera (Cockroaches, etc.), Hemiptera (Bugs), Mecoptera (Scorpion flies), Siphonaptera (Fleas), Diptera (Flies), Coleoptera (Beetles), Hymenoptera (Wasps, etc.), and possibly Trichoptera (Caddis flies). The insect fauna is capable of yielding a considerable amount of information on the palaeo-environment, but only a few salient points will be noted here.

The mayflies are very closely related to modern cold-adapted genera which are always shallow-water dwellers. Stoneflies are found solely in cold, well-aerated waters, and the only ones able to survive in standing waters live in subalpine lakes, although a species immediately related to the Koonwarra form can survive in cold-water lagoons and backwaters in the presence of prolific submerged vegetation

(E. F. Riek, pers. comm.). The dragonflies and damselflies occur in a variety of situations, the former tending to live on the mud and the latter in weed growth.

The aquatic larvae of the scorpion-fly *Nannochorista* lives at the present time in the silt of shallow backwaters or at the margins of lakes. The gerrid water bugs found at Koonwarra generally dwell in quiet-water regions. Although water beetles breed in a variety of aquatic situations those found at Koonwarra represent lacustrine or paludal environments. No coleopteran species characteristic of fast-flowing waters are known from Koonwarra (E. F. Riek, pers. comm.).

From this assemblage Riek has submitted (pers. comm.) that: 'The assemblage of aquatic insects in the Koonwarra sediments is such that they must have lived in the shallow margins of a cold lake or in a shallow backwater on a cold stream.'

With regard to aquatic arthropods other than insects, Crustacea (Orders Conchostraca and Anostraca) are abundant and a single limulid is known. The conchostracans were referred to the genus *Cyzicus* by Talent (1965) and the limulid is to be described by E. F. Riek and E. D. Gill.

Conchostraca are, according to Williams (1968) '... of rather sporadic occurrence in Australia, and they are by no means common animals ... they occur as free-swimming animals in lakes, ponds, dams and temporary freshwater pools'. *Cyzicus* is a living genus occurring commonly in Australia (Williams, 1968). The Koonwarra species is variously preserved, some individuals being isolated and others occurring in large numbers on a single bedding plane. All occur in the claystone laminae, often with both valves of the carapace still joined together.

Anostracans may occur in a variety of environments ranging from hypersaline to freshwater, '... but their usual habitats appear to be small still waters such as ponds, pools, ditches, farm dams and small lakes' (Williams 1968).

The arachnoids are represented by a limulid which has little ecological significance (Talent 1965) as limulids are known from freshwaters today and from freshwater sediments in the past (Størmer *et al.* 1955).

The non-aquatic fauna yields some information, but not in as detailed a form as the aquatic fauna. The carabid and staphylinid beetles are of a type commonly found at the present day around lake margins. The leaf-hopper (Order Hemiptera) is very similar to present-day species living on eucalypts (E. F. Riek, pers. comm.). The two genera of fleas indicate the presence of mammals; or, less probably, other vertebrates.

## THE FLORA

Dr. J. G. Douglas has studied the flora (Douglas 1969) and some results of discussions with him are summarized below.

Preservation is principally as impression but compressions weathered to a varying degree are occasionally found. About 50 separate plants have been found, but perhaps 10–15 of these may be different parts of plants (e.g. seed, leaf, stem, etc.). 30 or more natural plant species are certainly represented.

The Bryophyta appear to be represented only by the liverworts. 4 of these have been described (Douglas, MS.). 1 plant has been allocated to the Isoetales and cones tentatively attributed to a small, probably prostrate lycopod are common.

Pteridosperms are very common and may have reached a height of a few feet. *Taeniopteris daintreei* McCoy seems to have corresponded in some ways to the 'bracken' of the present day. This species is characteristic of the middle zones of the Victorian Upper Mesozoic.

Sphenopsids (equivalents of the modern *Equisetum*) were also present, 2 species having been distinguished. Conifer remains, both vegetative and fertile, are plentiful, with several species represented. These include a species much like the 'hoop-pine' (*Araucaria*) of the present time.

*Ginkgoites* leaves are common in some laminae and, like the conifer remains, probably belonged to trees of substantial size, possibly up to 30 m in height.

Angiosperms are represented by about 4 types of dicotyledon, but no monocotyledons have been observed. Only one of the dicotyledons has been found elsewhere in Victoria.

Notably absent are the Bennettitales, an extinct group present in Zones A, B, and basal C of the Victorian Lower Cretaceous beds.

The palaeo-environment envisaged is one of a limited area of water with small, aquatic, or near-aquatic angiosperms in and round the perimeter, possibly accompanied by sphenopsids. Slightly removed from the water's edge would be a region occupied by *Taeniopteris* and perhaps small conifers, and beyond this a back forest of larger conifers and *Ginkgoites*. The last-named probably resembled the present-day *Ginkgo* in size. The bryophytes would have occupied damp areas such as stream banks or on decaying logs. Rooted growth has been noted, but is very rare. Seeds of an angiosperm much like *Trapa* are congregated in groups and have evidently fallen from the plant directly into the area of preservation. The conifers and ginkgos were close enough to the lake to have contributed fronds and leaves in a comparatively complete state, and were probably not more than about 30 m away from the shore. The conifers are well represented by wind-dispersed seeds.

From this evidence Douglas proposes precipitation of perhaps 100–150 cm per annum. There is no botanical evidence pointing conclusively to freezing, arid, or tropical conditions, but the lack of evidence from cuticular material must be remembered in this connection. The Koonwarra flora must have originated from a specialized environment or have been preserved under unusual conditions, however, as there are about 12 species of plant present which have not been found elsewhere in the Victorian Upper Mesozoic.

*Ginkgoites* leaves and conifer seeds are found in the claystone laminae, stratigraphically very close to the position of the fish. Present-day *Ginkgo* and conifers lose leaves and seed in the autumn and it is probable that their Cretaceous counterparts were embedded in the clay at Koonwarra just before the periodic mortality of the aquatic fauna.

With regard to age, Douglas (1969) and Dettmann (1963) basically agree that the deposit is Aptian–Albian in age. The Koonwarra beds fall within Dettmann's 'speciosus' zone, which is approximately equal to Douglas's 'Zone C'.

# THE GEOLOGY OF THE KOONWARRA FISH-BED AND SURROUNDING SEDIMENTS

*Stratigraphy.* The fish-bed is part of a stratigraphic thickness of 7.1 m of mudstone occurring within a succession of fine-medium grained arkose which makes up most of the 124 m length of the road-cutting. The succession in the cutting is summarized in Table 4. The whole succession dips at 35–40°, striking 230–235°.

As may be seen from Table 4, the arkose is current-bedded, and contains layers of clay-galls, impersistent siltstone, and carbonaceous bands, as well as considerable amounts of plant breccia. No vertebrate material has been found in the arkose at Koonwarra, but this may be due in part to the search for fossils having been concentrated in the fish-bed.

The fish-bed is divided into two parts. The lower is laminated, much as in the upper bed, and includes larger fish than are found in the latter. It is 0.23 m thick. Between the lower and upper parts of the fish-bed is a stratum of siltstone which is laminated only in the sense that it may be split into thin sheets perhaps 6–12 mm thick. The upper part of the fish-bed is 1.24 m thick in the quarry above the road-cutting and contains a very large number of complete fish and arthropods, as well as plant material, although the fish tend to be more prolific in the top 0.6–0.9 m of the bed. The mudstone succession above the upper fish-bed is severely weathered, and little detail is observable. It has weathered to a stiff clay and is succeeded vertically by further non-laminated mudstone.

As the two parts of the fish-bed are so close stratigraphically it would be artificial to separate them and they are, therefore, known as 'The Koonwarra Fish-Bed'. As may be seen from the discussion of the duration of the fish-bed environment, the sediments between the 2 parts may only represent a very few years, or possibly less, and may be regarded as a minor interruption in the fish-bed environment.

TABLE 4

## *The Stratigraphic Succession in the Koonwarra Road-cutting*

		<i>m</i>
<i>Upper Arkose</i>	Medium-grained arkose with clay-galls and plant remains. At least	5.60
	Very thin, imperisistent, carbonaceous band, less than	0.03
	Medium-grained arkose with clay-galls often occurring in bands. Current bedded	2.20
	Impersistent blue-grey siltstone with carbonaceous fragments	0.31
	Medium-grained current bedded arkose with clay-galls	16.70
	Fine arkose with mudstone weathering blue-grey	0.93
	Medium-grained arkose	3.72
	Fine arkose containing about 6 carbonaceous layers	0.10
	Fine arkose with mudstone weathering blue-grey	0.67
<i>Mudstone Succession</i>	Arkose with narrow bands of silty and carbonaceous material	4.03
	Laminated siltstone/claystone which includes the fish-bed	7.13
<i>Lower Arkose</i>	Lower medium-grained arkose with clay-galls and plant remains. At least	11.50

Measurements represent actual stratigraphic thicknesses. The measurements of the Upper and Lower Arkoses are terminated at each end of the road-cutting.

TABLE 5

*Detail of the Mudstone Succession (see Table 4)*

upper arkose			
<i>local unconformity</i>			
	<i>m</i>		<i>m</i>
Mudstone with plant fragments (estimated thickness)	3.04	which begins 0.23 m above the lower margin	1.24
Laminated siltstone/claystone	0.13	Siltstone—irregularly laminated—holds water	0.10
Grey sandy clay	0.08	Fine arkose	0.23
Laminated siltstone/claystone	0.08	Mudstone	0.03
Grey clay	0.03	Fine arkose	0.03
Yellow sandy clay	0.05	Mudstone	0.08
Laminated siltstone/claystone	0.31	Mudstone with fine arkose stringers	0.13
Blue-grey clay	0.05–0.08	Mudstone	0.08
Laminated siltstone/claystone	0.31	Uncompacted fine arkose	0.10
Blue-grey clay	0.10	Ochreous and grey clay	0.08
Laminated siltstone/claystone—the upper part of the Koonwarra fish-bed, plants in lower part	1.24	Variegated mudstone	0.05–0.08
Mudstone with insects, anostracans, plants. Includes lower part of fish-bed		Fine arkose	0.03
		Cross bedded mudstone and arkose	0.13
		Ochreous and carbonaceous clay	0.08
		<i>local unconformity</i>	
		lower arkose	

Progressing north-east along the strike of the fish-bed the mudstone succession begins to wedge-out between the two arkoses. In the southern wall of the railway cutting, which runs approximately parallel with the road-cutting (see map), the thinner mudstone succession is clearly visible, the laminated upper part of the fish-bed still being present and yielding *Leptolepis*. Although not much material has been removed from this part of the bed, *Leptolepis*, the conchostracan *Cyzicus* (Talent 1965), and plant fragments have all been found. The mudstones are reduced to a stratigraphic thickness of 2.79 m and the condensed sequence is given in Table 6.

TABLE 6

upper arkose			
<i>local unconformity</i>			
	<i>m</i>		<i>m</i>
Weathered grey clays	1.86	Mudstone, with a little sand	} 0.77
Fish-bed: laminae very thin	0.15	Mudstone, penetrated vertically by underlying arkose	
		<i>local unconformity</i>	
		lower arkose; clay galls near contact	

*The Lamination and its Origin.* The fish-bed sediments have been studied by means of both thin (Pl. 13, figs. 1, 2) and ground sections made at right angles to the bedding. Within the mudstones there is a degree of cyclic sedimentation. In the lower-middle region of the succession, mudstone and fine arkose alternate, while above the fish-bed the alteration is between laminated mudstone and grey clay (see Table 5).



It is, however, within the fish-bed that the finest examples of rhythmic sedimentation are to be seen. The fish-bed is clearly laminated, the layered appearance being given by alternate light and dark layers of mudstone. The lighter layers consist of pale grey siltstone which becomes progressively finer vertically, grading into a claystone of a darker grey colour. Above each claystone layer there is typically a sharp contact with a further light grey siltstone layer which in its turn exhibits the fine gradation previously mentioned. There are 166 such couplets of light and dark laminae in the fish-bed, and this is the simplest form of lamination found within the sequence.

It is most likely that this sedimentation pattern represents seasonal change of an annual nature, each pair of light and dark laminae representing a single year. De Geer (1912) instituted the term 'varve' for the distinctly marked annual deposit of a sediment regardless of its origin (statement by Bradley 1929, quoting Antevs 1925) and assuming this definition the Koonwarra fish-bed may be described as a varved claystone-siltstone. The term 'non-glacial varve' (Bradley 1929, 1937) is not applicable to Koonwarra. Bradley stated (1937, p. 32) 'Apparently the most reliable characteristic of non-glacial varves . . . is the presence of organic matter in one lamina of the varve' and also that this matter may be either a 'bitumen-like substance or parts of siliceous or calcareous organisms'. This is totally unlike the sedimentation present in the fish-bed.

De Geer (1912) did not use the term 'glacial' in his definition of varves, but most of the work on this subject has been carried out on varves formed by glacial action, i.e. by true glaciation. For example, Pennington (1947, p. 140) stated that varves are '... annual laminations formed by the seasonal deposition from glacial drainage into standing water'. It is not proposed in the present study that the Koonwarra palaeolake was glacier-fed, or that permanent glaciers or ice-sheets were present. Winter snow and ice in higher regions together with a freezing of the watershed is all that is envisaged.

The literature on varves is considerable, but among references consulted have been: Antevs 1951, Berkey 1905, Bradley 1929, 1937, 1948, Burwash 1938, Fraser 1929, Johnston 1922, Kindle 1930, Pennington 1947, Reeds 1927, Rittenhouse 1934, and Sayles 1919, 1928.

Within a single clay lamina there may be several minor layerings, due to minute differences in grain-size (Pl. 13, figs. 1, 2). I have referred to these as 'microlaminae'. They may be due to minor fluctuations in water temperature during the winter, causing variations in the rate of precipitation of the finest material. Slight warm spells in late winter might also have caused a minute ingress of waters containing fine sediment (Fraser 1929, Kindle 1930). If the lake were situated at a much lower altitude than the majority of its catchment area, it may have thawed a little earlier than the higher regions. Wind and wave action could then have stirred up some of the finer top layers of sediment before the arrival of the main meltwaters. If the sediments have been disturbed and redeposited, each successive microlamina should show a decrease in grain-size. I can only say that the microlaminae consist of clay-grade particles of sericite (white mica) less than  $4\text{ }\mu\text{m}$  across. Kuenen and Migliorini (1950) noted that the fine laminations within varves may be due to variations in melt-water discharge from rivers.

Above the clay fraction of a siltstone/claystone couplet there may be other minor

clay and/or silt layers, perhaps as many as 10 in 25 mm (Pl. 14, fig. 1). It is likely that these represent structures described as follows by Pennington (1947, p. 141): 'Difficulties may arise in the measurement of varves owing to the presence of deceptive bands resembling the winter layers. Such layers which De Geer calls digraphs and trigraphs, can often be distinguished by the absence of the typical sharp winter-spring junction. . . . It is very difficult to distinguish these structures at Koonwarra as there seems to be a thickness-series ranging from probable digraphs and trigraphs up to lamina couplets of varve type. The origin of the minor ones may be similar to that of the micro-laminae, differing only in magnitude, i.e. the possibility of 'thaw-freeze-thaw' conditions before the onset of a complete thaw. Small sedimentary influx in certain years may account for some of the narrower pairs of laminae.

Thin layers of the coarsest sedimentary fraction sometimes occur, consisting of angular quartz grains of similar size. These bands probably represent shoreline sands washed out on to the clays in late autumn by sudden rainstorms or similar phenomena.

There is also a single thick band (about 25 mm in thickness) of unsorted clay and silt which may be due to rapid influx and deposition of sediment. It is overlain by a clay lamina representing the final slow deposition of the fine material. Such a thick lamina may be comparable with 'drainage varves' (Antevs 1951, pp. 1257-1258), due to a greater sedimentary influx than normal. Possibilities include: river or stream capture providing a greater sediment load, a change in river channel bringing the region of sedimentary ingress closer to the fish-bed environment, subaqueous slumping, and heavy rainfall in the catchment area.

The problem of translating the lamina-couplets into years is difficult due to the digraphs and trigraphs, which are of uncertain significance. Reeds (1927, p. 54) noted that '... a sharp line of demarcation in between the top of the "winter" layer and the base of the succeeding "summer" layer . . . [is] of value . . . in separating the seasonal layers into varves or annual deposits'. Kindle (1930, p. 85) mentioned that cold periods within the summer causing variation in stream flow '... may complicate the problem of translating the record into years', and also noted that in deeper regions of a glacial lake (about 11 m in that particular case) fine sediment may remain in suspension for more than 1 year. This would further confuse the counting of varves in that a sharp contact would not be formed under such conditions. However, Rittenhouse (1934, p. 111) and Fraser (1929, p. 59) cited Antevs as stating that flocculation would account for the precipitation of all material, and Johnston (1922, p. 380) referring to the glacial Lake Louise, Alberta, Canada, stated that the water is clear by the spring, the fine material having settled out.

It seems to be generally accepted that whatever the mechanism involved, all sediment in most regions of a very cold lake is deposited before the arrival of thaw-material in the spring. It follows, therefore, that in the majority of cases the winter-spring contact will be a sharp one.

At Koonwarra some small 'laminae' have sharp contacts whereas others do not, so that any count of annual layers must be an approximation. Including these minor 'laminae', but excluding the microlaminae, there are 166 couplets of laminae within the fish-bed. Assuming all of these to be annual, that figure represents the duration in years of the bed. Such an assumption may well be invalid (due to the inclusion of the minor 'laminae') and it seems far more likely that the 1.24 m thickness of the

upper bed represents less than 50 years of deposition. There is no evidence of an hiatus in the mudstones, apart from the minor (local) unconformities against the arkose at top and bottom of the succession.

*Conditions for the Formation of Laminated, Graded Bedding.* Most work of this nature has been carried out with regard to varve origins and is applicable to this study.

Some essential conditions for the formation of laminated clays of the diatactic type (Sauramo 1923) were stated by Fraser (1929) in his laboratory experiments on varve-deposition. (Diatactic structure [Fraser, loc. cit., citing Sauramo] is the effect of sorting of particles according to their size and specific gravity, coarsest at the bottom and finest at the top.)

1. Unflocculated material of assorted sizes.
2. Sedimentation in water of low temperature.
3. Low concentration of electrolytes.
4. Periodic supply of material.

Fraser (loc. cit.) stated that the grading of varves is caused by low temperatures retarding the fall of fine particles, that the maximum salinity in which coarse clay varves will form is 1/50th that of normal sea-water, and that varve-like sediments can be reproduced in the laboratory, if unflocculated material is sedimented in fresh water near a temperature of 0 °C.

Any of these conditions could have occurred at Koonwarra.

Kuenen and Migliorini (1950) produced various kinds of graded bedding in the laboratory, some of which resemble those present at Koonwarra. They stated that the grading of varves is due to the slow rate of settling in cold waters and the gradual grain-size decrease after the spring thaw.

The fineness of the particles (silt and clay) implies that deposition was far removed from the point of influx of material into the lake; or, that only particles of this size ever entered the lake. The perfect preservation of the laminae indicates an absence of burrowing fauna and of much rooted vegetation, and that the fauna died before coming into contact with the bottom sediments.

The wedging out of the mudstones and condensation of the laminae in the north-eastern exposure of the bed resembles the 'microdistal' varves of De Geer (1940) which, to quote Pennington (1947, p. 142) '... he supposes to have been deposited, ... , at a great distance from the ice border'. Pennington (loc. cit.) has used this hypothesis to explain the very thin varves of Lake Windermere in northern England.

A similar explanation may also be used for the north-eastern part of the Koonwarra fish-bed in that this area may have been furthest from the region of the main inflow of sediment. Its narrowness implies that it represents a rise in the floor of the lake, possibly towards the shoreline. Pennington (loc. cit., p. 142) mentioned that: 'Undisturbed varved clays extend into very shallow water—i.e. to within a few yards of the edge of the lake in sheltered positions in the bays; ...', although she thought that the lake level might have been higher when the varves were laid down, as slight shore erosion would have prevented the settling of fine material.

Were the evidence of the laminae to be considered apart from other factors there would be little doubt as to their formation under conditions similar to those of glacial

varves, i.e. in the deeper regions of cold, freshwater lakes. As may be seen in the evidence of the invertebrate fauna in particular, there is an apparent conflict between geological and zoological evidence. It must be noted that depth of water is only required in order to provide stillness. If this last factor may be provided in another way, then the need for proposal of a deep lake is obviated.

*Disturbance of the Sediments.* Only 2 types of disturbance are known at Koonwarra and both of these appear to be mechanical. No organic disarray of the laminae has been noted (i.e. absence of burrows, trackways, etc.).

*Folding.* A single sample of minor folding (Pl. 13, fig. 3) has been collected from the laminated sediments and it appears that the folding occurred contemporaneously. Laminae above and below the fold remain unaffected. This small fold was due to subaqueous slumping on a small scale, either gravity slumping, or by the action of a later turbidity current (cf. Kuenen and Migliorini 1950; Kuenen and Menard 1952).

*Faulting.* Throughout the sequence of laminae there are occasional examples of minor faults with throws of 1–3 mm, probably caused by post-depositional differential compaction of the laminae. A similar occurrence was noted by Antevs (1951, p. 1238) in a varve from Steep Rock Lake, Ontario, Canada. The only structures known from the bedding are conchoidal in shape. The laminae pass through them and they may be due to differential compaction (Pl. 14, fig. 2).

Disturbances of the laminated sediment occur at the contact with the lower arkose, due to water and sediment being squeezed out of the latter during compaction (Pl. 14, fig. 3).

During a laboratory experiment carried out on the rate of decay of small fish in bottom-muds, Koonwarra mud was used as the substrate. This was allowed to settle at temperatures of between 65° and 75 °F in a large gas-jar filled with tap water. At these temperatures the mud completely settled out fairly rapidly (within 3 days), in contrast to the very cold water experiments of Fraser (1929) and Kindle (1930), and formed an imperfectly graded deposit which was very well bonded together. The surface film of the clay appeared to be strongly adherent, so much so that a fish embedded close to the surface remained in position when the water was agitated. This adherence was probably due to flocculation of the fine particles by the comparative warmth of the water. No electrolytic action is postulated as Melbourne's water supply is remarkably free of dissolved salts. Flocculation of the winter clay fraction in cold lakes could well lead to their possessing the 'glue-like' quality noticed in the above experiment, protecting the laminae from the disturbing effects of incoming sediments.

*Mineralogy.* Edwards and Baker (1943) analysed many examples of the (then regarded as Lower Jurassic) Lower Cretaceous sediments of southern Victoria. They maintained from comparisons with the proposed source rocks that the arkoses had been derived mainly from igneous rocks of several ages and areas, whereas the mudstones resulted from the erosion of Palaeozoic sediments, mainly Ordovician and Silurian, but probably also Permian.

The coarser laminae of the Koonwarra mudstone consist mainly of angular quartz

with plagioclase feldspar, some orthoclase feldspar, and mica, both biotite and white mica (muscovite/sericite). In the claystone laminae the minute size of the grains makes identification very difficult. Edwards and Baker stated (loc. cit., p. 208) of the mudstones that they '... range ... to extremely fine-grained rocks in which little other than sericite can be made out with the microscope'.

*The Origin and Termination of the Fish-bed.* The arkose above and below the mudstones appears to be of fluviatile origin, being cross-bedded and containing large numbers of clay-galls, which often occur in well-defined layers. Fragments of wood and other plant breccia also occur in the arkose.

The upper arkose contains two sub-parallel bands of fine-grained sediment apart from and coarser than the central mudstone succession. Clay-galls are particularly common.

The contact between the arkose and mudstone is very clearly defined, both at top and bottom of the section, and it is evident that the mudstones were laid down while the arkose was in a fairly fluid condition. Specimens in the Monash University collection show the mudstone as having been forced apart into separate blocks by the arkose as compression of the sediments occurred, the arkose being squeezed vertically through fissures and also horizontally between bedding planes (Pl. 14, fig. 3).

Above the mudstone succession the arkose reappears along a well-defined but irregular contact. The most reasonable theory to account for the origin and termination of the mudstone succession is that of the speed and direction of a river undergoing some kind of alteration.

1. A river changing its point of entry into a lake might well have left an area which could have become a shallow lake arm, possibly even with a sandbar or other barrier left by the departed river between the lake arm and the main lake. The lake arm would persist in the manner suggested, until the river returned to its original course, flooding the mud floor of the lake arm with coarse breccia-bearing sediments. The clay-galls within this coarser material may have been derived from other similar mudstones through which the river had cut.

2. A mature river changing course in its meander-belt, thereby creating an 'ox-bow' lake or 'billabong'. The lake would persist until again overrun by the river.

3. The deposit may represent a backwater of a river, perhaps originally occupied by an inflowing tributary, but permanently joined to the region of flowing water.

4. A sudden interruption of the water course by physical means, such as a landslide, would create lacustrine or paludal conditions. Termination of that environment would occur when the dam was breached, or when the water reached a sufficiently high level to allow flowage around the dam, thereby restoring moving-water conditions.

All of these theories have one factor in common, that is, a region of flowing water has become comparatively still for a period of time, and has then reverted to a fluviatile condition. The second and third theories could really be grouped together, because the concept of an ox-bow lake is qualified in this case by stating that it must be connected with flowing water at some time of the year in order for sedimentation to occur.

With regard to the third theory, it is possible that the lake occupied an old tributary

backwater, not connected with the main river except during the flood season. Possibly this small lake or pond received its fine sediment from the tributary itself, which would only flow during that season. Linkage with the main river would then occur due to the rise in water level, thereby allowing faunal repopulation to occur.

Theory 4 would account for the deposition of the 7.1 m thickness of the mudstones by a continual rise in water-level, rather than by a continuous depression of the land. On the occurrence of a landslide most of the fluvatile sediment-load would immediately be deposited due to the change in current velocity. The lake would then increase in size (the rate being dependent upon the size of the river) and due to this a 'still-water barrier' would form between the river and the dam itself. Sedimentation would, therefore, become progressively finer close to the dam. As the lake grew in size only the finest sediment would be deposited in the distal portion of the lake. The theory is unsatisfactory in that it fails to explain the very sharp junction between the lower arkose and the base of the mudstone succession. It has been argued that the 'landslide-lake' idea is geologically instantaneous and does satisfactorily explain this contact. I would strongly contest this view in that it reveals a basic confusion of thought between geological time and sedimentation time. Such a landslide would be geologically instantaneous in its effects, but would not be sudden enough to provide such a sharp contact on its upstream side as is present at Koonwarra. An interruption of this nature would cause a gradation, possibly an uneven gradation, from coarse below to fine above as turbulence gave way to stillness. This does not occur. No decrease of particle size has been noted in the arkose, even at a distance of a few millimetres from the contact.

The landslide concept is useful, however, in that it may be used in a reverse fashion. Such an event could block the flow of a stream or river. The sediment-load of the river downstream from this dam would then be deposited rapidly due to the rapid decrease in velocity (to nil).

A variety of circumstances could then account for the sedimentation of the mudstones somewhere along the now depleted watercourse.

Among the most likely of these is that a string of lakes and ponds would be left in the depressions of such a watercourse, perhaps linked to a lake at their lower end. The Koonwarra deposit may have been formed in a pond or lake in the river-bed close to a larger lake. During the flood season the larger lake would 'back-up' the river valley and be temporarily linked with the smaller one. The lake would be filled from other unblocked watercourses and not from the blocked one, or the laminated sediments would be destroyed.

Gradual breakdown of the dam would eventually restore fluvatile conditions similar to those existing prior to the mudstone succession. It may be significant to note that clay-galls appear to be commoner in the upper than in the lower arkose, above the upper contact. This may be due to some violent fluvatile action, possibly connected with breaching of an obstacle by the river.

To sum up it may be said that whichever of these occurrences gave rise to paludal or lacustrine conditions, such occurrence must have been rapid, in that the supply of fluvatile sand was cut off sharply and replaced by silt and clay. If the sand possessed good water-holding properties ('quicksand'), then it would retain its waterlogged nature until the silt/clay was deposited. The mudstone-sandstone contact may be

described as a local unconformity, representing a small hiatus (Billings 1954, pp. 245, 247). Billings (loc. cit.) has stated: 'In the deposition of continental sediments, such as gravels, sands and clays, the streams may wander back and forth across the basin of deposition. At times of flood these streams may scour out channels scores of feet wide and many feet deep. As the flood subsides, or some days or even years later, the channel may be filled up again. Such an unconformity is local in extent and, in most instances, cannot be identified beyond the limits of the outcrop in which it is found. The time interval is short.'

Whether or not the beds at Koonwarra represent this exact state of affairs is uncertain, but the mode of formation of the fish-bed may have been similar.

#### THE PALAEO-ENVIRONMENT OF THE FISH-BED

It is most convenient to summarize the evidence for the nature of the palaeo-environment as a number of independent factors. From these may be derived certain possible conclusions, and in turn a general summary of conditions present in the palaeo-lake may be arrived at.

*Observation 1.* The fish-bed is formed of a large number of paired laminae with microlaminae occurring within this pairing. The pairing is due to a decrease in particle size vertically. This is followed by a sharp junction with the next coarse lamina. The particle-sizes range from silt to clay-grade.

*Conclusion:* The paired laminae represent cyclic or rhythmic sedimentation. It is not possible to state with absolute certainty whether this is seasonal, but the evidence is consistent with a seasonal rhythm. Sediment would have been deposited by an increase in water flow at a particular time of year, followed by a period of lesser influx, and slow settling of the finer particles. The cycle would then be repeated.

Such a type of sedimentation would require exceptionally still conditions during the period of little or no influx of material, allowing the fine clay to settle out.

The microlaminae may result from a variety of causes, including storms bringing in additional sediment, wave-action on sediment already laid down, or minor fluctuations of temperature.

*Observation 2.* The laminae are composed of clay and silt only.

*Conclusion:* That the region of deposition was a considerable distance from the point of entry of the water-borne sediments into a main basin. Alternatively, only fine material may have been introduced into the region of deposition at any time.

*Observation 3.* The biota is preserved in a large number of the paired laminae but is almost always found within the claystone layer, often close to the junction with the overlying siltstone (coarse) layer.

*Conclusion:* The biota was entombed during the still part of the cycle and sank into the uncompacted clay to be covered by more of the fine material before the onset of the next sediment-bearing period.

*Observation 4.* The fauna is generally completely and delicately preserved without decomposition or disintegration.

**Conclusion:** Such fossilization is usually regarded as being only possible in anaerobic situations, as otherwise rapid destruction of tissues occurs.

A second implication is that the fauna represents a life assemblage. In the case of many of the aquatic arthropods a journey of even a few yards after death would have resulted in at least partial disintegration, but this has not occurred. Once the fauna was dead and resting on the sediment already laid down, it must have remained undisturbed for such preservation to have been possible, i.e. the corpses must have been covered in some way. It may also be stated that such perfect preservation will not occur at high temperatures (see below, and Zangerl and Richardson 1963). These authors stated that of all factors present, temperature is the most important.

*Observation 5.* There is no disturbance of the laminae by organic causes.

**Conclusion:** The fauna must have been dead before coming to rest on the bottom-mud as any death-throes would have affected the lamination. Also no burrowing forms inhabited the sediments.

*Observation 6.* Decayed or rotted fish showing evidence of gas release are very rare (Pl. 16, fig. 1).

**Conclusion:** That most of the fish died and were preserved in an environment which was not conducive to the rapid production of putrefaction gases, i.e. a cold, anaerobic environment.

*Observation 7.* There is a total absence of black shale, peaty or carbonaceous bands within the fish-bed. Sulphides are also totally absent.

**Conclusion:** The period of anaerobicity was of insufficient duration for these phenomena to occur. It is probable that no hypolimnion or monimolimnion type of environment existed.

*Observation 8.* There is periodic mortality repeated throughout the fish-bed, this being true mass-mortality (Brongersma-Sanders 1957), numbers of fish and aquatic invertebrates often occurring on a small area of a single bedding plane.

**Conclusion:** A regularly occurring phenomenon caused the death of the aquatic fauna and caused no disturbance of the corpses, possibly even protecting them from such disturbance. To obtain such a repetitive mortality, regular repopulation of the fish-bed region must be postulated, or that not all fish were killed by the mortality mechanism.

*Observation 9.* The cause of mortality has left absolutely no material trace of itself in the sediments.

**Conclusion:** The cause of mortality was ephemeral, such as in the following examples: extremes of temperature; noxious gases or vapours; algal or protozoan blooms; bacterial, fungal, or oil films; ice-covering, etc.

*Observation 10.* Nearly all of the fish preserved are of similar small size. To judge from 2 larger fish found elsewhere in the same sequence, those of the fish-bed are juveniles or young adults. This applies not only to the shoal fish such as *Leptolepis*, but also to the other genera.



**Conclusion:** In present-day bodies of fresh water the shallows are inhabited by mainly juvenile fish, and I have assumed a similar situation at Koonwarra, i.e. the fish lived, died, and were buried in a region of shallow water.

It is evident that the mortality occurred at a similar time in each cycle, the fish having reached a similar growth-stage before being killed. This implies that at some time after the death of the fauna, repopulation of the environment occurred, i.e. the cause of the mortality was transient.

*Observation 11.* Leaves of the gymnosperm *Ginkgoites* occur only in the claystone laminae, often slightly below the layer bearing a fish.

**Conclusion:** It is probable that the life-cycle of *Ginkgoites* was much like that of the modern *Ginkgo*, the leaves being shed in the autumn. If this assumption is valid then at least a part of each clay layer was deposited in the autumn and the fish died and were buried between autumn and spring of the following year. The leaves are invariably completely preserved without signs of wear, implying no great distance of travel.

*Observation 12.* A well-developed terrestrial arthropod fauna is preserved, the elements of which are usually fossilized in an undamaged state.

**Conclusion:** The preservation indicates a very short distance of post-mortem travel, but the distance travelled before death is not known. It seems more likely that most of the terrestrial arthropods were not carried (or did not venture) far from the shore as their concentration is comparatively high. The terrestrial fauna would presumably have become sparser proceeding in an offshore direction.

*Observation 13.* 2 genera of fleas are known from the deposit.

**Conclusion:** The presence of fleas implies that mammals were among the terrestrial fauna.

*Observation 14.* Among the aquatic fauna there are both plecopteran (stonefly) and ephemeropteran (mayfly) larvae.

**Conclusion:** The water was completely fresh, both types of larvae being intolerant of even minor salinity.

*Observation 15.* *Ceratodus* is present.

**Conclusion:** The water was fresh.

*Observation 16.* A limulid ('king-crab') is known from the deposit.

**Conclusion:** This is not diagnostic of the freshness or salinity of the water. Most limulids of past ages have been freshwater in habitat but most existing species are marine. The living genus *Carcinoscorpius*, however, ranges into freshwater (Størmer, Petrunkevitch, and Hedgpeth 1955). Limulids are capable of migration when the environment becomes intolerable (Riek, pers. comm.). Some factor, therefore, prevented the limulid from leaving the waters of the Koonwarra fish-bed. Conditions for life may have deteriorated so rapidly that the animal had insufficient time to escape, or alternatively it may have died of 'natural causes'. I consider it to be significant that the limulid is preserved in a claystone lamina, as this indicates death during the same period as the rest of the fauna.

*Observation 17.* There is a general lack of predation in the fauna, and absence of gut contents in all the fish examined.

*Conclusion:* The fauna may have died simultaneously after a period of fasting, the aquatic predators having had no time to feed on the dead or dying fish or the invertebrate fauna. Alternatively, the cessation of feeding may be due to illness before death. Some phenomenon must also have prevented terrestrial necrophages from reaching their prey. The most likely type of obstruction would have been some form of covering, either sedimentary or organic. Another type of barrier could have been a sheet of ice, and a covering of salt has also been suggested. An alternative suggestion is that some factor rendered the corpses unpalatable to even carrion-feeders.

*Observation 18.* There is a complete absence of true mudcracks, mudcurls, rain-pits, or tracks from the fish-bed.

*Conclusion:* At no time did the fish-bed become even partly dried out.

*Observation 19.* Progressing along the strike of the bed toward the south-east, the band becomes very much thinner, representing a condensed sequence. The paired laminae are also very much thinner, and finer grained (Pl. 13, fig. 4).

*Conclusion:* This is indicative of the region of deposition being at a greater distance from the entry-point of the sedimentary material than the thicker part of the band. As the facies remains the same the environment has not undergone a change of any magnitude.

From these statements the following main conclusions may be derived.

1. The palaeo-environment formed a shallow part of, or was periodically linked with, a larger body of water (e.g. lake or river) from which it received a periodic repopulation of its aquatic fauna.
2. Conditions within this environment were of the still-water type, or nearly so, for most of the period of sedimentary deposition.
3. Mass-mortality occurred periodically, and the fauna has been perfectly preserved due to temporary anaerobic conditions.
4. It seems likely that a surface film of some sort caused:
  - (a) Perfect stillness allowing settling of the fine fraction of the sediment, which would have taken considerable time (several months).
  - (b) An anaerobic environment.
  - (c) Protection from predation by an outside fauna.

The film was also the probable cause of,

- (d) The death of the fauna.

*The Mortality Mechanism and the Connection with Preservation.* When deriving such a mechanism, it must be remembered that the phenomenon must fulfil all the conditions listed as (a)–(d).

The main possibilities seem to be as follows:

1. A heavy algal and vegetal mat formed of living flora—a 'flotant' such as is found at the present day in the bayous of Louisiana (see Zangerl and Richardson 1963).

2. If the lake had dried out, then it has been proposed that a fine film of salt brought up through underlying sediments by capillary action could have preserved the fauna.
3. Sufficiently rapid settling of the clay fraction could have formed a film over the already dead fauna and thereby preserved it.
4. A thinner algal, fungal, bacterial, or protozoan scum, fortified by adherence of the fine clay particles and windblown dust.
5. A film of oil, derived from a seepage or other source.
6. Possibly no film existed and the conditions may be explained by a hypolimnion or monimolimnion environment.
7. A freezing over of the surface of the shallow arm of water, i.e. an ice surface film or sheet.

*The Flotant Hypothesis.* The idea of a vegetal mat or 'flotant' (Zangerl and Richardson 1963) possibly forming a covering of the water surface is perfectly feasible in theory. It would have given an oxygen-rich layer beneath the flotant, but bottom conditions would have been anaerobic. It is certain that if such a thick mat had occurred, some traces would have been found on the claystone bedding planes which have yielded such a delicately preserved biota. No carbonaceous bands, films, or black muds occur within the fish-bed. A further disadvantage of this theory is that such mats tend to be permanent and not cyclic. This hypothesis must be discarded as being completely without supporting evidence.

*The Salt-Crust Hypothesis.* This idea, proposed to me by a co-worker, assumes that even the freshest of naturally occurring waters contains some salts in solution and that any salts deposited by evaporation would protect the sediment beneath from total dehydration and the preserved biota from necrophages. This salt layer would then be dissolved away by the next ingress of water and the coarser sediments of the spring laid down on the fine sediment of the year before. Not all of the salt would be derived from the standing water, but some of it would be brought up by capillary action from the underlying sediments.

The theory is also based on the assumption that the death of the fauna was caused by heat and deoxygenation, a suggestion which does not agree in any way with the evidence. Also, if the salt film had been as thin as the theory suggests, it would undoubtedly have occurred intermittently over the sediment surface and certain areas would have dried out completely, showing dehydration phenomena. These are absent. If, on the other hand, the film had been thicker, then recognizable crystallization would have occurred, perhaps in the form of salt 'hopper' crystals. There is no evidence of any crystallization at Koonwarra.

Fossilized larvae of the insect orders Plecoptera (stoneflies) and Ephemeroptera (mayflies) are well known from the fish-bed and such larvae at the present day are extremely intolerant of even slight salinity. If the water was fresh enough to allow the growth of these larvae, the amount of salt precipitated on evaporation of a reasonable depth of water would have been virtually nil, invalidating the hypothesis.

*The Clay-Settling Hypothesis.* After death the fauna would have sunk into the soft, unconsolidated ooze of the finer sediments. Fine material still settling out would

then be deposited on top of the fauna giving the anaerobic environment required for the type of fossilization found and doing away with the necessity for a water-surface film.

If the water were sufficiently shallow then wind-action would have kept at least some clay particles in suspension, providing a blanketing effect until the coming of the next sedimentary influx.

If this theory is to be upheld, then certain points must be investigated. For example, a separate mortality cause must be found as none is provided for in this theory. If the lake-arm were very shallow, then disturbance of the fish and sediment would have occurred, firstly by wind and wave-action, and secondly by predators.

This hypothesis fills only one of the requirements previously stated, that of the anaerobic environment, and even that is doubtful as it is not certain whether a thin clay film would stand up to wave-action in nature, or foil predators. This hypothesis seems to be unsatisfactory as a complete explanation.

*The 'Scum' Hypothesis.* Thin surface 'scums' may form over the surface of small bodies of water and may be reinforced by fine sedimentary particles, both air and water borne.

It is most unlikely that a film of this sort would create an anaerobic environment in the water. From observations of a film in a large laboratory tank, it is evident that such a scum would be rapidly destroyed in nature by wind-wave action. It could conceivably cause death of the aquatic fauna by the formation of toxins, but would certainly not fulfil the other conditions as laid down herein.

*The Oil-Film Hypothesis.* An oil film would create an at least partly anaerobic environment beneath itself, but would have to be periodic and well developed, and as such, would undoubtedly have left geological traces of its presence somewhere in the Koonwarra mudstones.

This idea could fulfil most of the listed requirements. The oil-film would have lessened the effects of wind-wave action, could have caused sufficient deoxygenation to kill and preserve the biota and would have rendered the corpses unpalatable. However, this is purely an imaginary hypothesis as there is no trace of oil anywhere at Koonwarra.

*The Hypolimnion or Monimolimnion Hypothesis.* The Koonwarra sediments could represent those of a deep lake. This is based on evidence provided by the sediments alone. The hypolimnion is the bottom water-stratum of a lake, generally subjected to periodic overturn with surface waters, whereas the monimolimnion is also such a bottom layer, but is permanent to all intents and purposes, i.e. it does not engage in overturn.

Indeed, if one examines rock from Koonwarra the resemblance to varves laid down in deep glacial lakes is immediately apparent, as previously noted. However, there the resemblance ends. I have been unable to locate references to mass-mortality in varves (except within the Green River Eocene non-glacial varves which are completely different in type from those at Koonwarra). A clear explanation of this mortality is necessary. There are 2 mortality mechanisms which may explain the

facts: (a) possible heating of surface layers of the water driving the fauna down into the toxic hypo- or monimolimnion where they would be killed and anaerobically preserved; and (b) during spring and summer overturn of the epilimnion (upper aerobic layers) the fauna might have received sufficient toxins from the hypolimnion to cause death and subsequent preservation of the fauna. Both theories appear feasible at first glance, but neither takes into account the environmental and preservation evidence of the invertebrates in particular. As Riek has clearly stated (pers. comm.), the aquatic invertebrates are characteristic of fresh, cold, shallow waters, and, moreover, we have observed that these aquatic forms are invariably perfectly preserved and often in considerable numbers. How then do these invertebrates come to be preserved in deep, anaerobic lake sediments? As they could not have lived in such a situation they must have been carried in. This concept is untenable because the aquatic invertebrates are complete, down to their finest structures. The most minute cerci, less than two microns in width, have been impeccably preserved *in situ*, which definitely indicates lack of transport.

In 'normal' circumstances laminated pairs of graded silt-clay bands occur only in the deep, undisturbed, de-oxygenated regions of cold lakes. It is evident, however, that conditions in the Koonwarra deposit were anything but 'normal' and seemingly incompatible, if one refuses to admit that such perfect laminae may be laid down in shallow water if somehow protected. After all, the only reason for invoking deep water is for sediment-protection and if this can be simply supplied by other means then there is no need for deep water theories. The 'abnormality' of the Koonwarra deposit lies basically in its mass-mortality combined with laminated sediments—a rare occurrence. Bradley (1929) proposed deep conditions for his Green River (Eocene) varves which contain an excellent fauna, but in that case there is good evidence of hypolimnion or monimolimnion conditions, e.g. '... Consistent presence of finely granular pyrite . . .' (Bradley 1929, p. 103).

Further to the question of the hypo-monomolimnion theory: why (with two exceptions) are all the fish of the fish-bed of similar size? In a deep lake of some size one would expect to find fish of all sizes (i.e. ages) preserved, but at Koonwarra this does not occur. A mortality mechanism operating in a lake of this proposed type would surely represent a cross-section of the fish population. If it were a deep lake, one would expect there to be a marked component of more adult fish. In fact there are only 2 specimens known of larger size, a fragmentary ?coccolepid and a single specimen of *Koonwarria*.

It is also exceedingly unlikely that such a high percentage of superbly preserved terrestrial arthropods would be preserved in deep waters. Surely it is far more likely to find such a concentration close to shore, rather than at a distance and at depth?

*The Freezing Hypothesis.* It is possible that the shallow, isolated, lake-arm became frozen over during part of the year. This would not necessarily imply the freezing over of the main body of water of the lake.

A covering of ice would fulfil all of the specified conditions and may be used to form the basis of a theory of mortality and preservation. It is the only hypothesis that does not conflict with any of the available evidence as far as I know, and is, therefore, proposed as the most likely cause of this facies.

The fish-bed is assumed to represent a shallow arm of a cold, freshwater lake, partly separated from the main lake by a subsurface sandbar or similar obstacle. During the spring, summer, and autumn there was contact between the 2 regions, with a well-developed population of small fish and aquatic invertebrates inhabiting the shallow arm.

With the advent of winter the shallow waters rapidly grew cooler on the surface and an ice-film appeared. The fauna was alive at this time. As winter set in the ice thickened, and abutting against the subsurface obstacle of the main-lake side, effectively isolated the shallow arm. The situation would then have been one of a fauna inhabiting a totally sealed-off environment. During the course of the winter the available oxygen decreased and death of the fauna from anoxia ensued. This is a familiar phenomenon in Canada, for example, and is known as 'winterkill' (Greenbank 1945). A snow-cover to the ice (or the presence of cloudy ice) is necessary if photosynthesis and hence oxygen-formation is to be prevented.

The conditions of very cold water and anaerobicity were perfect for preservation as the fish sank down into the bottom-clays. Very fine sediment continued to precipitate through the latter part of the winter, covering the corpses with a layer of finer clay.

In the following spring the ice-layer melted away, the water level rose by thawing of feeder streams and snow in higher regions, and silt covered over the finer layers beneath. Such a cycle would then have been repeated.

Even though the palaeo-topography is unknown, it seems most likely that the lake was situated at the foot, or in the foothills, of a range of high hills or mountains which became partly snow-covered in winter. The watershed from this range probably also froze, thawing in spring to release water and sediment into the lower levels, including the Koonwarra main basin. The fish-bed arm of the lake or river would have been well away from the entry of the sediment-laden water, only the finer grades (silt and clay) being carried into it. At the present time sedimentation in cold, still waters continues throughout the winter. The 'Freezing Theory' is extremely simple in concept, fulfils the conditions laid down by Sauramo (1923) and Fraser (1929) for the deposition of laminated clays, and also encompasses the 4 listed conditions which characterise the whole Koonwarra fish-bed preservation.

*Palaeo-ecological Evidence from the Vertebrates: The Evidence Derived from Preservation.* The mode of preservation of the fish is of direct significance in the understanding of the palaeoenvironment, as preservation takes a number of forms. It should be noted that although large numbers of fish have been collected, a number of these are incomplete due to breakage during collection. This applies particularly to many of those collected by earlier workers with the aid of explosives. However, sufficiently large numbers of intact specimens are available for detailed examination.

Studies on post-mortem preservation of vertebrates have been very few, the most recent being by Zangerl and Richardson (1963) who have dealt with some problems of decomposition in aerobic or anaerobic conditions. It is evident from this and other studies that for preservation of nearly perfect, articulated skeletons (Pl. 15, fig. 2; Pl. 17, fig. 3), anaerobic conditions are required and that probably the most important single factor is that of temperature.

Prompted originally by a suggestion that the mass-mortality of the Koonwarra fish was caused by drying up of the lake arm in the heat of the summer I carried out two small experiments on fish in the laboratory. Small European carp (*Cyprinus carpio*) were placed in a large tank filled with freshwater and the temperature slowly raised. The fish exhibited signs of discomfort at 38 °C, and at 40–41 °C death ensued with only the most minor death-throes on the bottom of the tank. The fish then floated to the surface within a few hours and overnight released the gases of putrefaction and sank down to the tank floor. When the corpses were examined the next morning it was immediately evident that the visceral region had virtually exploded, the fish were in most cases decapitate, and no specimen was in even a remotely complete state of preservation. Within a few more hours all the fish had disintegrated, many completely. This is obviously far removed from the mode of preservation found at Koonwarra. It might be remarked that 40–41 °C appears to be an unrealistic temperature for lake waters, but it must be remembered that very shallow areas of bodies of water in Victoria at the present day may often reach this temperature in the summer.

A second experiment was performed using a small, freshly killed carp which was placed in a large gas-jar filled with tapwater and left in the laboratory. The fish floated to the surface after several hours, became distended, and overnight had sunk to the clay which had been placed on the floor of the jar. The fish had come to rest obliquely, with its head slightly lower than the rest of the body. The clay (from Koonwarra) was stirred without disturbing the fish too much, until the water was sediment-laden, and the jar then left untouched for three days. On re-examining the jar it was found that the clay covering the fish was of 'glue-like' consistency and even when the water was agitated, the clay remained comparatively undisturbed. Stirring of the water was necessary to create any marked disturbance, although the very finest particles were dislodged during agitation. The fish was apparently intact, apart from the loss of some scales. The temperature of the laboratory ranged from about 18 to 24 °C during the course of the experiment.

The sediment in the gas-jar was allowed to dry out completely without the use of artificial heat sources and the condition of the sediment noted. It was found that the clay layers exhibited a tendency to curl up and separate from the underlying silt layer. Vertical cracking also occurred and this often penetrated both clay and silt layers (Pl. 16, fig. 5). The fish and sediment immediately surrounding it were removed from the jar, placed in a Petrie dish and water added carefully so as not to cause any disturbance. The material absorbed water at a rapid rate and, due to the absence of surrounding matrix, quickly crumbled into a heap around the fish. Hydration was then allowed to proceed for about 3 hours, after which time the contents of the dish were slightly agitated. It was observed prior to this agitation that the caudal region had become separated from the trunk of the fish. The fish was then removed from the Petrie dish and examined. Little damage had occurred to the fish, apart from the loss of the caudal region. The skull, axial, and appendicular regions were hardly disturbed, except that one or two of the branchiostegal rays had become dislodged. The body wall was seen to be distinctly ruptured laterally between pectoral and pelvic fins and had lost all scales in that region, rendering the ribs clearly visible. The fish was preserved in the sediment with the ruptured side downwards. Evidently, after having risen to the surface and vented the gases of putrefaction through the body wall, the fish had rotated 180° on its longitudinal axis before coming to rest on the bottom sediment. Such preservation is very rare at Koonwarra, if indeed present at all; once again indicating that conditions necessary for this form of preservation were not generally present in the Koonwarra claystones.

Complete fish undoubtedly represent the majority of individuals at Koonwarra. It is proposed that these died of anoxia in the winter beneath the ice-layer. They became covered by clay settling during the winter and were then further entombed by the silt of the following spring. This is typical preservation.

Fish found in the siltstone laminae of the fish-bed are poorly preserved, firstly due to the coarser grade of matrix, secondly to the apparently aerobic conditions existing during silt precipitation, and thirdly to the probability of disturbance by wind and muddy water currents. That they are preserved at all well is almost certainly due to rapid burial by spring-thaw silt, and it is proposed that their death was due to 'natural causes' such as disease, rather than any mass-mortality mechanism. These fish may have died outside the shallow arm and been carried in during the spring thaw, or have perished during repopulation of that shallow arm. It is even possible that the first

few fish to enter the arm after the winter may have suffered anoxia and died at that time, being buried in silt rather than clay. This is feasible as it has been noted by several authors that during artificial oxygenation of oxygen-depleted waters many fish have been killed by the admixture of poorly oxygenated and deoxygenated waters. This may be due to a high biochemical oxygen demand in upwelling bottom waters (Patriarche 1961, Halsey 1968) and the presence of hydrogen sulphide. Greenbank (1945), Puke (1949), and Halsey (1968) have remarked that the combination of hydrogen sulphide-bearing waters with those containing oxygen will reduce the amount of dissolved oxygen due to oxidation of hydrogen sulphide (Hutchinson 1957). A high biochemical oxygen demand in the mixing waters might have killed some fish before the pool became properly oxygenated.

A few slightly decayed fish are known (Pl. 10, fig. 4; Pl. 16, fig. 3), either lacking scales, or with disarticulated skulls. These specimens probably represent isolated fish which died of causes other than anoxia before the ice-sheet was properly formed, or actually died beneath the ice while oxygen was still present. The very cold water would have inhibited rapid decomposition of the fish.

Also known is an individual example of a fish which has apparently voided its gases of putrefaction with some violence through the ventral body wall between the skull and pelvic fins (MUGD 3643AB; Pl. 16, fig. 1). Apart from the disruption of the scales, one-half of the pectoral girdle is also preserved well away from its original position. The fish is preserved dorso-ventrally, in contrast to most of the other fish at Koonwarra and it is probable that it was either very close to the bottom or actually resting on it, when the venting occurred. This conclusion is derived from the arrangement of the scales and pectoral girdle elements with reference to the body. The unusual dorso-ventral position may be due to the fish floating belly-upwards, and then releasing the gas, sinking directly into the mud without changing position. The last two examples could be due to fish floating to the surface in the spring (Greenbank 1945).

2 specimens are known with only the caudal region preserved, the rest of the fish apparently having disappeared (MUZ 3161AB, 3036AB) (Pl. 17, fig. 1). In MUZ 3036AB portions of other fins are preserved in their natural positions. I assume that these fish were lightly adherent to the mud surface and then drifted away, possibly with the currents of the spring thaw. It is significant that the last few vertebrae and the tail are preserved in each example. This ties in very well with cases quoted by Saito (1936) for fish preserved in the Mesozoic deposits of Chao-Yang, Jehol, Manchuria, which also exhibit evidence of decomposition in the caudal region.

It is of interest to note that it is only the distal portions of the lepidotrichia of each fin (with the exception of the caudal) which are preserved. Evidently the fish were sufficiently intact for the long proximal fin-ray joints to remain attached to the body.

A single specimen (MUZ 3165A) (Pl. 18, fig. 1) is not preserved anterior to the cleithrum. Having observed the preservation of recently dead fish in mud, it may be mentioned that the head sometimes comes to lie a little lower in the sediment than the rest of the body and any disturbance after a short decay period could well result in the skull being left in the mud when the corpse drifts away. In this manner, isolated skulls are occasionally found in the matrix, with the rest of the body having apparently disappeared, or in some cases lying near by, e.g. MUZ 3031 (Pl. 17, fig. 2).



There are a few examples of pieces of fish skin and scales which have apparently adhered to the mud. The skin is from the mid-flank of the fish, carrying the lateral line—the area of skin most likely to be preserved in such a case, e.g. MUZ 3162AB—(Pl. 17, fig. 4).

Examples of fish having died an agonized death are rare at Koonwarra. However, 2 specimens are preserved in what may possibly represent such a state; 1 (*Wadeichthys*, MUGD 3648) with the body thrown into an arc, concave ventrally (Pl. 18, fig. 4); and the other (*Leptolepis*) being sinuous in form (MUZ 3159AB; Pl. 18, fig. 2). Saito (1936) has cited examples from Chientao, Manchuria, which resemble the latter in form and has ascribed their attitudes to death struggles.

One or two examples of a number of fish entombed in close contact on the same bedding plane are known from Koonwarra, the best of these being MUGD 3654AB, where 4 medium-sized *Leptolepis* are preserved in contact, with a fragment of a fifth nearby. On 3655AB there are also 5 similar *Leptolepis* preserved, together with a very large number of *Leptolepis* scales and skeletal elements which belong to a sixth individual of the same species (Pl. 15, fig. 3).

MUZ 3035AB, is a possible example of predation, having lost a portion of the antero-dorsal region between the dorsal fin and occiput. Disturbed ends of neural spines protrude into the cavity and it appears as if a piece of flesh has been torn out (Pl. 18, fig. 3).

Zangerl and Richardson (1963) discussed the mode of occurrence of disarticulated specimens of fish from Upper Carboniferous black shales, Indiana, U.S.A., and concluded that many of their specimens represented ejected prey, gastric residues, or faecal masses. At Koonwarra it is difficult to be certain of the exact cause of many of the disarticulated specimens, but I consider that most of these are due to causes other than predation. However, in one or two cases predation would seem to be the most likely explanation.

There is a single example of a fish in an advanced state of disintegration, although its body shape is still approximately determinable (MUGD 3644AB; Pl. 15, fig. 1). It is possible that this is a partly digested fish which has been orally ejected from the digestive tract of a predator (Ejected prey—see Zangerl and Richardson 1963). An alternative idea is that the fish died in early winter or late autumn and was subjected to aerobic decay.

MUGD 3655AB (Pl. 15, fig. 3) could possibly be an example of the gastric residue type (Zangerl and Richardson 1963).

3 specimens of coprolites are known from Koonwarra and seem to correspond to the 'irregular compact form' of coprolite mentioned by Zangerl and Richardson (loc. cit., p. 141). They are MUZ 3163AB, 3164, and 3165AB (Pl. 16, figs. 2, 4, 6). All are small, the largest, 3164, being 21 mm long, with a maximum width of 9 mm. 3165 consists of small, thin bones, impressions of vertebral centra, and scales identified as *Leptolepis*. 3164 is made up of denser material which has been weathered, and does not reveal very much detail. However, it is possible that a part of a cleithrum is contained in this specimen together with some rhomboid scales which could belong to *Wadeichthys*. One or two small bones are also present. 3163 is the smallest of the three, and the best preserved. It is formed of scales, ribs, and spines of a small fish. The scales are again referable to *Leptolepis*, and some appear to have been partially

digested in that they have a curiously flexible appearance not usually seen *in situ*. One of the scales preserved is from the lateral line and shows no such softening. On the outer rim of this coprolite is a darker, greyish area, which may represent fluid organic matter from the coprolite itself. Several of the 'softened' scales are present in this region together with what appear to be the last few segments of an insect abdomen with attached cerci.

A specimen is known from Koonwarra consisting of a small slab bearing a mélange of skull elements (e.g. opercular, dermosphenotic, hyomandibular) all apparently of *Wadeichthys* (MUZ 2879AB). This may well represent a gastric residue of a fluid type, as two very small scales of *Leptolepis* are also present on the slab in the midst of the *Wadeichthys* elements. Alternatively, the skull bones could have belonged to a decomposing fish which drifted on the surface with the disintegrating skull hanging downward. These elements are preserved in a siltstone layer, and so would have been laid down in spring or summer.

Isolated bones are rare although hundreds of isolated scales have been found. However, 1 hypural element has been found associated with a number of large scales of *Koonwarria*. Only 1 scale of the enamelled, rhombic, *Wadeichthys* type has been found isolated, whereas cycloid scales are common. Cycloid scales drift away from fish corpses with the slightest current (personal observation), and these would probably have been wafted away from fish which died before the ice-sheet appeared, or after it had melted.

In an area of the lower region of the mudstone exposure there is a minor association of large, disarticulated skull elements of ?*Coccolepis* sp. (Pl. 2, fig. 5; Pl. 3, fig. 3; Pl. 4, figs. 1-5). Their exact provenance is unknown but this preservation is consistent with a dead fish floating on the surface releasing skull elements as decay ensued.

*Comparable Preservation in other Assemblages.* It is stressed that the sites discussed are only a few examples of those of an Upper Mesozoic age which exhibit preservation of fish comparable to that known from Koonwarra. No attempt has been made to give discussions of faunas exhibiting taxonomic similarities, with the exception of the Talbragar fauna. As the Archaeomaenidae and Koonwarriidae are limited to Australia and the taxonomic status of many species of *Leptolepis* is doubtful, the historical summaries previously given for each family are considered sufficient. Liu (1957) provided a map of the distribution of the Coccolepididae, and Lehman (1966) gave the distribution of the Ceratodontidae.

As the exceptional preservation of the Koonwarra fish is very rare for a freshwater deposit it may be worth while to consider possibly comparable fossil beds elsewhere.

When thinking in terms of varved or laminated fish-beds, those of the Eocene Green River Series in Wyoming, U.S.A., immediately come to mind (Bradley 1929, 1948). However, these deposits, although seasonal, only superficially resemble their Koonwarra counterparts, the varve structure being organic and totally different from that at Koonwarra, except that anaerobicity undoubtedly caused the excellent preservation of the fish.

Beautifully preserved fish occur in the Kimmeridgian (Upper Jurassic) lithographic limestones of both France and Germany (Saint-Seine 1949) but the environment has

been generally regarded as that of a coastal lagoon. With many of the described fossil fish deposits of the world it is often very difficult to decide from the literature whether the palaeoenvironment was marine or freshwater.

In two well-known examples within the Jurassic-Cretaceous, however, there is little doubt of the freshwater nature of the deposit. These are the Jurassic-Cretaceous fish-beds of Eastern Asia (Cockerell 1925, Saito 1936, Takai 1944) and the ?Jurassic fish-bed of Talbragar, New South Wales, Australia (Woodward 1895*a*, Wade 1941, 1953).

Saito (1936, pp. 3-4) discussed the mortality and preservation of fish from 2 localities in Jehol, Manchuria: Ling-Yuan and Chao-Yang. In the former the fish were described as '... extremely abundant, often packed on bedding-planes'; while in the latter they are found in lesser numbers. The Ling-Yuan fish show no signs of decomposition whereas the Chao-Yang specimens are mostly distorted by 'swelling... as a result of decomposition'.

Saito proposed that the Ling-Yuan fauna may have been overwhelmed by volcanic dust or water-lain mud before decomposition could begin. The Chao-Yang fishes were believed to have been either exposed to the air, or left unburied for a time in shallow water where they partly decomposed before being embedded. At a third locale, Chientao, most of the fish are distorted. A single specimen is known from this deposit, bent to an 'S-shape which is taken to imply... a last death struggle'. All these fish are embedded in paper shales, originally a fine-mud bottom to their place of burial. Assemblages within sediments of this age in Eastern Asia are freshwater ones consisting of molluscs, arthropods, fish, amphibia, and plants associated with a terrestrial biota which includes reptiles, insects, and plants (Takai 1944).

The Talbragar deposit of New South Wales is probably Jurassic in age; its fish-fauna has been described by Woodward (1895*a*) and Wade (1941, 1953), and the stratigraphy by Dulhunty (1937). It has been designated a freshwater deposit on the basis of the flora, but no palaeoecological studies have been published. There are no records of any other biota apart from the fish and plants and I cannot add to this even after examination of a large amount of material. The fish fauna is closely comparable to that of Koonwarra, but the mode of preservation is slightly different, much larger concentrations of fish occurring on single bedding planes than at Koonwarra. As at Koonwarra fish associated on bedding planes are generally closely similar in size. There is no published work on the sedimentology of the Talbragar deposit, but the beds should be studied with reference to the mass-mortality of the fish.

Ghekker (1948) discussed the biota of the Upper Mesozoic Karatau beds of Kazakhstan, U.S.S.R., and illustrated the palaeoniscoid *Pteroniscus*. Some specimens are preserved in sinuous fashion, the position apparently having been caused by water-currents. The fish are also often grouped together on one bedding plane, unlike specimens of *Coccolepis* from Koonwarra. It is possible that *Pteroniscus* may have been a shoal fish, at least in the juvenile stages. A specimen of *Pholidophorus netchkini* (Gorizdro-Kulczycka 1926) from a similar locality is also preserved in a contorted position, but this seems to be exceptional, as at Koonwarra.

*The Biological Evidence.* The presence of a lung-fish at Koonwarra is entirely consistent with the ideas put forward for the palaeo-environment. Edwards and Baker

(1943, p. 219) stated that '... the presence of *Ceratodus* ... in the sediments [Korumburra Group] points to warm rather than cold conditions'. This statement assumes that because Australian lung-fish live naturally only in Queensland freshwaters at the present time, in a warm-hot climate, this situation has always existed. I do not consider that any evidence of climate may be derived from the lung-fish.

Lung-fish are regarded as primary division freshwater dwellers (for references see Schaeffer 1952) and the presence of *Ceratodus* at Koonwarra is the only vertebrate evidence for the freshwater nature of the palaeoenvironment.

The fish fall into three categories:

- (i) The insect or plankton feeders, i.e. *Leptolepis*, *Koonwarria*, *Wadeichthys*.
- (ii) The predators, i.e. *Coccolepis*, and the large fish ?*Coccolepis* sp.
- (iii) ?Crustacean feeders, i.e. *Ceratodus*.

The 3 genera comprising the first type have toothless jaws, and possess upturned mouths, particularly *Leptolepis*. They are regarded as feeding on the anostracans, aquatic insect larvae, and any terrestrial or aerial insects alighting on the surface of the water.

*Coccolepis* was undoubtedly the predator. With its large teeth and streamlined body it may well have filled the niche occupied today in the Northern Hemisphere freshwaters by the Esocidae (Pikes).

The extant Australian lung-fish *Neoceratodus forsteri* Krefft feeds on the mollusc *Corbiculina* which lives on the water plants in some rivers of eastern Queensland such as the Burnett and the Mary (I. D. Hiscock, pers. comm.). No molluscs of any kind are known from Koonwarra and where present elsewhere in the Korumburra Group they are excessively rare. The Koonwarra lung-fish may have fed on the conchostracans which were so abundant at that time, and may have ingested large amounts of water-weed in order to extract the attached fauna of invertebrates. *Neoceratodus* of the present day behaves in the latter fashion while feeding on *Corbiculina* (I. D. Hiscock, pers. comm.). Dissection of the gut of *Neoceratodus* which has been living in the natural state usually reveals a mass of plant material. (For discussion of the feeding habits of *Neoceratodus* see Longman 1927, pp. 166-167.)

With the exception of *Ceratodus* which was found in the topmost layer of the fish-bed, all of the fish of the upper fish-bed are of small size. Examination of the scales of *Leptolepis* often reveals the presence of growth rings. Most of the scales indicate fish which died during their first or, very rarely, their second year of life. These young scales show none of the effects associated today with spawning or regeneration of scales.

The upper part of the fish-bed contains only small scales and small fish, while the lower part is similar, but for the presence of a single, larger specimen of *Koonwarria*. It has been proposed that the absence of larger scales of *Leptolepis* indicates death after spawning, which may have occurred at the age of 2 years. Whilst this is possible, I feel that it is more realistic to regard the absence of large fish in the bed as being due to the shallowness of the water in the lake arm and to the obstacle proposed to partially separate this arm from the main lake.

In one *Leptolepis* (MUZ 3030AB) from the lower fish-bed there is evidence of

regeneration and/or disease in the scales, particularly those of the anterior region, but the significance of this is uncertain.

None of the many hundreds of specimens of fish examined from Koonwarra possesses any gut contents, implying that either these have not been preserved, or that they were not present when the fish became entombed. The latter is the more plausible suggestion in that were gut contents present the delicacy of fossilization would have preserved them. One can only assume that the alimentary tracts of the fish were empty when they were buried, i.e. no feeding had occurred for quite some time before death. This may have been due to the increasing discomfort caused by the mortality mechanism.

*Winterkill.* Possibly the most comprehensive paper on this topic has been that of Greenbank (1945) which dealt with many aspects of winterkill, or winter suffocation as it is sometimes known. Many incidences of winterkill were cited and the mechanism and its effects on the fauna described and discussed. Since that time a number of papers have appeared, mainly dealing with investigations into methods of preventing the phenomenon (see Halsey 1968).

Most of these studies have been carried out on shallow, eutrophic lakes. Characteristically such lakes are horizontally thermally stratified and have a bottom ooze rich in organic material. A number of factors contribute to the formation of an oxygen-depleted environment in such a situation when the lake becomes frozen over in winter. Among the most important of these according to Greenbank (*loc. cit.*) is '... bacterial decay of organic matter, which is largely derived from dead plankton, and is either suspended or dissolved in the water or lies in the form of a mucky deposit on the lake bottom'. Apparently respiration of the biota does not play a significant part in depleting the amount of oxygen present. 'The greatest ... fluctuations occur in shallow, extremely eutrophic lakes', but quantities of oxygen present in deeper, less eutrophic lakes remain nearly constant beneath the ice-cover (Greenbank 1945, p. 389).

At Koonwarra the clay laminae have no visible organic content, although finely brecciated plant fragments are found in the silt fractions of the laminae. It is not necessary to have a layer of organic matter preserved in the sediments if the original component is easily metabolized or disintegrated (Greenbank 1945). There are a number of organisms (e.g. algal blooms) which could be broken up in this way, leaving no trace, apart from the indirect evidence of the physical presence of a dead fauna. The presence of a well-developed phytoplankton, deprived of its means of existence, could well provide the conditions necessary for an anaerobic environment and would leave little or no trace of its presence. Deprivation would most likely take the form of snow covering the surface ice, thereby preventing the access of sunlight necessary for photosynthesis and causing death of the phytoplankton (Greenbank 1945). For references see Halsey (1968).

Mackereth (1966) has stated (pp. 167-8) that organic matter synthesized in a lake may be used up within the sediment very quickly by available oxygen (*cf.* Lake Windermere, northern England). Probably only the tough, lignified plant material brought in from outside the aquatic environment would survive and be preserved. Such durable material is seen in coal-bands and carbonaceous layers in the arkoses

of the Korumburra Group, but does not occur in the fish-bed or elsewhere in the mudstone succession.

It is evident that no external supply of organic material reached the clay-deposition environment during the settling of the clay, and any produced within those waters was oxidized, thereby providing a cause for the low oxygen concentration and winterkill. Halsey (1968, p. 81) has also added '... that incomplete autumnal oxygenation is a cause of "winterkill" of fishes'.

With regard to the winterkill of invertebrates little seems to be known, but Greenbank (loc. cit., p. 387) quoted Kofoed (1903) as recording a near total extinction of 'plankton' in a winterkill in parts of the Illinois River. Greenbank also stated that due to '... winter eggs or other resistant forms ...' populations will not be erased and 'Benthic invertebrates, such as aquatic insect larvae and nymphs no doubt are affected to some extent'.

It seems, therefore, that winterkill can provide a complete explanation for the events recorded in the Koonwarra sediments.

In conclusion: 'It need scarcely be pointed out that, regardless of the volume of evidence at hand, we are never in possession of *all* of it. Hence, ... conclusions presented ... are simply those that do not conflict with any of the evidence presently at hand' (Zangerl and Richardson 1963, p. 4).

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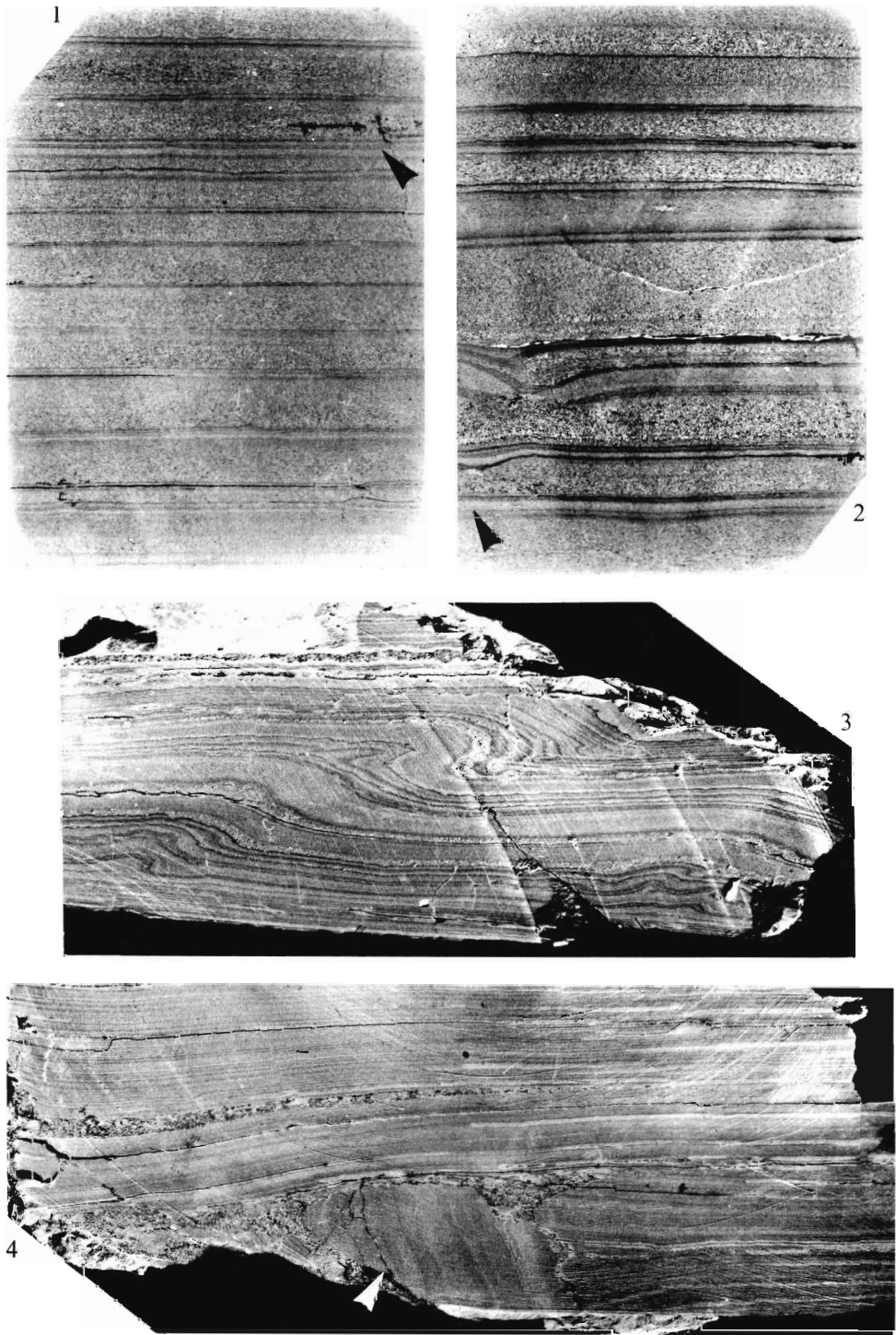
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#### EXPLANATION OF PLATE 13

Figs. 1, 2. Thin-sections (MDV 9038, 9042) of the fish-bed, showing microlaminae (arrowed) within claystone laminae,  $\times 1.6$ .

Fig. 3. Minor fold in the fish-bed, perhaps caused by contemporaneous slumping,  $\times 1.2$ .

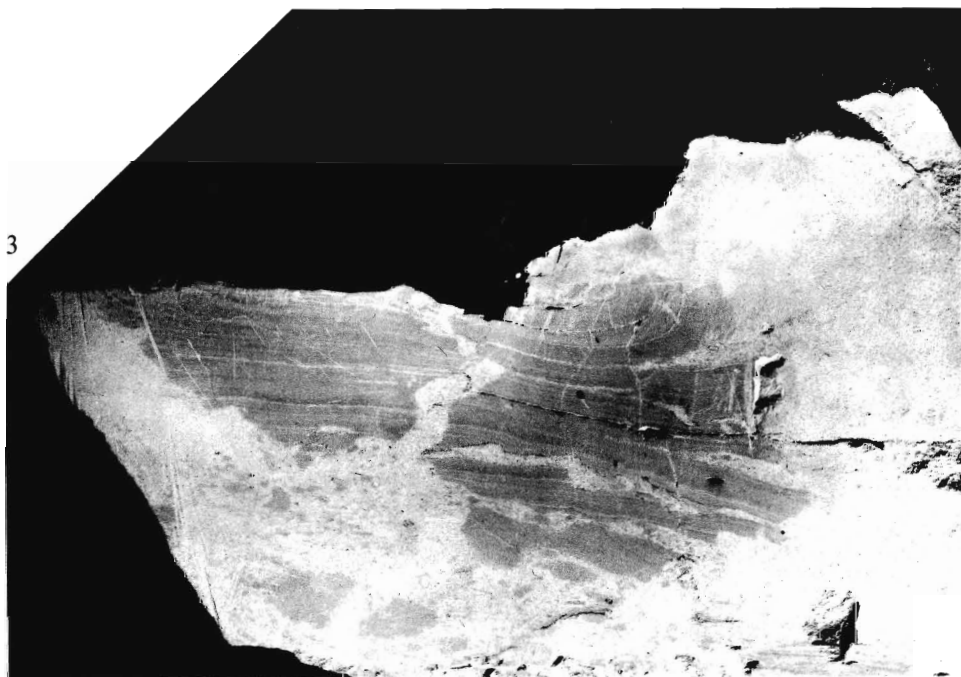
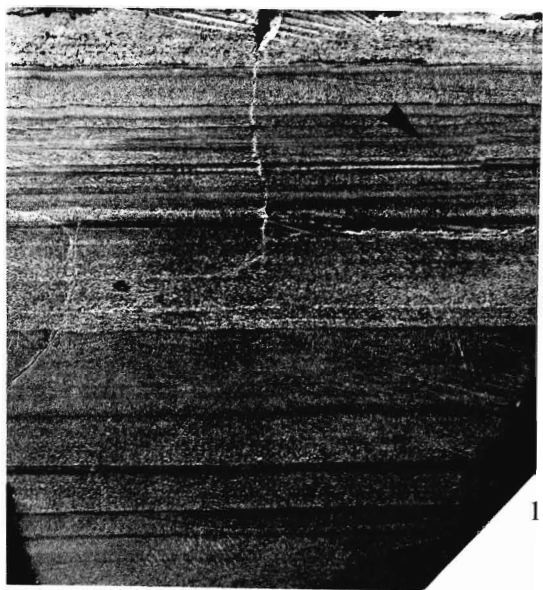
Fig. 4. Lower laminae from the condensed sequence at the northern exposure of the fish-bed. Note penetration of coarser arkose into the mudstone and displacement of part of the latter (arrowed),  $\times 1$ .



WALDMAN, Fish-bed sediments

#### EXPLANATION OF PLATE 14

- Fig. 1. Section of fish-bed mudstone, to show many minor clay-silt layers (arrowed),  
× 1·3.
- Fig. 2. Conchoidal fracture of the mudstone, × 2·7.
- Fig. 3. Part of the contact between the fish-bed mudstone (dark) and the underlying  
arkose (pale). Note horizontal and vertical penetration by the arkose, × 0·5.



WALDMAN, Fish-bed sediments



EXPLANATION OF PLATE 15

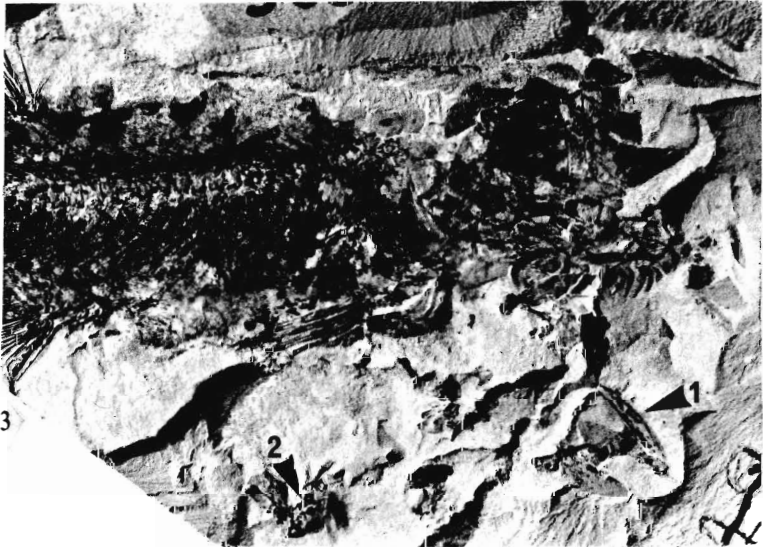
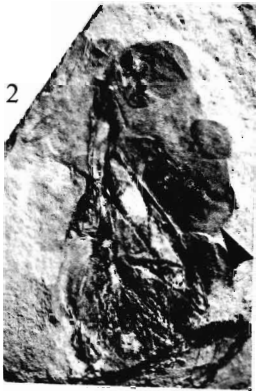
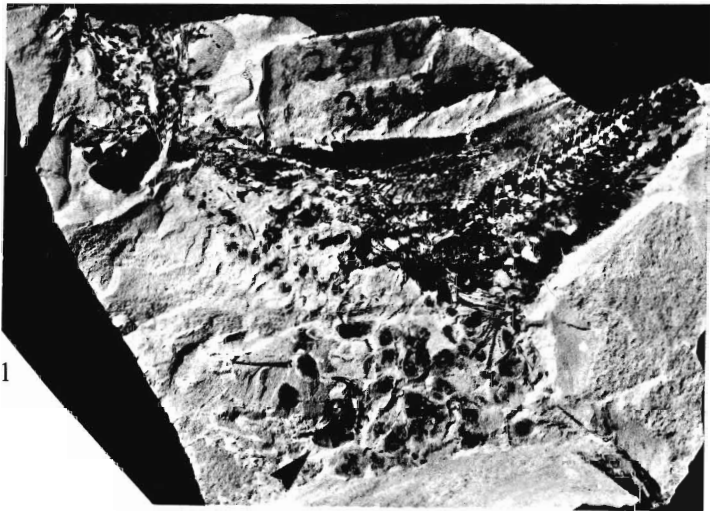
- Fig. 1. *Leptolepis koonwarri*. MUGD 3644B. Disarticulated fish retaining some semblance of its original form. Note that caudal fin-rays have remained in position,  $\times 1.5$ .
- Fig. 2. *Wadeichthys oxyops*. MUZ 2106A. Preservation with fins in the 'closed' position,  $\times 1.3$ .
- Fig. 3. *Leptolepis koonwarri*. MUGD 3655B. A number of fish and a mass of scales associated on the same bedding plane,  $\times 1$ .



WALDMAN, Fish preservation

EXPLANATION OF PLATE 16

- Fig. 1. *Leptolepis koonwarri*. MUGD 3643B. Violent disruption due to putrefaction. Note distance of displacement of pectoral girdle (arrowed),  $\times 1$ .
- Figs. 2, 4, 6. Coprolites or gastric residues. (MUZ 3163A, 3164, 3165B). In fig. 2, note the presence of scales of *L. koonwarri*, including a large lateral line scale (arrowed). Magnifications  $\times 4.5$ ,  $\times 3.4$ ,  $\times 3$ , respectively.
- Fig. 3. *Leptolepis koonwarri*. MUGD 3636A. Partial disintegration of skull. Some elements remain in their original positions, but others have drifted away. e.g. dentalo-splénial (arrow 1) and hyomandibular (arrow 2),  $\times 1.8$ .
- Fig. 5. A small carp, *Cyprinus carpio*. An attempt to reconstruct fossilization in drying mud,  $\times 1.8$ .



WALDMAN, Fish preservation

#### EXPLANATION OF PLATE 17

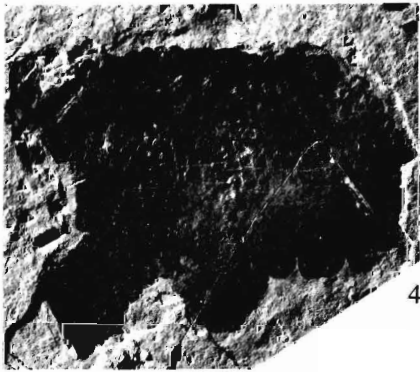
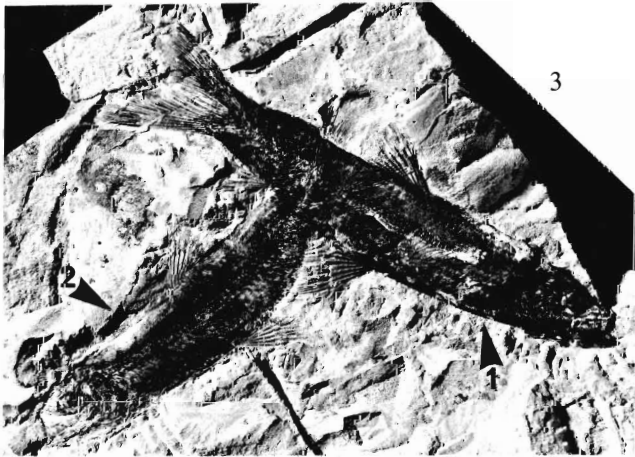
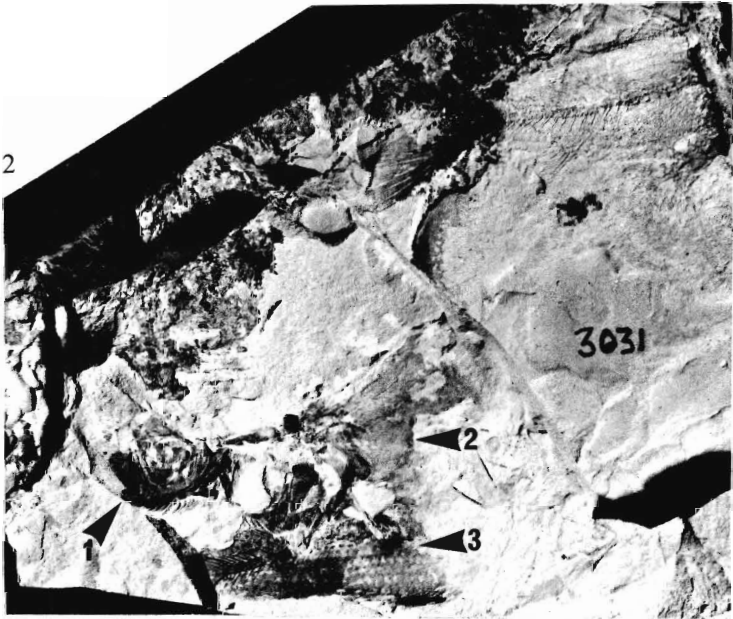
Figs. 1-4. *Leptolepis koonwarri* sp. nov.

1, MUZ 3036A. An isolated caudal region, the anterior portion of the fish having drifted away. The original position of the latter is indicated by the positions of the distal fin ray joints of the dorsal, pelvic, and pectoral fins (arrows 1-3),  $\times 2$ .

2, MUZ 3031. An isolated skull (arrow 1), which probably belongs to the doubled-up and broken body beside it (arrows 2, 3),  $\times 0.7$ .

3, MUZ 3207B. Two specimens preserved on the same bedding plane. Note that the caudal region of specimen 1 overlies that of 2,  $\times 0.7$ .

4, MUZ 3162A. An isolated patch of flank skin and scales, including the lateral line,  $\times 2$ .



#### EXPLANATION OF PLATE 18

Figs. 1-3. *Leptolepis koonwarri* sp. nov.

1, MUZ 3165. A headless trunk, the skull having been broken away at its junction with the cleithrum,  $\times 1$ .

2, MUZ 3159A. The sinuous shape may imply agonized death throes in a toxic environment,  $\times 2$ .

3, MUZ 3035A. A possible example of predation. Note neural spines and supraneurals protruding into the gap in front of the dorsal fin. Deep-bodied appearance is due to oblique compression during preservation,  $\times 1.1$ .

Fig. 4. *Wadeichthys oxyops*. MUGD 3648. A possible example of an agonised death,  $\times 0.9$ .

