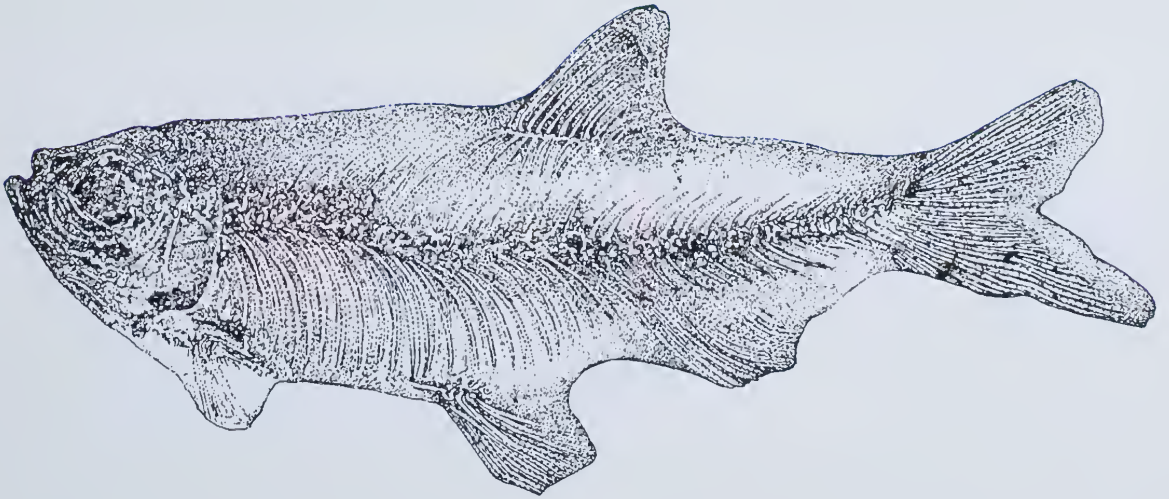


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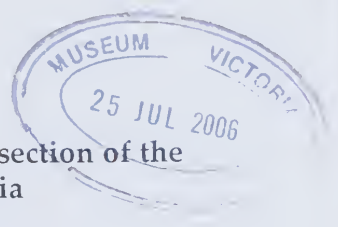
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Cover: The leptolepid fish *Cavenderichthys talbragarensis* from the Late Jurassic of New South Wales.
Drawing by Jill Ruse.



The fishes of Lake Kununurra, a highly regulated section of the Ord River in northern Western Australia

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Abstract – The Ord River, situated in the east Kimberley region of Western Australia, is regulated by two dams that supply irrigation water for tropical agriculture. The regulation of water in the 55 km span of river between these dams has resulted in this section now resembling a lacustrine rather than riverine environment that is reflected in its name, Lake Kununurra. Utilising various sampling techniques we captured/observed 4157 fish from 19 species in 13 families, whilst the presence of a further three species was confirmed by reliable sources. *Nematalosa erebi*, *Craterocephalus stramineus* and *Melanotaenia australis* were the three most widespread and abundant species, being encountered throughout the lake and representing ~66% of all fish recorded. *Ambassis* sp., *Arius midgleyi*, *A. graeffei*, *Glossamia aprion*, *Amniataba percoides*, *Hephaestus jenkinsi*, *Glossogobius giurus* and *Toxotes chatareus* were found throughout the lake but generally at fewer sites and in smaller numbers (~30% of all fish) than the three dominant species. The remaining species *Neosilurus ater*, *Strongylura krefftii*, *Leiopotherapon unicolor*, *Syncomistes butleri*, *Lates calcarifer*, *Mogumda mogumda*, *Oxyeleotris lineolatus* and *Ambassis macleayi* were generally found at few sites and in low numbers, and accounted for less than 4% of the overall catch. The regulation of the Ord River has apparently altered the species composition and abundances in Lake Kununurra. For example, marine/estuarine species, commonly encountered in the freshwaters of large northern Australian Rivers, are largely absent, while species such as *L. unicolor*, which is one of the most abundant species in nearby rivers and tropical Australian rivers in general, contributed to <1% of the total catch.

INTRODUCTION

The Ord River, situated in the east Kimberley region of Western Australia, has an arid and semi-arid monsoonal catchment of over 50 000 km² that extends into the western Northern Territory. The 650 km long river, which originates northwest of Halls Creek and drains into the Cambridge Gulf near Wyndham, has a mean annual stream flow of 3940 GL (into Lake Argyle), the second largest in Western Australia (Water and Rivers Commission 2000). The river is regulated by two dams that supply irrigation water for tropical agriculture. Completed in 1963, the Kununurra Diversion Dam was built across the Ord River and created Lake Kununurra. Approximately 55 km upstream of the Diversion Dam, the Ord River Dam that forms Lake Argyle, was completed in 1973.

Operation of the Kununurra Diversion Dam spillway gates, along with continual water release from the Ord River Dam, maintains relatively constant water levels in Lake Kununurra throughout the year. Thus, these dams have essentially altered the flow regime of this section of

the river from lotic to lentic conditions. Such modification often results in changes in fish communities, such as a reduction in the relative abundance of species that favour faster flowing reaches of rivers along with a concomitant increase in the abundance of those species restricted to slower flowing sections. Dams also often impede species migrations within river systems (Bunn and Arthington 2002).

Constant water levels within the lake have encouraged the development of profuse riparian vegetation. The inundation of surrounding lowlands also has resulted in many fringing swamps that are characterised by rich aquatic plant growth, large woody debris and extensive stands of emergent vegetation, such as the bulrushes *Typha domingensis* and *Eleocharis* spp. (Jaensch 1993). In recognition of its significance as a dry-season refuge for waterbirds, due to the consistency in the water level of the lake and its varied habitats, Lake Kununurra is now classified under the Ramsar convention as a “wetland of international importance”.

Despite its listing as a wetland of international importance, and noting the likely effects of habitat change and large dams on the teleost fauna, no literature exists detailing the lake's fishes. Thus, the primary aim of this study was to determine the fish fauna of Lake Kununurra. The distributions and broad habitat associations of the species in the lake are also discussed.

MATERIALS AND METHODS

Sample sites

The term 'Lake Kununurra', in the present study, refers to the 55 km-long body of water between the Lake Kununurra Diversion Dam and the Ord River

Dam, including the tributaries and associated perennial swamps and lagoons (Figure 1) (Jaensch 1993). In order to capture representatives of each species within Lake Kununurra extensive sampling was undertaken at 16 sites throughout its length in a variety of habitats (Figure 1).

Sampling methods

Sampling was conducted during day-light hours in November and December 2002. During this time the fish fauna of the sites were sampled using a variety of methods, including monofilament gill nets (50, 100, 125, 150 and 200 mm stretched mesh), seine nets (5 and 15 m nets of 3 mm woven mesh), rod and line, and visual surveys (e.g., mask and

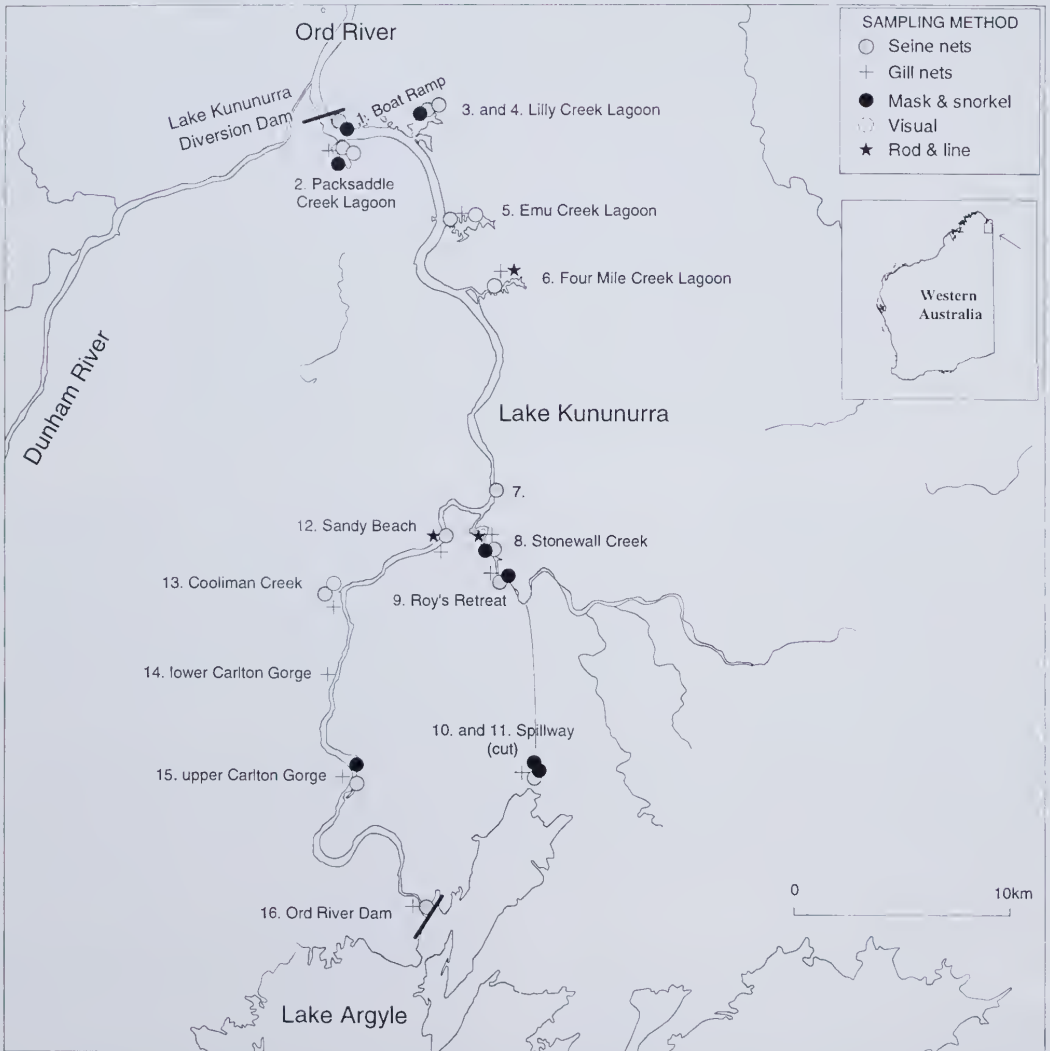


Figure 1 The sites sampled and the methods used to survey the fish fauna in Lake Kununurra.

snorkel). On capture, fish were identified, the number of each species recorded and the majority then released. A global positioning system (GPS) was used to determine the longitude and latitude of each site, and these data were then used, in conjunction with the computer program MapInfo (MapInfo Corporation 1998), to produce a map showing their location (Figure 1).

RESULTS

A total of 4157 fish from 19 species in 13 families were captured/observed in Lake Kununurra during the present study (Table 1). Three species dominated catches at the majority of sites within the system and accounted for 66% of the total catch. Bony Bream *Nematalosa erebi* (Günther, 1868) accounted for 27.3% (1133) of captured fish and was recorded at 11 of the 16 sites sampled. The Strawman *Craterocephalus stramineus* (Whitley, 1950) and Western Rainbowfish *Melanotaenia australis* (Castelnau, 1875) represented ~20.1% (837 individuals) and ~18.6% (775 individuals), respectively, and were each recorded from 12 sites (Table 1). The first of these species was most common in shallows near deep water where groups were observed feeding over sand or gravel substrates whereas the two smaller species were typically caught along the well-vegetated margins where they congregated in moderate to large schools near the surface in areas of low flow.

A further seven species were also widely distributed, and accounted for just over 30% of the total catch (Table 1). In decreasing abundance were Northwest Glassfish *Ambassis* sp. (~8.5%, 356 individuals, 6 sites), a species associated with areas of little water flow and copious growths of aquatic vegetation and was formerly referred to as *Ambassis muelleri* Klunzinger, 1880, by Allen and Burgess (1990); Silver Cobbler or Shovel-nosed Catfish *Arius midgleyi* Kailola and Pierce, 1988 (4.8%, 201 individuals) was captured at nine sites, from below the Ord River Dam downstream to Packsaddle Creek Lagoon; Mouth Almighty *Glossamia aprion* (Richardson, 1842) made up almost 5% of the total catch and was found throughout Lake Kununurra (198 individuals, 8 sites), where it was generally associated with aquatic vegetation; Barred Grunter *Amniataba percoides* (Günther, 1864) was widespread and relatively common (~3.2%, 134 individuals, 11 sites), forming aggregations in the shallows over gravel, sand, or mud in fast (e.g., upper Spillway Creek) to slow flowing or still waters (e.g., Lilly Creek Lagoon); Jenkin's or Western Sooty Grunter, or colloquially Black Bream *Hephaestus jenkinsi* (Whitley, 1945) represented ~2.8% of the total catch (117 individuals) and was captured in nine sites from Packsaddle Creek Lagoon to Carlton Gorge where it was often associated with deep water and

structure in the form of submerged roots, logs, rocks or vegetation; Flathead Goby *Glossogobius giurus* (Hamilton, 1822) was relatively common and widespread (~2.4%, 98 individuals, 8 sites) and was most often found in the shallows on sandy bottoms; Lesser Salmon or Blue Catfish *Arius graeffei* Kner and Steindachner, 1867 was captured at six sites from Carlton Gorge downstream to Packsaddle Creek Lagoon (~2.3%, 96 individuals) and was also common in the lower Ord River and Lake Argyle (Rowland unpublished data); Seven-spot Archerfish *Toxotes chatareus* (Hamilton, 1822) was relatively common and widespread throughout Lake Kununurra (~1.6%, 66 individuals, 8 sites), where it was commonly observed patrolling the surface near river banks or around riparian vegetation.

The remaining seven species encountered during this study, i.e., Black Catfish *Neosilurus ater* (Perugia, 1894); Freshwater Longtom *Strongylura krefftii* (Günther, 1866); Spangled Perch *Leiopotherapon unicolor* (Günther, 1859); Butler's Grunter *Sycomistes butleri* Vari, 1978; Barramundi *Lates calcarifer* (Bloch, 1790); Northern Trout Gudgeon *Mogurnda mogurnda* (Richardson, 1844); Sleepy Cod *Oxyeleotris lineolatus* (Steindachner, 1867) and Macleay's Glassfish *Ambassis macleayi* (Castelnau, 1878), were caught in low numbers and/or at few sites and in total contributed less than 4% to the overall catch (Table 1).

Three further species not captured during this study have been reported from Lake Kununurra; these were Freshwater Sawfish *Pristis microdon* Latham, 1794 (Thorburn *et al.* 2003), Rendahl's Catfish *Porochilus rendahli* (Whitley, 1928) (G. Allen and M. Allen unpublished data) and Giant Glassfish *Ambassis gulliveri* (Castelnau, 1878) (S. McIntosh personal communication).

DISCUSSION

The results of this study demonstrate that, although Lake Kununurra is a highly modified section of the Ord River, the number of freshwater species inhabiting the lake is comparable to those found elsewhere in the Kimberley. For example, the capture of 18 freshwater species, not including the catadromous *L. calcarifer*, during this study, in addition to reports of two other species from reliable sources, compares with 23 freshwater fish species found throughout the entire Fitzroy River (Morgan *et al.* 2002), 18 species from the Prince Regent River (Allen 1975), 19 from the Drysdale and Carson Rivers (Hutchins 1977), and nine from the Mitchell River (Hutchins 1981).

Of the 4157 fish caught in the present study the most abundant and commonly encountered species, *Nematalosa erebi*, *Craterocephalus stramineus*, *Melanotaenia australis*, *Ambassis muelleri*, *Arius midgleyi*, *Glossamia aprion*, *Amniataba percoides*,

Table 1 The number of each fish species caught at each of the sites sampled in Lake Kununurra. NB. Site 1 Swim Beach boat ramp; 2, Packsaddle Creek Lagoon; 3, Lilly Creek Lagoon (boat ramp); 4, Lilly Creek Lagoon; 5, Ernu Creek Lagoon; 6, Four Mile Creek Lagoon; 7, main channel (opposite Stonewall Creek); 8, Stonewall Creek (mouth); 9, Stonewall Creek (Roy's Retreat); 10, Spillway Creek (below spillway); 11, Spillway Creek (upper); 12, main channel (Sandy Beach); 13, Cooliman Creek; 14, main channel (lower Carlton Gorge); 15, main channel (upper Carlton Gorge); 16, main channel (below Ord Dam). * Although no *N. erebi* were captured at Site 16 during the present study they were seen there on a previous trip. (See Figure 1 for site locations).

Total Species	Site																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	individuals	cont.	sites
Clupeidae																			
<i>Nematalosa erebi</i>		533	550		16	8		3	7			2	7	5	2	*	1133	27.3	11*
Ariidae																			
<i>Artus graeffei</i>		3			10	25		19					8	31			96	2.3	6
<i>Artus midgleyi</i>		1			8	18		5		150		1	5	12		1	201	4.8	9
Plotosidae																			
<i>Necasilurus ater</i>		2						1		50							53	1.3	3
Belontiidae																			
<i>Strongylura krefftii</i>		1	30		3				1		8						43	1.0	5
Atherinidae																			
<i>Craterocephalus stramineus</i>	50	20	110		5	6	57	45	189	60	250	41			4	837	20.1	12	
Melanotaeniidae																			
<i>Melanotaenia australis</i>	76	50	185	100	207	25	14	5	10			27	58	18		775	17.6	12	
Ambassidae																			
<i>Ambassis macleayi</i>																	1	<0.1	1
<i>Ambassis</i> sp.	100			112	7			28				30	80			357	8.6	6	
Centropomidae																			
<i>Lates calcarifer</i>											4					4		<0.1	1
Terapontidae																			
<i>Amniataba percooides</i>	21	1	6		6			33	3	25	30	1	4		2	132	3.2	11	
<i>Hephaestus jenkinsi</i>		3			5			2	41	15	45	2	1	3		117	2.8	9	
<i>Leiopotherapon unicolor</i>					1	2		3	16		5	1	1			29	0.7	7	
<i>Sycomistes butleri</i>								12				2				14	0.3	2	
Apogonidae																			
<i>Glossamia aprion</i>	1			13			55	45				65	12	5	1	197	4.7	8	
Toxotidae																			
<i>Toxotes chatareus</i>	10		41		3	5		3	2			1	1			66	1.6	8	
Eleotridae																			
<i>Mogurnda mogurnda</i>				3												3	<0.1	1	
<i>Oxyeleotris lineolatus</i>				1												1	<0.1	1	
Gobiidae																			
<i>Glossogobius giurus</i>	34		13		8		1	15	6			18		3		98	2.4	8	
Total (species)	6	10	7	5	11	8	4	14	9	5	6	10	12	4	6	4	4157		

Hephaestus jenkinsi, *Glossogobius giurus*, *Arius graeffei*, *Toxotes chatareus*, were all recorded from the lower-most regions of the lake (Swim Beach Boat Ramp and/or Packsaddle Creek Lagoon) and, with the exception of *Ambassis* sp., *Arius graeffei* and *T. chatareus*, were also found in the upper-most sites (i.e., upper Carlton Gorge and /or immediately below the Ord Dam). The last three species were, however, captured at Cooliman Creek and/or lower Carlton Gorge, sites that are in the upper third of the lake.

Nematalosa erebi, *C. stramineus* and *M. australis*, in addition to being widespread throughout the system, were the most numerous and frequently encountered fishes caught during this study. However, whilst *N. erebi* was often associated with the deeper main channel, the smaller species *C. stramineus* and *M. australis* were usually observed in the shallow vegetated littoral zones. The fact that much of the Lake Kununurra environment consists of the preferred habitat of *N. erebi*, i.e. still or slow flowing vegetated waterbodies with mud/sand substrate (Bishop *et al.* 2001) would help explain why this species is so abundant and widespread within the lake. In the case of *C. stramineus* and *M. australis*, the dense emergent and submerged littoral vegetation would provide not only a refuge for these small fish from predators, but also a rich source of terrestrial and aquatic insect prey.

The rarer species encountered in Lake Kununurra include *Ambassis macleayi*, *Leiopotherapon unicolor*, *Sycomistes butleri*, *Mogurnda moguruda* and *Oxyeleotris lineolatus*. Some are genuinely rare throughout parts of their range such as *A. macleayi* (Merrick and Schmida 1984), whilst others, such as *O. lineolatus*, are generally cryptic species that hide amongst snags (Allen *et al.* 2002) and are difficult to catch, and thus are possibly under-represented in our samples. However, *L. unicolor* is usually one of the most numerous species encountered in freshwaters throughout the Pilbara and Kimberley (Morgan *et al.* 2004; Morgan and Gill 2004), yet is very rare in Lake Kununurra. A possible explanation for this observation is that in *L. unicolor* the stimulus to spawn is apparently associated with flood events (Llewellyn 1973; Beumer 1979), which, due to regulation, are minimised within the main body of Lake Kununurra. An examination of *L. unicolor* capture locations lends support to this explanation as the majority of *L. unicolor* were captured from sites in Stonewall and Spillway creeks, i.e. watercourses that resemble naturally flowing Kimberley streams and are subjected to flood flows during the wet-season. Such an explanation is also supported by the work of Bunn and Arthington (2002) who noted that some Australian freshwater fish species, as a result of life history strategies evolved in direct response to natural flow, are likely to suffer

recruitment failure when subjected to altered flow regimes and impoundment conditions.

Although the fish fauna of the Lake Kununurra section of the Ord River is relatively rich, it is likely that it would have been even more diverse prior to damming. For example, the 20 m dam wall provides an insurmountable barrier to the movement of catadromous species, such as Bullshark *Carcharhinus leucas* (Valenciennes, 1839), Freshwater Sawfish *P. microdon*, Freshwater Whipray *Himantura chaophrya* Monkolprasit and Roberts, 1990, Tarpon *Megalops cyprinoides* (Broussonet, 1782), Barramundi *L. calcarifer* and various others, including mullets (Mugilidae), all of which are present either immediately below or within five kilometres of the dam wall (Thorburn *et al.* 2003; Doupé *et al.* 2005). The occurrence of four *L. calcarifer* above the Diversion Dam is likely the result of escapes from aquaculture in Lake Argyle (Doupé and Lymbery 1999) or by their release into Lake Kununurra by recreational anglers. The current debate regarding the development of Lake Kununurra as a barramundi fishery has raised the issue of the feasibility of building a fishway between Lake Kununurra and the lower Ord River, either directly at the Diversion Dam, or indirectly via Packsaddle Plain and the Dunham River (Doupé and Bird 1999; Doupé *et al.* 2005). If such a scheme was to proceed, then it is possible that movement of catadromous species into the lake will occur. This may lead to the fish community above the Diversion Dam returning to a more natural condition, i.e. one that more closely mirrors that which would have been present before the dam was constructed.

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Distribution of the spotted minnow (*Galaxias maculatus* (Jenyns, 1842)) (Teleostei: Galaxiidae) in Western Australia including range extensions and sympatric species

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Abstract – *Galaxias maculatus* was captured from a number of rivers outside its previously known range. In Western Australia, it was formerly only known from rivers and lakes between the Goodga River (Two People's Bay, 30 km east of Albany) and the Dailey River (50 km east of Esperance), with additional records from the Boat Harbour Lakes (Kent River). An intensive survey of the inland fishes in rivers and lakes along the south coast of Western Australia has extended its distribution east by 50 km (Thomas River), west by approximately 40 km (Walpole River) and north by 400 km (Harvey River). The Western Australian Museum also has a specimen from the Canning River, a further 100 km north. Field salinity tolerance of *G. maculatus* was high, with fish found alive in 81 mScm⁻¹ (~45 ppt). The freshwater piscifauna east of, and including, the Pallinup River is depauperate, with *G. maculatus* being the only freshwater species present. All sympatric teleosts are tolerant of salinity and, with the exception of the introduced *Gambusia holbrooki*, are estuarine, including *Pseudogobius olorum*, *Leptatherina wallacei* and *Acanthopagrus butcheri*.

INTRODUCTION

The Spotted Minnow, Common Galaxias or Common Jollytail (*Galaxias maculatus* (Jenyns, 1842)) is a small, elongate, partially translucent, scaleless, osmeriform fish (Figure 1). It is one of the most widely distributed freshwater fishes in the world (Berra *et al.* 1996; Waters *et al.* 2000), with populations occurring in Australia, Lord Howe Island, New Zealand, Chatham Islands, Falkland Islands and South America. Both land-locked (i.e. complete their life-cycle in inland waters) and catadromous (with a marine larval phase) populations are recognised, and this widespread distribution has been attributed to the presence of catadromous populations throughout its range in eastern Australia, New Zealand and South America, with the larvae moving into the sea after hatching (Benzie 1968; Pollard 1971; McDowall *et al.* 1975). The presence of *G. maculatus* in Western Australia was first reported by Coy (1979) and McDowall and Frankenberg (1981), where the distribution was thought to extend from the Goodga River in the west to the streams around Esperance (see Figure 2). Jaensch (1992) later reported a single specimen to the west of the Goodga River in the Boat Harbour Lakes (Kent River) (Jaensch 1992) (Figure 2).

This paper presents new data on the distribution of *G. maculatus* within Western Australia and extends the range of the species in this State.

MATERIALS AND METHODS

This study focused on sampling the fish fauna in the rivers and lakes east of, and including, the Pallinup River on the south coast of Western Australia, excluding estuaries. Fish were sampled primarily using a combination of fine mesh seine nets in 148 sites between the Pallinup River and Poison Creek (east of the Thomas River, see Figure 2). Data presented in Morgan *et al.* (1998) were used for the distribution of *G. maculatus* to the west of the Pallinup River, while the unpublished reports by Morgan and Beatty (2003a, b) were utilised for the occurrences of *G. maculatus* in the Walpole and Harvey rivers, respectively.

Species distribution maps were created using site latitude and longitude data in the program MapInfo (MapInfo Corporation 1998).

Dissolved oxygen, temperature and conductivity were measured *in situ* with a WTW Multiline P4 meter. Unless otherwise stated, measurements were made immediately below the water surface.

RESULTS

Distribution of *Galaxias maculatus* in Western Australia

During this study *G. maculatus* was captured from the following rivers and lakes within its previously known range: Goodga and Angove



Figure 1 The spotted minnow (*Galaxias maculatus*).

rivers (Morgan *et al.* 1998), Pallinup, Bremer, Gairdner, Fitzgerald, Hamersley, Phillips, Steere, Jerdacuttup, Oldfield, Munglinup, Torradup, Young, Lort and Dalyup rivers; Yallobup, Kateup, Coramup and Bandy creeks; Moates, Gardner, Angove, Wheatley, Mullet and Woody lakes (Figure 2). Additionally, *G. maculatus* was captured from: Lake Boolenup and the Thomas River, approximately 100 km east of Esperance; the Walpole River, approximately 140 km west of the Goodga River; and in a drainage canal of Bancell Brook, a tributary of the Harvey River, approximately 580 km west and north from the Goodga River by coast (Figure 2).

Sympatric species

The estuarine Swan River Goby (*Pseudogobius olorum*) was found in the majority of systems between the Pallinup and Thomas rivers; the Western Hardyhead (*Leptatherina wallacei*) was found from the Pallinup River to Bandy Creek; Black Bream (*Acanthopagrus butcheri*), was captured with *G. maculatus* in the Oldfield River and in Wheatley and Woody lakes; and the introduced eastern Mosquitofish (*Gambusia holbrooki*) was found only in the Pallinup River (Figure 3).

Environmental variables

Galaxias maculatus was captured in conductivities ranging from 0.3 to 94.4 mScm⁻¹, and temperatures from 12 to 30°C, however, all fish found in conductivities greater than 88 mScm⁻¹ were dead, yet in all salinities <81.6 mScm⁻¹ (~45 ppt) they were alive. Field measurements and repeated observations revealed that when dissolved oxygen levels were less than 1.5 mg l⁻¹ at 30 cm depth, *G.*

maculatus approached the surface to respire aerially. In these instances the surface dissolved oxygen concentration was always marginally higher than that at 30 cm. Furthermore, dead fish were recorded on several occasions when water temperatures were >30°C and salinity was <2 ppt.

DISCUSSION

During this study the range of *G. maculatus* was extended considerably, i.e. east to Lake Boolenup and the Thomas River, approximately 100 km east of Esperance; west to the Walpole River, approximately 140 km west of the Goodga River; and, in a drainage canal of Bancell Brook, a tributary of the Harvey River, approximately 580 km west and north from the Goodga River by coast (see Figure 2). The data presented here highlights the absence of studies of the inland fish fauna on the south coast of Western Australia.

There is a marked reduction in the number of species of native freshwater fish from west to east along the south coast of Western Australia. Ten freshwater fish species occur in the region with a moderate Mediterranean climate to the west of, but not including, the Pallinup River (Morgan *et al.* 1998; Allen *et al.* 2002), whereas only one freshwater species (i.e., *G. maculatus*) occurs in the region with a dry Mediterranean climate east of the Pallinup River (this study) (Figure 2). The ranges of *G. maculatus* and the estuarine *P. olorum* extend to the eastern most river on the south coast, i.e. the Thomas River (Figures 2 and 3), while the estuarine *L. wallacei* extends as far east as Bandy Creek. The species composition of the rivers east of, and including, the Pallinup River is a reflection of the higher natural salinities of these lower rainfall

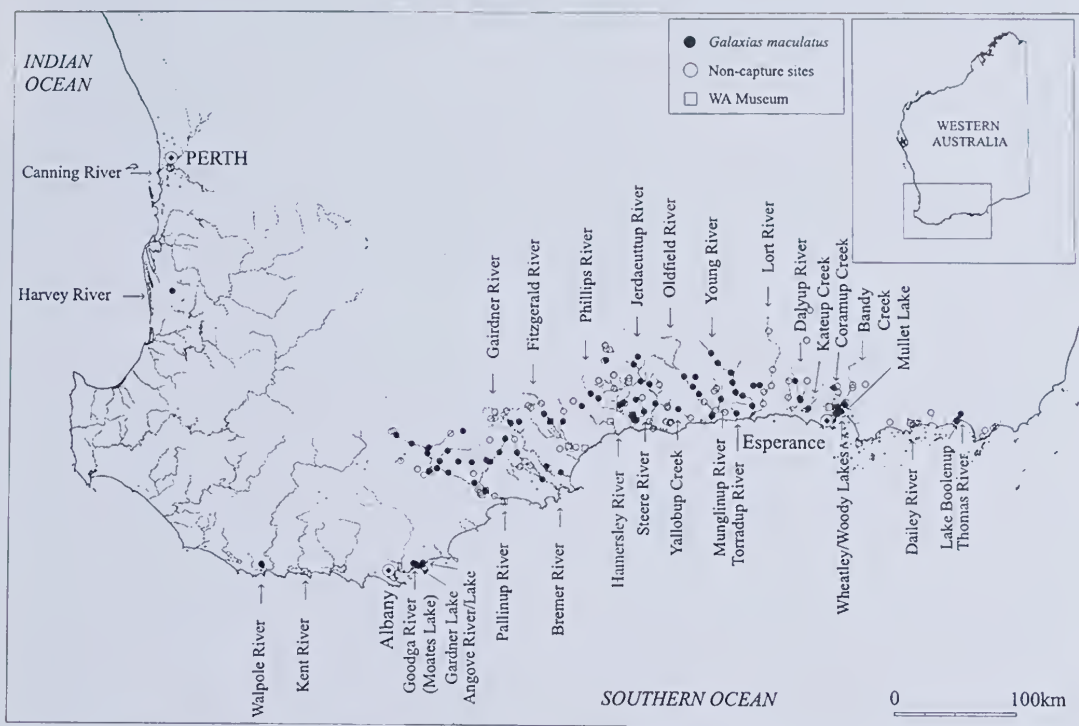


Figure 2 The sites that *Galaxias maculatus* were captured at during this study and from those specimens housed in the Western Australian Museum.

systems than for those rivers to the west. Thus, only species that are salt tolerant are found in the rivers east of the Pallinup. The feral *G. holbrooki* is able to tolerate salinities up to ~60 ppt (Morgan *et al.* 2004) but does not currently extend east of the Pallinup River however it is found in most of the river systems west of the Pallinup and north to the Hutt River, approximately 450 km north of Perth (see Morgan *et al.* 1998, 2004). This species is known to seriously impact other small south-western Western Australia fishes (Gill *et al.* 1999), yet it is not clear what impacts it has on the species in the Pallinup River. It is probably inevitable that it will eventually be introduced into other rivers on the south coast of Western Australia.

During the current study, the number of *G. maculatus* captured at those sites within its previously known range was far greater than those recorded to the west of its previously known range (i.e., Walpole and Harvey rivers). For example, despite extensive sampling, only four and one individuals were captured in the Walpole and Harvey rivers, respectively (Morgan and Beatty 2003a, b). Therefore, these individuals, particularly in the case of those in the Harvey River, are either indicative of populations with very low abundances

or are simply marine stragglers. It is likely that the establishment of new, self-maintaining populations is only achieved when adequate numbers migrate into these systems and environmental tolerances, particularly salinity and possibly temperature, are not exceeded. For example, while *G. maculatus* is extremely tolerant to high salinity (acute LD₅₀ of 45 ppt, Chessman and Williams (1975) and supported by field observations in this study), water temperatures experienced on the west coast of Western Australia (e.g., Harvey and Canning rivers) may often exceed 30°C during summer, a temperature that Richardson *et al.* (1994) suggest is lethal to at least some New Zealand populations.

Previous workers have faced uncertainty whether Western Australian *G. maculatus* were land-locked or diadromous, though on the basis of an inland breeding record from the Pallinup River, the former was suspected (Allen 1982). A recent detailed study on the biology of *G. maculatus* in south-western Australia that included populations in the Goodga, Phillips, Oldfield and Jerdacuttup rivers confirms that, over most of its range in Western Australia, *G. maculatus* has a self sustaining, land-locked breeding strategy (Chapman 2004). Further evidence for this is the presence of fish in the

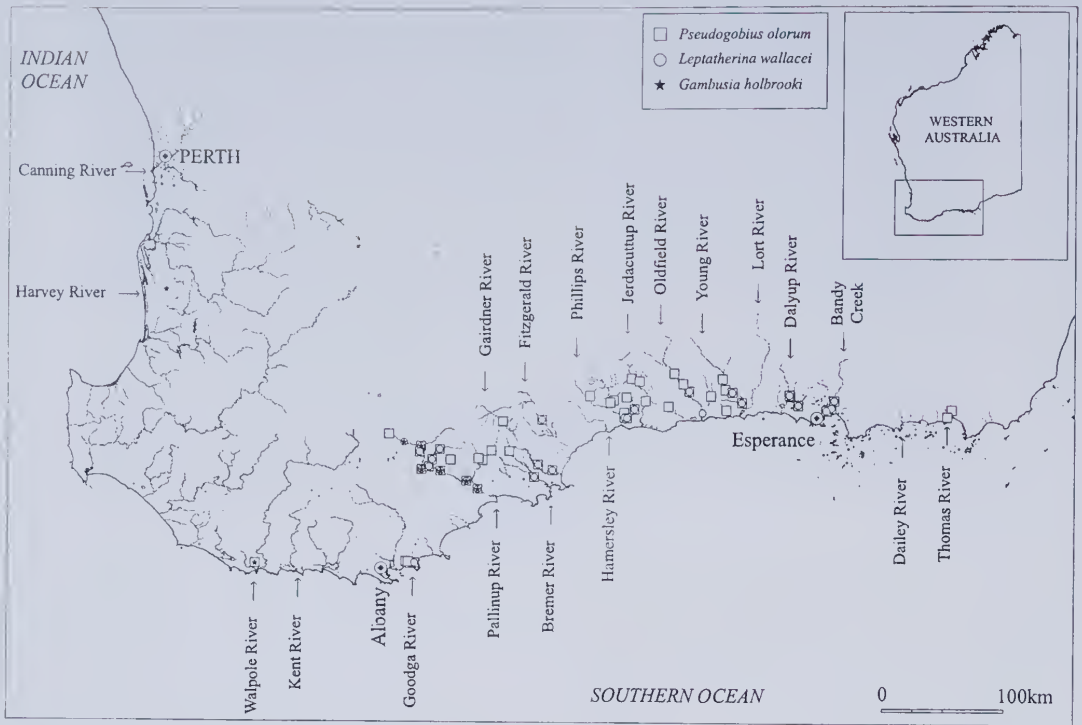


Figure 3 The distribution of the three sympatric species captured within the main range of *Galaxias maculatus*.

Jerdacuttup River, which has probably not had contact with the sea for 6 000 years (Hodgkin and Clark 1990). In other rivers, occasional contact with the sea by either adult or larval fish is a possibility as raised beach bars can either be breached by flooding, vigorous winter flow or human intervention (artificial excavation).

McDowall (1988) considered that diadromous galaxiids represented the primitive or ancestral stock and that freshwater limited populations were a more recently derived phenomenon. Waters *et al.* (2000a) proposed that the loss of the primitive marine juvenile phase may be an important mechanism of galaxiid speciation. It is very likely then that on the south coast of Western Australia the land-locked strategy has developed from diadromous stock in response to changes to local coastal geomorphology over recent geological time, with most of the rivers of the region now being only intermittently open. For example, Culham Inlet, previously the Phillips River estuary, where *G. maculatus* is confirmed to undergo a land-locked life-history (Chapman 2004), was permanently open to the sea as recently as 3 500 years ago but is now better described as a coastal salt lake (Hodgkin 1997). Most of the region's rivers are now open to the sea only after major rainfall events.

Although the presence of diadromous populations of *G. maculatus* in rivers on the south coast was not demonstrated during the present study, its presence in the Walpole River, which enters the sea via a permanently open channel at the mouth of the Normalup Inlet (Hodgkin and Clark 1988), suggests that there is at least the potential for diadromy in Western Australia.

Recent allozyme (Berra *et al.* 1996) and mitochondrial (Waters *et al.* 2000b) studies have demonstrated the considerable powers of dispersal, due to a marine larval stage in some populations, of *G. maculatus*. For example Berra *et al.* (1996) considered that gene flow continues to occur between Australia, New Zealand and South America, and whilst Waters *et al.* (2000b) confirmed gene flow between Australia and New Zealand, they were less convinced that dispersal occurred across the Pacific. It is likely that the presence of *G. maculatus* in the Walpole and Harvey rivers, is a result of larval drift via ocean currents from either outside Western Australia or from a south coast river. The collection of more mitochondrial data is required to test which of these hypotheses is the more likely. Such data would also permit comparisons of the genetic structure of populations within Western Australia, and between Western Australia, eastern Australia, New Zealand and

South American populations, i.e. is there regular gene flow between systems?

ACKNOWLEDGEMENTS

We would like to thank the Natural Heritage Trust, Murdoch University, Department of Fisheries, Water and Rivers Commission, Harvey River Restoration Trust and Fishcare WA for providing funds towards this project. Thanks to CALM for providing permits to sample in National Parks and A Class Reserves. Thank you to Charlotte Morgan for help with sampling.

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A new species of *Lechytia* from eastern Australia (Pseudoscorpiones: Lechytiidae)

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Abstract – The first Australian representative of the chthonioid family Lechytiidae, *Lechytia libita* new species, is described from Queensland where it appears to favour tree bark microhabitats in rainforest habitats.

INTRODUCTION

Members of the family Lechytiidae have a sporadic distribution around the world with ten species recorded from the Americas, six species from Africa, one species from Turkey and five species from Asia and the Pacific region (Harvey 1991), extending as far east as Hawaii (Muchmore 2000). The sole genus *Lechytia* Balzan has usually been placed in its own tribe (e.g., Beier 1932; Chamberlin 1929; Muchmore 1975) or subfamily (Morikawa 1960; Murthy and Ananthakrishnan 1977) within the Chthoniidae, but Harvey (1992) proposed the Lechytiidae as a family distinct from the remainder of the extant Chthonioidea, the Chthoniidae and Tridenchthoniidae. Muchmore (1975, 2000) divided the genus into two species-group, the *L. arborea* species-group for *L. arborea* Muchmore, *L. sini* Muchmore and *L. sakagamii* Morikawa, and the *L. hoffi* species-group for *L. hoffi* Muchmore. The type species *L. chthoniiformis* (Balzan 1887) was recognised as a member of the *L. arborea* group by Mahnert (2001), but the remaining species of the genus have not yet been placed. A new species of *Lechytia* has been recently detected in eastern Australia which extends the distribution of the family for the first time into the Australian region. This new species is the subject of this paper.

The specimens examined as part of this study are lodged in the Queensland Museum, Brisbane (QM) and the Western Australian Museum, Perth (WAM). Specimens were examined using dilute lactic acid under a compound microscope, and all have been returned to ethanol. Terminology largely follows Chamberlin (1931) and Harvey (1992). In particular, I have followed the naming conventions applied by Harvey (1992) based upon perceived homologies in the trichobothria. In this case, this affects the names of the trichobothria of the movable finger which are here termed *st*, *sb*, *b* and *t* (from the most basal to the most distal). In previous systems they are termed *b*, *sb*, *st* and *t*.

SYSTEMATICS

Family Lechytiidae Chamberlin, 1929

Genus *Lechytia* Balzan, 1892

Lechytia Balzan 1892: 499; Harvey 1991: 186 (full synonymy).

Type species

Roncus chthoniiformis Balzan, 1887, by original designation.

Remarks

Members of the family Lechytiidae share a number of unusual features, the most peculiar of which is the arrangement of the trichobothria where *eb* and *esb* are situated on the dorsum of the chelal hand. In all other chthonioids, these trichobothria are situated at the base of the chelal finger. This feature will serve to distinguish them from all other chthonioids.

Species of *Lechytia* have been recorded from many parts of the world (Harvey 1991), including South and central America [*L. chthoniiformis* (Balzan, 1887), *L. chilensis* Beier, 1964, *L. delamarei* Vitali-di Castri, 1984, *L. kuscheli* Beier, 1957, *L. martiniquensis* Vitali-di Castri, 1984 and *L. trinitatis* Beier, 1970], North America (*L. arborea* Muchmore, 1975, *L. cavicola* Muchmore, 1973, *L. hoffi* Muchmore, 1975 and *L. sini* Muchmore, 1975), Asia (*L. anatolica* Beier, 1965, *L. asiatica* Redikorzev, 1938, *L. himalayana* Beier, 1974, *L. indica* Murthy and Ananthakrishnan, 1977 and *L. madrasica* Sivaraman, 1980), Africa [*L. dentata* Mahnert, 1978, *L. garambica* Beier, 1972, *L. leleupi* Beier, 1959, *L. maxima* Beier, 1955b, *L. natalensis* (Tullgren, 1907) and *L. serrulata* Beier, 1955a] and the Pacific region (*L. sakagamii* Morikawa, 1952). A single species, *L. tertiaria* Schawaller, 1980, has been described from Tertiary Amber deposits in the Dominican Republic (Schawaller, 1980). The species described below is the first to be found in Australia.

Lechytiya libita sp. nov.

Figures 1–14

Material examined

Holotype

♂, Windsor Tableland, Queensland, AUSTRALIA, 16°16'S, 145°08'E, 1160 m, site 2, pyrethrum, 27 December 1988, E. Schmidt and ANZSES (QM S17220).

Paratypes

AUSTRALIA: Queensland: 1 ♀, same data as holotype (QM S67680); 1 ♀, Oakview State Forest, summit, 26°10'S, 152°20'E, 600 m, pyrethrum on trees, rainforest, 26 May 2002, G. Monteith (QM S64848); 2 ♀, Pearamon Scrub, 17°19'S, 145°37'E, 750 m, pyrethrum on trees, 9 December 1995, G. Monteith (QM S45776); 1 ♂, Mt Fort William, 6 km NE. of Kalpower, 24°39'S, 151°20'E, 700 m, pyrethrum, rainforest, 18 September 1989, G.B. Monteith (QM S41073); 3 ♂, 3 ♀, Bauple State Forest, 25°52'54"S, 152°37'12"E, tree hollow, 12 January 2001, M. Shaw (WAM T62601).

Diagnosis

Trichobothria *sb* and *b* (formerly *sb* and *st*) separated by about 1 areolar diameter; chelal teeth reduced to a lamina for most of finger length; chela 0.419–0.435 (♂), 0.462 (♀) mm in length, and 4.11–4.22 (♂), 3.76 (♀) times longer than broad; chelal hand 0.200 (♂), 0.210 (♀) mm in length.

Description

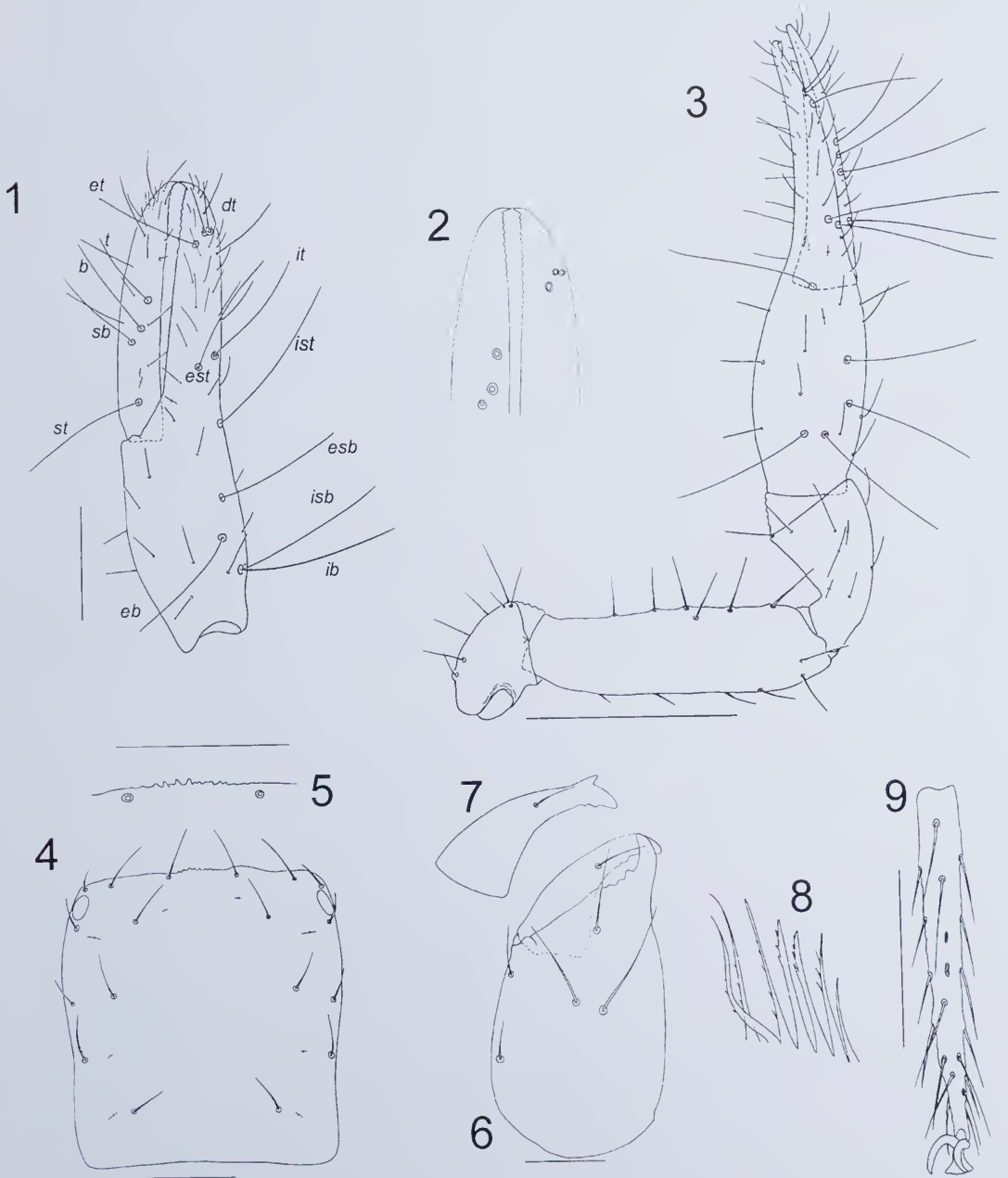
Adult: Colour pale brown. Pedipalp (Figures 1–3): trochanter 1.64–1.66 (♂), 1.55 (♀), femur 3.29–3.74 (♂), 3.17–3.90 (♀), patella 1.65–1.86 (♂), 1.60–1.90 (♀) and chela 4.08–4.36 (♂), 3.75–3.94 (♀) times longer than broad; chelal hand 1.86–1.96 (♂), 1.71–1.88 (♀) times longer than broad; movable chelal finger 1.24–1.35 (♂), 1.20–1.35 (♀) times longer than hand; femur with anterior face flattened so that a faint keel is present on the antero-dorsal and antero-ventral margins; chelal fingers with approximately 7 distal teeth, remaining teeth obsolete, fused into a lamina (Figure 1); fixed chelal finger and hand with 8 trichobothria, movable chelal finger with 4 trichobothria (Figure 1); *ib*, *isb*, *eb* and *esb* on dorsum of hand; *ib* and *isb* situated basally; *eb* and *esb* situated medially; *b* situated slightly closer to *sb* than to *t*; *b* and *sb* only about one areolar diameter apart; *xs* situated slightly distal to *et* near tip of fixed finger, each hair shorter than those of other trichobothria; venom apparatus absent. Chelicera (Figures 6, 7) with 5 setae on hand and 1 medial seta on movable finger; fixed finger with 3 small teeth, the distal-most tooth largest; movable finger much shorter than hand, with 2 small teeth; flagellum (Figure 8) consisting of 7 blades, the

subdistal blade strongly recumbent, others straight; galea of ♂ absent, that of ♀ a short rounded nubbin. Carapace (Figure 4) with 2 small corneate eyes; anterior margin finely denticulate (Figure 5); with 18 setae arranged 6: 4: 4: 2: 2; the pre-ocular seta about 50% length of other setae in anterior row; with 4 pairs of lyrifissures, one pair situated antero-medially, the second pair situated interno-lateral to the eyes, the third pair situated slightly interior to the sole pair of setae of the intermediate row, and the fourth pair situated exterior to the sole pair of setae of the posterior row. Tergites and sternites undivided; tergal chaetotaxy ♂, 6: 5–6: 5–6: 6: 6: 6: 6: 6: 4: 1T2T1: 0; ♀, 6: 6: 6: 6: 6: 6: 6: 6: 4: 1T2T1: 0; sternal chaetotaxy ♂, 10–11: (3)32–33(3): (3)8–10[4+4](3): 10: 7–8: 8: 8: 8: 2TT2: –: 2; ♀, 6: (3)6(3): (3)8(3): 10: 8: 8: 8: 8: –: 2. All setae bordering male sternite III bifurcate or trifurcate (Figure 13). Genitalia of male not studied in detail; of female weakly sclerotized with U-shaped frame. Pleural membrane smoothly plicate. Coxal chaetotaxy (Figure 10): ♂, 2+3: 4: 4–5: 4–7: 7; ♀, 2+3: 4: 5: 6–7: 7; manducatory process with 2 distal setae, about equal in length (Figure 10), the distal seta terminally bifurcate (Figure 11), plus an additional 3 setae situated close to trochanteral foramen; coxal spines and intercoxal tubercle absent (Figure 10); coxa I with small, triangular apical projection with single seta situated at base (Figure 12); other setae on coxa I situated near trochanteral foramen. Legs robust, femur+patella IV 2.03 (♂), 1.96 (♀) times longer than deep; heterotarsate; tarsi with two elongate gland openings along dorsal surface (see Muchmore 2000) each with crenulate margins (Figure 9); arolium slightly shorter than claws (Figure 9), claws simple.

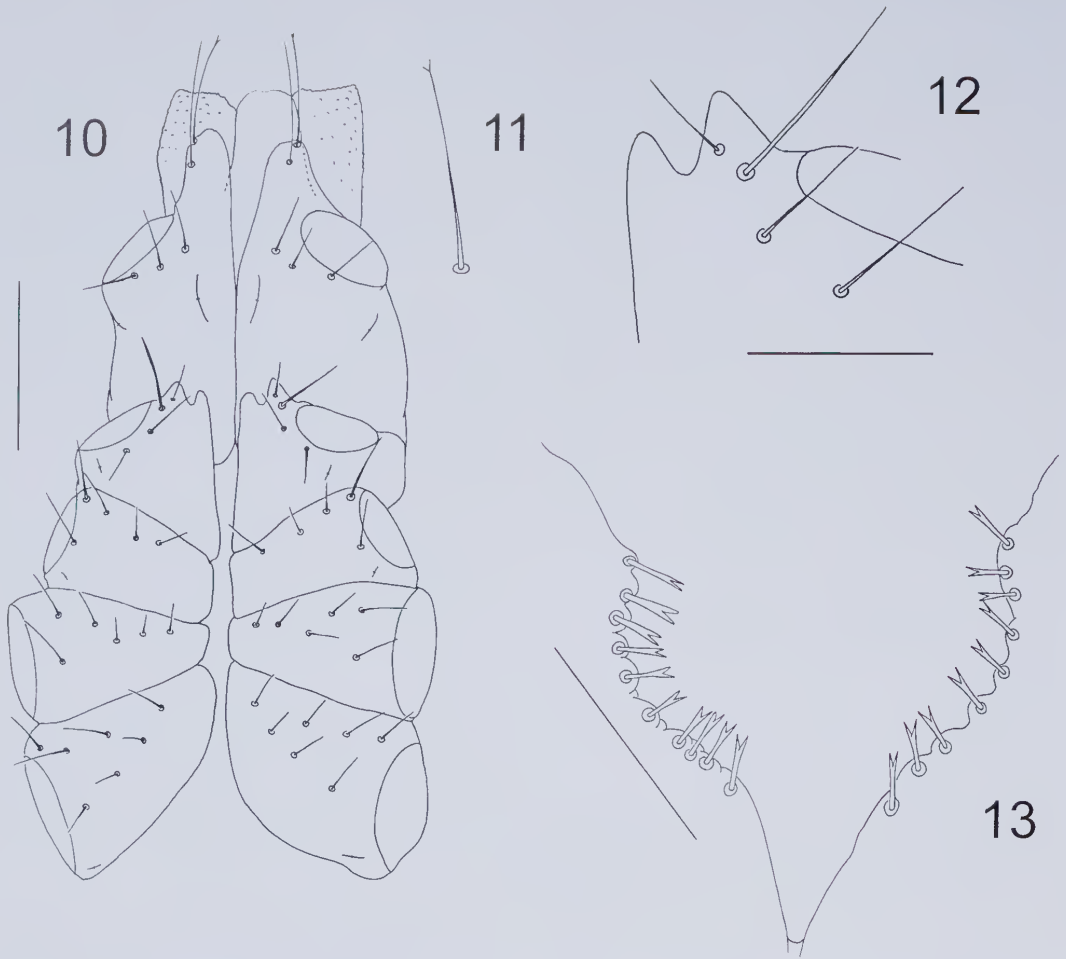
Dimensions (mm)

Males: Holotype (QM S17220) followed by other males (where applicable): Body length 1.17 (0.88–0.98). Pedipalps: trochanter 0.123/0.074, femur 0.288/0.077 (0.265–0.28/0.073–0.082), patella 0.160/0.092 (0.138–0.160/0.080–0.097), chela 0.435/0.103 (0.395–0.419/0.092–0.102), hand length 0.200 (0.175–0.200), movable finger length 0.256 (0.235–0.260). Chelicera 0.211/0.115, movable finger length 0.112. Carapace 0.315/0.307 (0.29–0.31/0.253–0.286); eye diameter 0.031. Leg I: femur 0.178/0.046, patella 0.090/0.053, tibia 0.109/0.035, tarsus 0.186/0.028. Leg IV: femur + patella 0.320/0.157, tibia 0.208/0.093, metatarsus 0.112/0.051, tarsus 0.186/0.029.

Females: Paratype (QM S67680) followed by other females (where applicable): Body length 1.22 (1.06–1.20). Pedipalps: trochanter 0.129/0.083, femur 0.304/0.096 (0.285–0.320/0.085–0.090), patella 0.166/0.104 (0.159/0.091–0.100), chela 0.462/0.123 (0.415–0.455/0.110–0.120), hand length 0.210 (0.198–0.225), movable finger length 0.262 (0.240–0.275). Chelicera 0.223/0.122, movable finger length 0.127. Carapace



Figures 1-9 *Lechyti libita*, sp. nov., holotype male unless stated otherwise: 1, left chela; 2, detail of distal portion of fingers; 3, right pedipalp; 4, carapace; 5, epistome; 6, chelicera; 7, movable cheliceral finger (paratype female); 8, flagellum; 9, right tarsus I (paratype female). Scale lines: 0.05 mm (Figures 6, 7); 0.1 mm (Figures 1, 4, 5, 9); 0.2 mm (Figure 3).



Figures 10–13 *Lechytiya libita*, sp. nov., holotype ♂ unless stated otherwise: 10, coxal region (paratype female); 11, distal seta of manducatory process; 12, left coxa I (paratype female); 13, male genital atrium. Scale lines: 0.05 mm (Figure 12); 0.1 mm (Figures 10, 13).

0.352/0.328 (0.290–0.340/0.285–0.345); eye diameter 0.023. Leg I: femur 0.188/0.051, patella 0.103/0.458, tibia 0.109/0.036, tarsus 0.186/0.026. Leg IV: femur + patella 0.315/0.161, tibia 0.224/0.070, metatarsus 0.122/0.056, tarsus 0.198/0.269.

Remarks

Lechytiya libita belongs to the '*L. arborea*' species-group as defined by Muchmore (1975), as the distal seta of the pedipalpal coxa is bifurcate (Figure 11), the chelal teeth are strongly reduced (Figure 1), tergite XI has a chaetotaxy of 1T2T1, the male galea is much reduced in comparison with the female (Figures 6, 7) and the tarsal gland openings are enlarged and possess crenulate margins (Figure 9) (Judson 1992; Muchmore 2000). It is most similar to those species of *Lechytiya* in which trichobothria *sb* and *b* are slightly separated from each other, usually

by about one areolar diameter, but it differs from all of these species by its smaller size: *L. chilensis* from Chile [e.g., chelal hand 0.24 mm (♀)], *L. kuscheli* from Juan Fernandez Island [e.g. chelal hand 0.25–0.26 mm (♂), 0.285 mm (♀)], *L. serrulata* from Zaire [e.g., chelal hand 0.24 mm (♂)], *L. maxima* from Kenya [e.g., chelal hand 0.28 mm (♂, ♀)], and *L. cavicola* from Mexico [e.g., chela length 0.51–0.52 mm (♂), 0.51 mm (♀), chelal hand 0.235–0.25 mm (♂), 0.24 mm (♀)]. In addition, the chelal teeth are reduced to a thin lamina in *L. libita*, *L. chilensis*, *L. kuscheli*, and *L. cavicola*, but are well-defined in *L. serrulata* and *L. maxima*. *Lechytiya libita* also differs from some of the lamina-bearing species by the relative dimensions of the chela: *L. chilensis* has a chela which is 4.8 (♀) times longer than broad, while the chela of *L. kuscheli* is 4.8 (♂), 4.3 (♀) times longer than broad; *L. libita* has a chela

that is 4.11–4.22 (δ), 3.76 (\varnothing) times longer than broad. Geographically, *L. libita* is closest to *L. sakagamii* from the Pacific region and *L. asiatica* Redikorzev from Vietnam. It differs from *L. sakagamii* by the relative positions of trichobothria *sb* and *b*, which are separated by about one areolar diameter in the Australian species and by about half an areolar diameter in *L. sakagamii* (Beier 1957: figure 3c; Morikawa 1960: plate 7, figure 10; Muchmore 2000: figure 5b). *Lechytia libita* also differs from *L. asiatica* in the positions of *sb* and *b*, which are contiguous in *L. asiatica* [Dr Mark Judson, in litt., has kindly examined the two syntypes (1 δ , 1 \varnothing) of *L. asiatica* which are lodged in Muséum national d'Histoire Naturelle, Paris].

Distribution

Lechytia libita is the first member of the genus to be found in Australia and has been recorded from rainforest habitats in eastern Queensland (Figure 14). All available records suggest that *L. libita* is a corticolous species as all known specimens were taken from tree habitats. Whilst a corticolous habitat is generally unusual for chthonioid pseudoscorpions – they are more abundant in leaf litter and soil – a corticolous environment is not unknown amongst lechytiids. *Lechytia arborea* has been collected from “base of leaf of cabbage palm” and “beating foliage” from south-eastern U.S.A., whilst some nymphs that were tentatively assigned to the species were collected from beneath the “bark of a pine tree” at two different locations in Florida

(Muchmore 1975). Some of the type material of *L. anatolica* from Turkey was taken under bark of a rotting pine (Beier 1965), and *Lechytia delamarei* was collected under bark on Guadeloupe (Vitali-di Castri 1984). *Lechytia himalayana* has been taken from the bark of *Rhododendron* and *Abies* (Schawaller 1987).

Etymology

The specific epithet is a Latin noun alluding to the pleasure of finding the first species of *Lechytia* in Australia (*libitus*, Latin, pleasing, agreeable).

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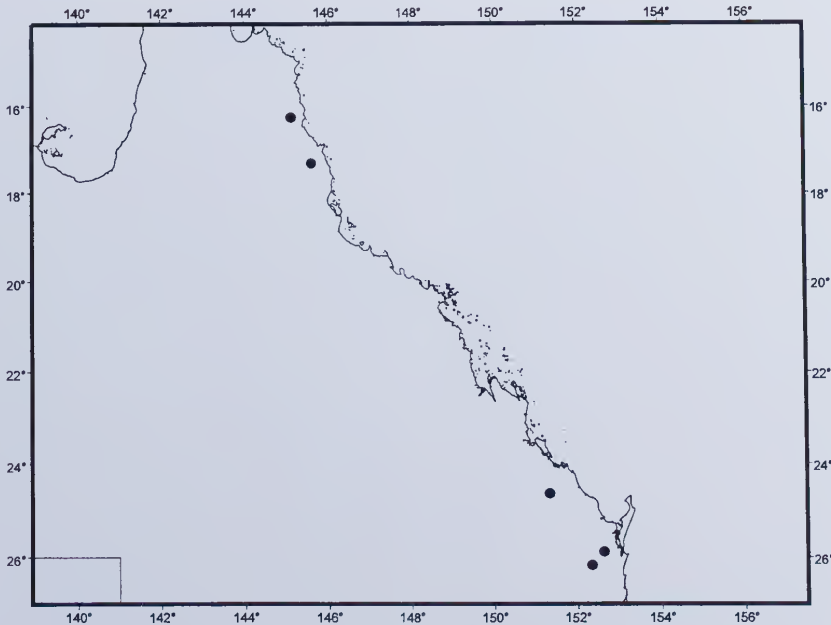


Figure 14 Distribution of *Lechytia libita*, sp. nov.

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Mulka's Cave Aboriginal rock art site: its context and content

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Abstract – The Mulka's Cave Aboriginal site, within "The Humps" Nature Reserve near Hyden, Western Australia, was recorded in detail prior to an overall tourist-orientated development of the Reserve. The site features 452 motifs, an extremely high number for the region where most sites have fewer than 30 motifs. The artwork is dominated by 275 handstencils, with 40 sprayed areas, 23 handprints, 23 paintings, 3 drawings and a single object stencil produced with a wide range of colours. The high diversity of art attributes is unusual in a region where the rock art is dominated by red handstencils. The site appears to have been of considerable importance to the Noongar people in the past and remains significant to them today. Its significance to the broader Western Australian community is evidenced by the high number of tourists it currently receives.

INTRODUCTION

The Mulka's Cave Aboriginal site is a decorated rock shelter with an occupation deposit within "The Humps" Nature Reserve near Hyden, Western Australia. The site's management is to be upgraded as part of an overall tourist-orientated development of the Reserve. In line with this upgrade, the site's rock art has been recorded in detail for research, interpretation and conservation needs. The name "Mulka's Cave" derives from the associated Aboriginal myth (see below). The site is currently promoted to the general public and is estimated to receive around 80,000 visitors per year, a very high level of visitation for an Australian rock art site (excluding the exceptionally popular tourist sites at Uluru and Kakadu; Gale and Jacobs 1987). The recording was undertaken as part of the Wheatbelt Heritage Management Strategy of the Department of Indigenous Affairs. The strategy aims to develop a procedure of consultation with local Noongar people with respect to the management of Aboriginal sites within the Noongar Native Title area.

THE SITE AND ITS CONTEXT

Mulka's Cave is 18 km north-east of Hyden (Figure 1) and 300 km inland from Perth. It lies 15 km north of Wave Rock, the region's, and one of the nation's, premier tourist attractions. While Mulka's Cave is a promoted tourist attraction, it is largely "riding on the back" of the very successful Wave Rock tourism development.

Mulka's Cave has formed beneath a large boulder at the base of an outcrop of Archaean granite now

known as The Humps (Figures 1 and 2). The outcrop is some 2 km x 1.5 km in area and rises to 80 m above the surrounding plain (Twidale and Bourne 2003). It is the highest of several granite inselbergs in the region that form notable landmarks in an otherwise flat landscape. These inselberg were important for the Aboriginal people as both navigational guides and water reserves (Bindon 1997). The rock consists of "variably textured, medium and coarse grained seriate granite and adamellite" (Geological Survey of Western Australia 2003). Small, deeply weathered areas of the outcrop on the eastern side form linear ridges and tors, and it is beneath one of these tors that Mulka's Cave has formed.

The mean annual rainfall for the region is 345 mm (Bureau of Meteorology web site for Hyden). Rainfall tends to be heavier in winter (June 52 mm) and lightest in December (mean 14 mm), but can occur throughout the year. The temperature extremes range from 48°C in summer to 5°C in winter. The interior of Mulka's Cave does not receive any direct sunlight and hence it is not subject to the extreme temperature changes that are a common factor in rock deterioration (Twidale 1980: 134). Run-off water flows through the cave making the interior floor damp and slippery for prolonged periods after rain. This run-off has doubtless also affected the integrity of the archaeological deposits at the main entrance. Water, both flowing through the shelter and percolating through the rock matrix, is probably the principal agent for the massive exfoliation occurring within the shelter that threatens the existing artwork (cf. Twidale 1980: 142; Thorn 2001).



Figure 1 Mulka's Cave, The Humps, near Hyden. Main entrance arrowed.

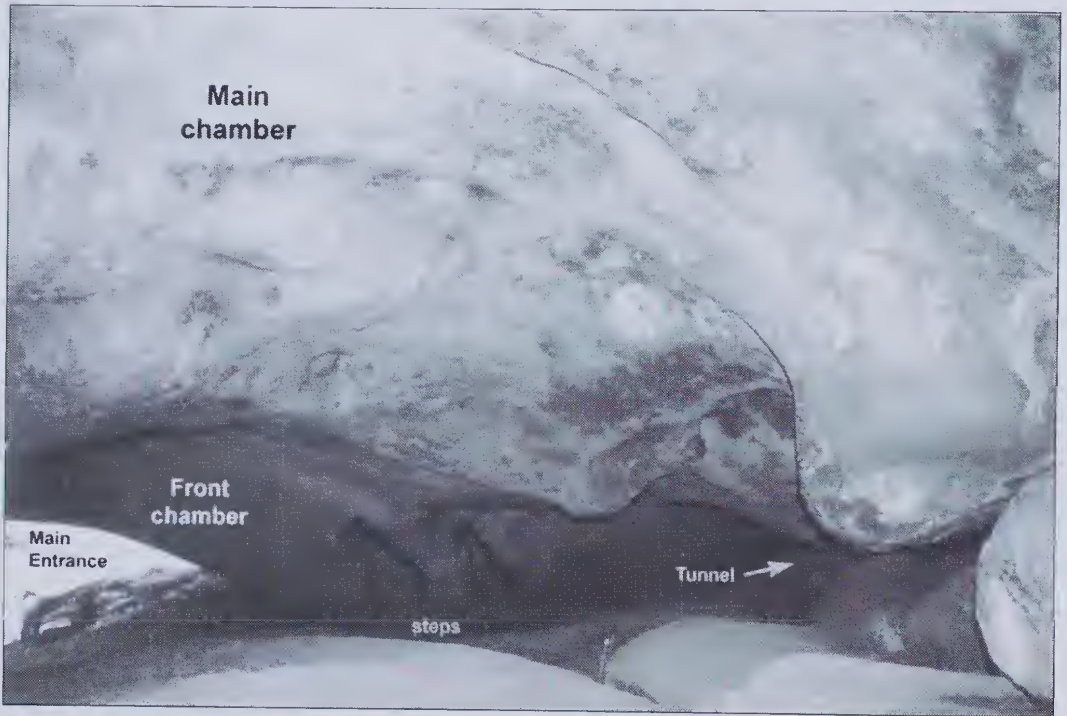


Figure 2 Interior of Mulka's Cave looking down to the main entrance from the main chamber.

The vegetation surrounding The Humps is essentially a mallee scrub with localised stands of salmon gums (*Eucalyptus salmonophloia*) (Bowdler *et al.* 1989), with pockets of relic

vegetation on The Humps themselves (Twidale and Bourne 2003). Yams and wattle seeds are the only plant foods whose use by Indigenous hunter-gatherers is documented in the region

(Bowdler *et al.* 1989). Early explorers (e.g., Roe 1852) found water and feed for their horses scarce throughout the region around Hyden, and sandalwood cutters relied upon the water they found in "granite rockholes" (Bowdler *et al.* 1989). As such they would have been of paramount importance to the Aborigines utilising the area (Bindon 1997).

The few early references to Aborigines around Hyden are scanty at best and have been interpreted as suggesting that the area was little visited because of its poor natural resources (Bowdler *et al.* 1989). However, the number and distribution of Aboriginal sites associated with gnammas across the region (Webb and Gunn 2004) suggests that the area was regularly visited following suitable rains.

Tindale (1974) placed the area around Hyden within the tribal area of the Njaki Njaki people who shared "overall cultural similarities" with the people of south-west Western Australia (Bowdler *et al.* 1989). Consequently, they were part of the south-western cultural group known as the Goreng (Tindale 1974) or, more usually, Nyungar or Noongar (Berndt 1980). The Njaki Njaki were also known by the names Kokor and Kikkar (Tindale 1974). Today the site is within the area of the South-West Aboriginal Land and Sea Council (SWALSC) which represent the various Noongar groups of the South-West.

Methods

The Western Australian Department of Indigenous Affairs (DIA) contracted the author to produce a detailed recording of the site. The Department undertook initial consultation for the project and received permission and approval from the local and regional Noongar representatives for it to proceed. DIA subsequently organised an on-site meeting between the consultant and the local Noongar representatives when the recording aims and methods were fully explained. The Department also gave their permission for the publication of this paper.

A plan of the site was prepared using handheld GPS, with finer detail mapped by tape and compass. Arbitrary key points were placed on the art panels and mapped onto the plan. These were later used to integrate the photographic record into a photomosaic.

The shelter interior, which is poorly lit on even the brightest days, was illuminated using generator-powered arc lights. The artwork was recorded by freehand sketching and photography, following published procedures (Gunn 1995a, 1995b) and a photomosaic subsequently prepared from which detailed drawings were made. Using the freehand sketches and the photographs, each image and area of pigment was allocated a discrete motif number.

Following Maynard (1977, 1979), a list detailing the attributes of technique, colour, form, type, condition and size for each motif was then compiled (Gunn 2004). Colour was generalised to orange-red, purple-red, brown-red, orange, yellow, cream and white. For hand stencils and prints, the knuckle size was measured on-site as an indicator of the size/age of the hand's owner. The maximum length of other distinct motifs was measured to the nearest half centimetre.

The Mulka Dreaming

Two versions of the story of Mulka have been published. The earliest is very brief:

The outcast Mulka, driven from the tribe because it was feared that his crossed eyes would bring a curse to those he looked upon, took refuge in the cave at the Humps (Meeking 1979).

The second comes from a brochure of the Department of Aboriginal Sites (DAS 1989):

Mulka was the illegitimate son of a woman who fell in love with a man to whom marriage was forbidden. As a result, Mulka was born with crossed eyes. Even though he grew up to be an outstandingly strong man of colossal height, his crossed eyes prevented him from aiming a spear accurately and becoming a successful hunter. Out of frustration, Mulka turned to catching and eating human children, and he became the terror of the district. He lived in Mulka's Cave where the impressions of his hands can still be seen much higher than those of an ordinary man. His mother became increasingly concerned with Mulka and when she scolded him for his anti-social behaviour, he turned on his own mother and killed her. This disgraced him even more and he fled the cave, heading south. Aboriginal people were outraged by Mulka's behaviour and set out to track down the man who had flouted all the rules. They finally caught him near Dumbleyung, 156 km south-west of Hyden, where they speared him. Because he did not deserve a proper ritual burial, they left his body for the ants; a grim warning to those who break the law.

Bowdler *et al.* (1989) consider this myth to be atypical of Aboriginal myths and consequently they dispute its origin. The author, however, has recorded similar myths in Central and Northern Australia, and considers this to be quite typical of local (non-travelling) myths, although even the longer version given here is likely to be a very much abridged rendition of a longer and more complex story. A myth with close similarities to the Mulka myth was also recorded by Meggitt (1962: 261–262) from the Warlpiri of Central Australia. [The Warlpiri are a Western Desert language group who share cultural links with the people to the east of the Noongar (see Gould 1969a; O'Connor *et al.* 1998, for maps)].

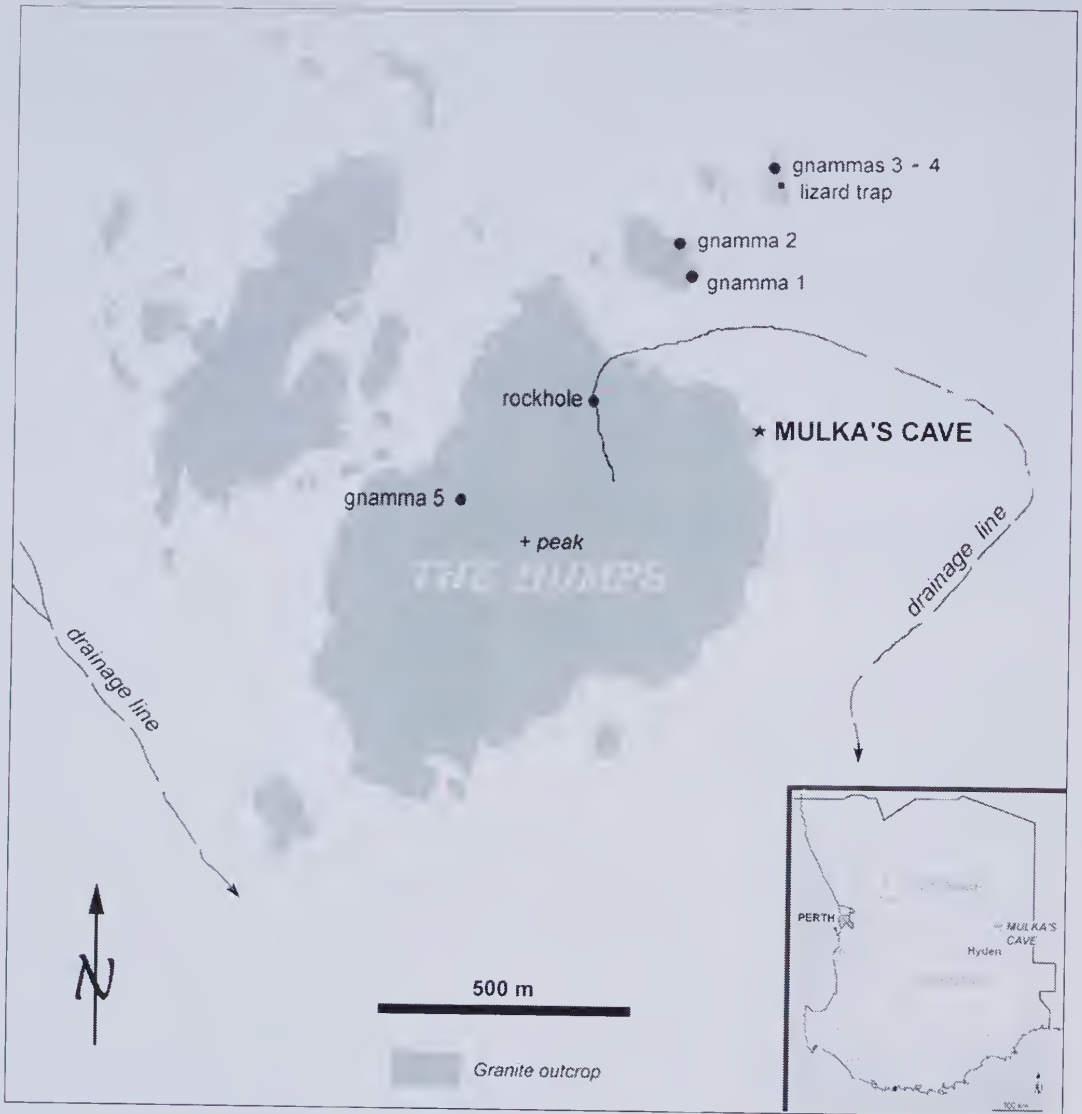


Figure 3 The Humps Reserve showing the location of the features of interest.

Mulka's Cave

Mulka's Cave is the only known rock art site within The Humps Reserve. In common with most Aboriginal rock art sites, Mulka's Cave is part of a larger site complex encompassing a range of other site types (cf. Gunn 1997). Here the associated sites consist of an adjacent open artefact scatter, a "lizard trap", five gnammas and a rockhole.

The Cave site lies at the base of the eastern slopes of the steep sided outcrop that forms The Humps hill (Figures 1, 3). The lizard trap, rockhole and four of the gnammas occur on flat granite pavements 300 m to the north of the cave. The fifth gnamma

lies on the northern mid-slope of the hill. This distribution of sites suggests that the principle area of Aboriginal interest was to the eastern side of the Reserve. While no further art sites or water reserves have been located on The Humps, no survey for stone artefacts has been undertaken to the west of the hill.

The first published account of the site was by R. B. Day (1951; quoted at length in Serventy 1952). Day mentioned that the site contained "hundreds of hand-marks done in red ochre...and the remnants of a large native drawing" but he did not provide any illustrations. Davidson had previously

recorded the site in 1938–1939 but he did not publish his findings until the following year (Davidson 1952: 113). He identified seven paintings, 92 stencilled hands, and 37 printed or drawn hands.

These are in red, white or yellow pigments. Davidson's study is the most detailed to date and is referred to further below. Serventy (1952), Wolfe-Okongwu (1978) and Flood (1990) also briefly

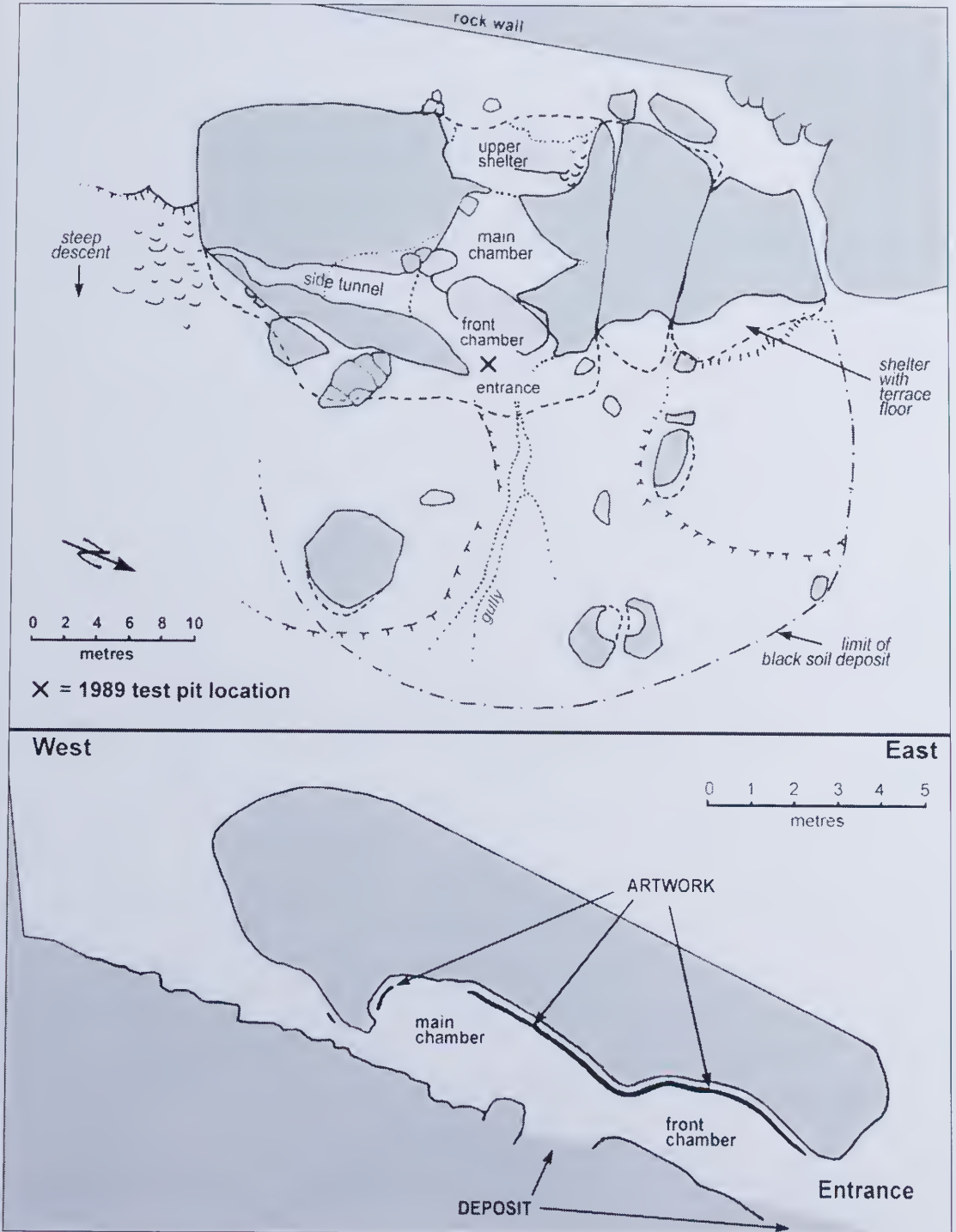


Figure 4 Mulka's Cave plan and section.

discuss the site but incorporate few new details into their descriptions. Internal reports of the then Department of Aboriginal Sites (DAS; now DIA) offer further descriptions of the site including note of "a recent-looking painting in orange (?ochre) which is probably not Aboriginal" that has not been mentioned by previous researchers. This large and imposing work of graffiti was almost certainly produced between 1952 and 1971 and is excluded

from the following description. A number of rock art conservation and management studies have been undertaken at Mulka's Cave (Randolph 1973; Clarke 1976; Haydock and Rodda 1986; Gunn 2003a) but these need not be discussed here.

The Shelter

Mulka's Cave is a tafone cavern underneath a large granite tor. A tafone (*pl. tafoni*) is a hollow or

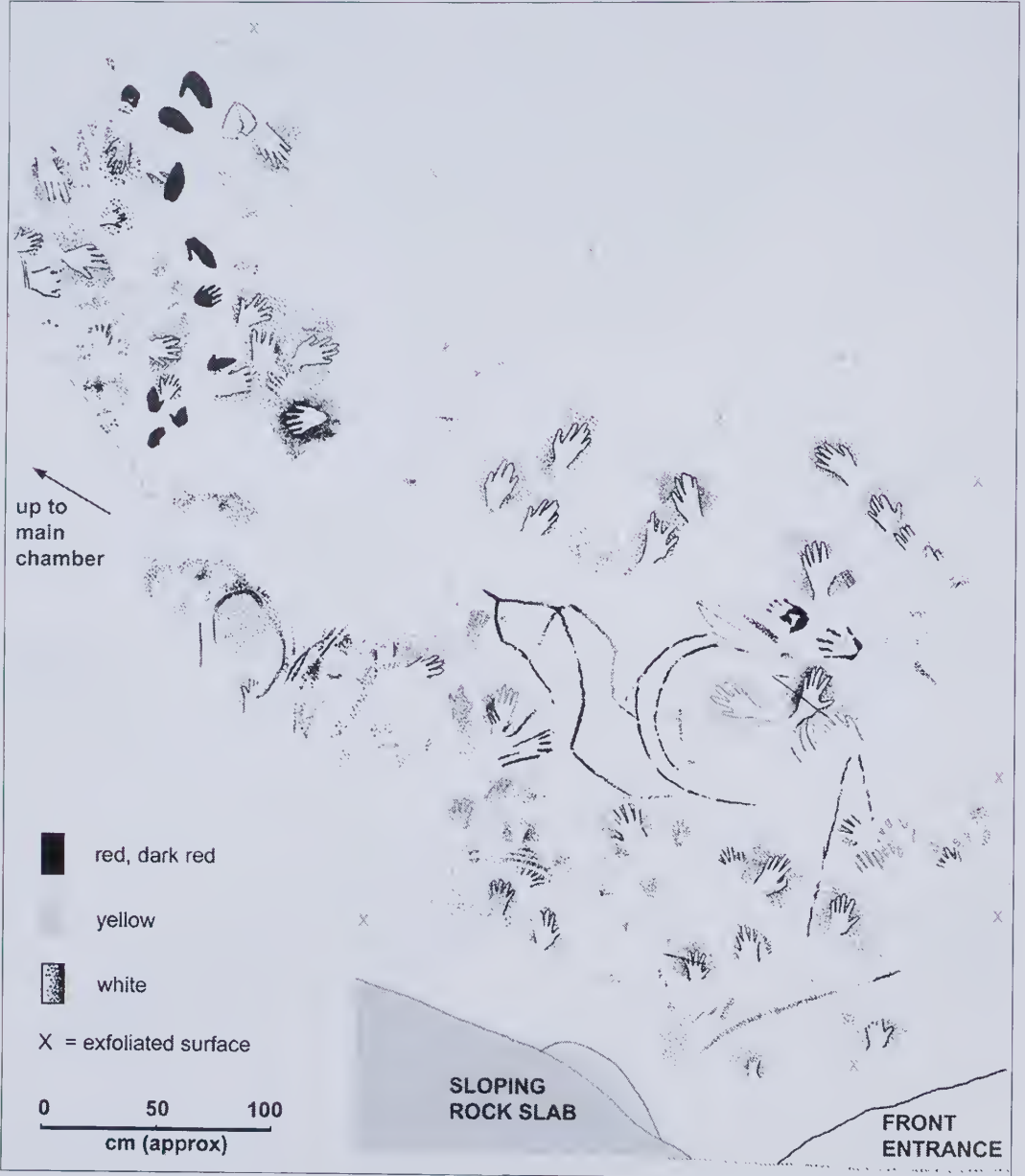


Figure 5 Front chamber artwork.

cavern that develops on the underside of a boulder (Twidale and Bourne 1975: 481), while a tor as used here, is an Australian term for a "boulder of weathering" (Twidale 1980: 95–105). The tor here is 25 m long by 18 m wide and 5 m high and irregular in plan and section (Figure 4). The top of the tor slopes steeply (20°) downhill such that rainwater run-off is directed down over the shelter mouth, contributing to the erosion of the deposits in front of the shelter. The cave is a steeply inclined tunnel beneath the tor, with low entrances on both the downslope and upslope. The ground in front of the shelter slopes very gently down to the east, forming a level area that radiates for about 20 m out from the downslope (and main) entrance. Behind the shelter, The Humps hill rises rapidly in a series of vegetated rock benches. A number of large water-retaining pans are at the southern end of one of these benches, some 50 m south of, and 20 m above, the shelter.

Mulka's Cave is 15 m deep by 9 m wide, with a

maximum height of 2.5 m above the floor. The interior is dark due to the low entrances and, while light penetrates through both entries, artificial light is required to see most of the artwork. For discussion and description, the cave is divided into five units on the basis of its interior morphology: main entrance, front chamber, main chamber, upper shelter and side tunnel (Figure 4).

The "front chamber" is immediately inside the main entrance (Figures 2, 4). It is 6 m wide and deep, with a domed ceiling up to 2 m high. Artwork covers most of the ceiling, with the exception of the actively eroding southern wall. The rear of the chamber is taken up with a large sloping block of granite. The chamber is divided from the main chamber by this block and a corresponding drop in the ceiling height. The floor consists of a flat deposit of grey sand in a narrow strip that runs diagonally back and into the side tunnel chamber. This was found to be rich in archaeological material (Bowdler *et al.* 1989; discussed below).

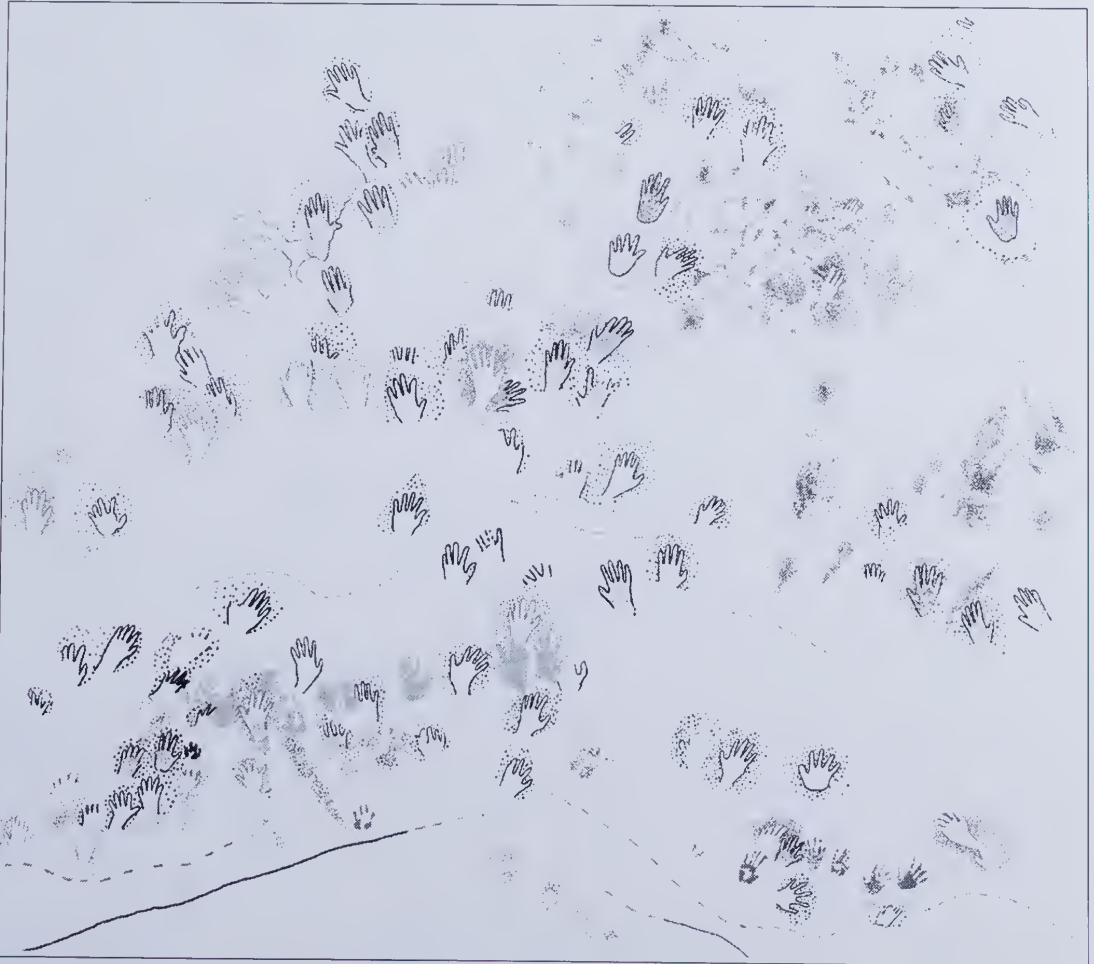


Figure 6 Main chamber artwork detail.

The "main chamber" is 6 m wide by 9 m deep, with a domed and undulating ceiling that rises to a maximum height of 2.5 m above the floor. The floor slopes steeply (c.20°) towards the entrance and at its lowest point is 1.5 m above the floor of the front chamber. Boulders cover most of the floor but there is a small area of flat soil at the lowest point. These boulders are convenient to sit on but there is little flat area suitable for sleeping. Towards the back entrance, the floor is covered by smaller, loose rocks (c.0.5 m diameter). Artwork covers most areas of the ceiling but with a denser concentration on the downhill side (facing uphill and away from the entrance; figure 2). This area of ceiling is the most obvious to decorate for people sitting in the cave.

The "upper shelter" is on the uphill side of the tor. Although it is 10 m wide, 5 m deep and 2 m high, the floor is both steep and rock strewn, making it unsuitable for occupation. A small panel of artwork occurs directly above this entry.

The "side tunnel" is about 12 m long. Although 1.5 m wide and high at its mouth, it decreases rapidly in width such that despite its flat soil floor, only the first six meters is comfortable to sit in. There is no artwork within the tunnel, whose ceiling and walls are actively deteriorating.

The Artwork

A total of 452 motifs were recorded from three alcoves within the cave (Figures 5 and 6). [The full list of motifs and their attributes is given in Gunn (2004).] The front chamber has 131 motifs, the main chamber 318, and the rear shelter three. The densest area is on the downhill face of the main chamber ceiling. The northern sidewall is most easily viewed

without artificial lighting. The quantity of artwork on the eastern face suggests that the Aboriginal artists would have worked with artificial lighting.

The absence of motifs within the side tunnel and the south wall of the front chamber is probably attributable to moisture and consequent rock deterioration. The small number of motifs within the rear shelter most likely reflects its unsuitability for occupation as well as its water-washed wall surface, while the total lack of extant artwork on the outside wall at the main entrance can be attributed to its water-washed surface.

A lack of artwork on the dry wall of an adjacent shelter to the immediate north of the cave, however, is less readily explained. This small shelter has a flat floor with a light scatter of stone artefacts, indicating that it was used in the past, presumably by the same people who decorated Mulka's Cave.

Motif types

Eighteen distinct motif types were recorded in Mulka's Cave (Table 1). Visually and numerically the artwork is dominated by hands (69%); these are primarily stencils but include a few handprints (Figures 5 and 6). Left hands outnumber right hands 108 to 72 (a ratio of 1.5:1). Similar ratios occur throughout Australia and are thought to reflect the proportion of left and right handed people in the population, as right-handed people tend to stencil their left hands and vice versa (Gunn in prep). While most of the hand stencils and prints are of the standard type with splayed fingers, a small number of the stencils are variants (cf. Walsh 1979), with the second (middle) and third (ring) fingers held together (Figure 7). Among the handprints, a

Table 1 Motif types by technique.

Motif Type	Print	Spray	Paint	Draw	Total
Unknown object		1			1
Spray area		37			37
Variant hand	9	11			20
Right hand	10	62			72
Unknown hand	14	99			113
Left hand	4	103	1		108
Band		1	1		2
Other apex element			2	2	4
Arc set			1	1	2
Bar set			5		5
Line single			3		3
Other element			2		2
Arc pair			1		1
V shape			1		1
Line pair			1		1
Simple design k1a			1		1
Simple design k1b			1		1
Simple design k3			1		1
Total	37	314	21	3	375
Fragments		75	2		77
%	8	86	5	<1	100



Figure 7 Group of red "variant" handstencils.



Figure 8 Group of red "variant" handprints, possibly imitating a trail of macropod tracks.

few have all their fingers closed together but with the thumb splayed, giving the shape of a kangaroo or other macropod track (Figure 8; and see McDonald 1983), but whether this resemblance was intentional or fortuitous is unknown.

Solid areas of pigment sprayed onto the wall (in the manner of a stencil but without stencilled object) are a feature of the artwork. Several are unusually large, up to 40 cm, and involve the use of a considerable amount of pigment. No ochre source is known in the immediate vicinity and hence it is assumed that the ochres used here would have to have been brought in from some distance away. Consequently the use of large quantities of ochre implies some particular value in the artwork produced even though no recognisable image is apparent. It is probable then that the importance was in the *application* of pigment to the wall rather than the production of any particular image. This would then fall into one of Ross's "associated rock art traditions" that include other non-image works such as abraded areas, scribble areas, etc. (Ross 2003: 89).

Two large, linear, simple designs in the front chamber are the most visually impressive motifs in the cave (Figure 9). Other motifs consist of small "geometric element" motifs: bars, lines and arcs, in either sets or other various combinations (Figure 10). This graphically simple repertoire is consistent with the pattern of rock art throughout much of southern Australia (Wolfe-Okongwu 1978; Gunn 1981, 1983, 2002).

Small numbers of large linear designs within a suite of numerous handstencils is now becoming apparent throughout south-west Western Australia (Hallam 1972; Gunn and Webb 2003). While all of the design motifs are similar in structure (linear), they are unique in their individual designs.

Techniques

Four art production techniques were recorded in Mulka's Cave (Table 2): spraying (86%), printing (8%), painting (5%) and drawing (<1%).

Table 2 Motif colour by technique.

Colour	Paint	Spray	Print	Draw	Total	%
Monochrome						
Red (brown-red)	6	2			8	2
Yellow	1	18			19	4
Red (purple-red)	8	199	18		225	50
White	3	106	2		111	25
Red (orange-red)	5	28	7	3	43	10
Orange		1	3		4	<1
Cream			7		7	2
Bichrome						
White+red		32			32	7
Yellow+red		2			2	<1
White+yellow		1			1	<1
Total	23	389	37	3	452	



Figure 9 The major paintings in the front chamber of Mulka's Cave. Motif 68 is in purple-red and overlies motif 67 in an orange-red. Motif 67 is 1270 mm and motif 68 is 830 mm. The colour scale is 10 cm.

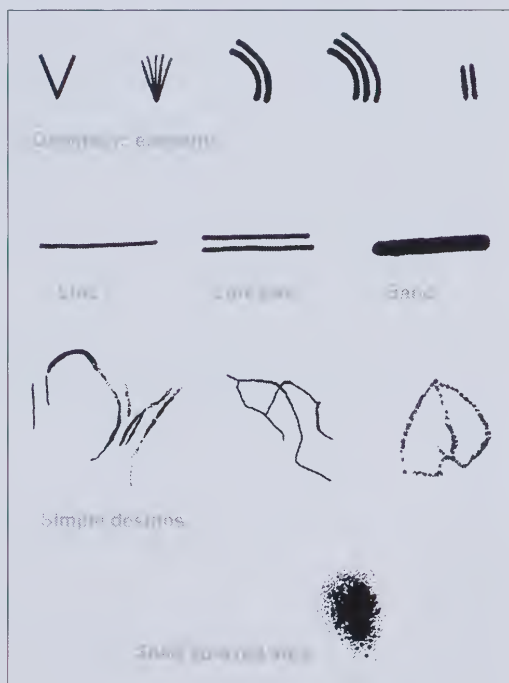


Figure 10 Freeform motif types.

Of the sprayed motifs, 38 are solid areas of sprayed pigment, while the others are sprayed over an object, most commonly a hand, that was then removed leaving a negative stencil image. Although

most of the stencils were produced on an area of bare rock wall, 35 were produced by placing the hand on a pre-pigmented surface (Figure 11). Although artworks produced by this technique are known elsewhere in Australia in small numbers, the number of examples here make the technique a feature of the Mulka's Cave art. In some instances this appears to be incidental overlap, but in a number of cases the placement is central to the pigment area and therefore probably deliberate. While it is not possible to determine whether or not the original pigment was applied immediately before the stencilling (and hence as part of the stencilled motif), or whether a previously sprayed area was deliberately chosen, a number of examples suggest the former. In these cases, red pigment was used as the underlying colour and white as the stencilling colour. Due to some unusual character of the pigment or the wall surface itself, the white pigment has dropped off the wall taking with it the underlying red pigment. What remains is a positive red image, of the negative stencilled hand, within a field devoid of pigment. Superficially these resemble handprints, yet the character of the hand is distinctly in the form of a stencil. Other examples in the cave demonstrate the intermediary stages of this deterioration process and clearly show the white overlying the earlier red layer.

In contrast to stencils which produce a negative image, printing produces a positive image by imprinting a pigment-laden object, again usually a hand, directly onto the rock surface. Here only handprints occur, both standard splayed hands and

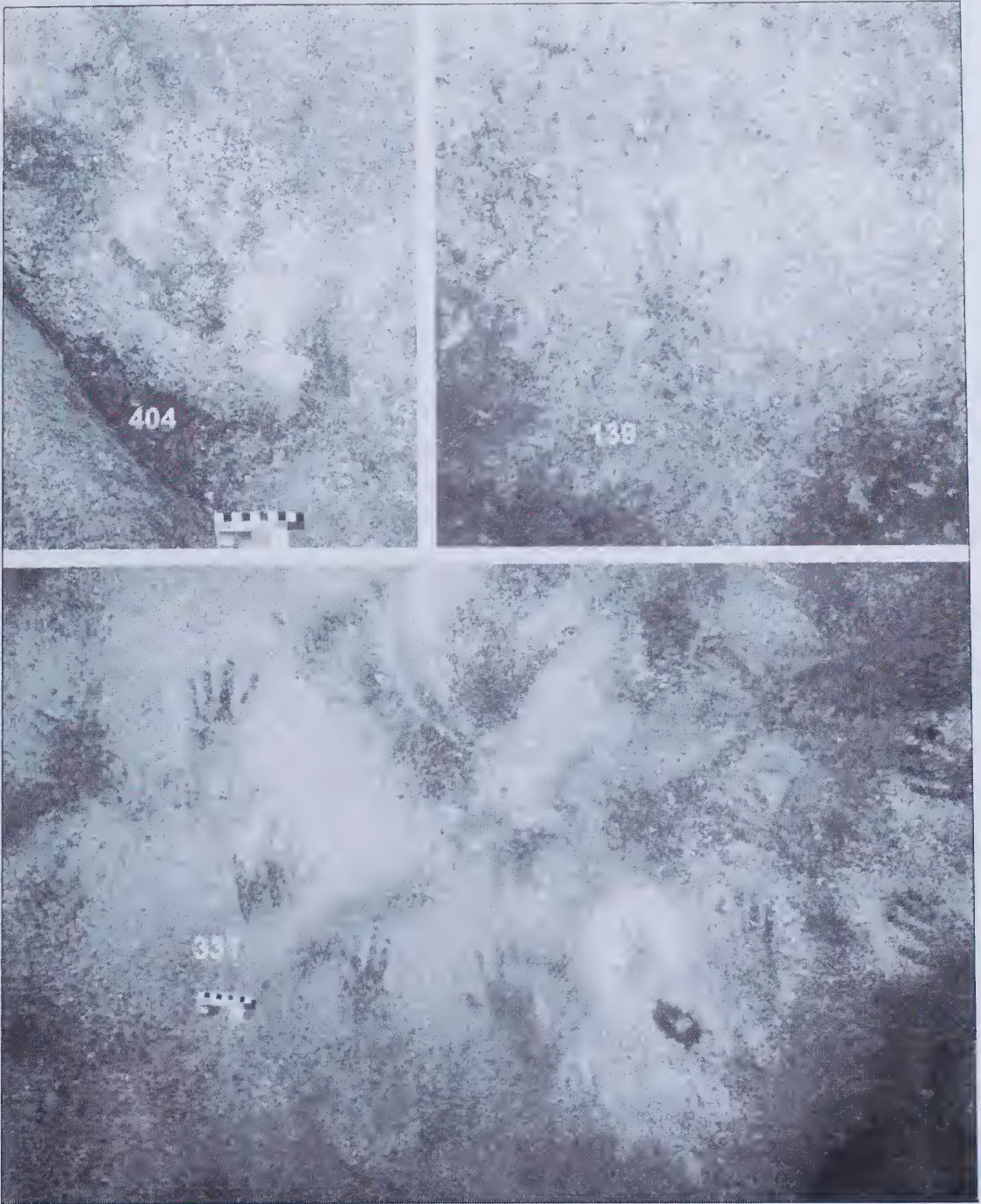


Figure 11 White handstencils over red pigment areas in Mulka's Cave. The white pigment and the underlying red have eroded away leaving a red positive hand on a bare rock surface. The motifs in the upper two photographs retain fragments of white pigment around the red hand.

some "variant" hands with non-evenly splayed fingers (Figure 8).

The paintings, due to the lack of any brush striations, appear to have been executed with a daubed finger rather than any form of brush. The drawings were produced using a dry ochre nodule, in the manner of a crayon.

The motifs tend to form two groups (Table 1):

- Paintings and drawings : Geometric elements and simple designs
- Sprays and prints : Hands, objects and spray areas

This is a common division in pictogrammic art (e.g., the "art" and "associated art traditions" divisions of Ross 2003) where "freeform" images (where the shape of the object is determined by the artist's mental image) are distinct from preform" images (where the shape of the image is derived from an actual object or by the technique itself)(see below).

Colour

Seven distinct colours were recorded (Table 2): purple-red (50%), white (25%), orange-red (10%), and brown-red, yellow, cream, and orange in smaller numbers. The three reds appear to be distinctly different hues, but analysis may show them to be the same colour in various stages of preservation. Purple-red is the most common colour among the sprays, prints and paintings.

Three bichrome colour combinations were also recorded: white+red, white+yellow, and yellow+red. These are all handstencils produced over an underlying colour. Cream is restricted to printing. However, as the number of motifs involved in these two groups is small, the

distinctions are not considered significant at this stage. On the other hand, the lack of yellow handprints and the very small number of white prints (two, cf 106 white stencils) appears culturally motivated, as the pigments were obviously readily available.

A matrix of colour and motif types shows that whereas hands and sprayed areas are made with a wide range of colours, geometric elements and designs use a limited range basically restricted to the three reds (Table 3). Contrary to Davidson (1952), who found that left and right hands occur in equal numbers with all colours, the author found that when all hands are included, left hands predominate over right in all colours in a ratio ranging from 1.5:1 to 2:1.

Motif forms

Six motif form types were identified (Table 4): handstencil (73%), solid (11%), handprint (10%), linear (6%), and single examples of an object stencil and an outline+infill painted motif. Motif form can be subdivided into *preforms*, where the form is dictated by the technique used, for example handstencils, and *freeforms*, where the form is independent of the technique, such as paintings. The preforms recorded here account for 93% of the motifs, and comprise hand and object stencils, handprints and sprayed areas. The freeform motifs are dominated by linear types, the most complex of which is a simple outline+infill design. Apart from the solid sprayed areas, and a single painted "hand" motif, there is a distinct separation of the motif types between freeforms and preforms (Table 4).

The single yellow object stencil is a narrow shaft about a metre long and 25 mm thick. Its simple

Table 3 Motif type by colour.

Motif Type	rb	rp	ro	w	y	w+r	c	o	y+r	w+y	Total
V shape	1										1
Line pair	1										1
Arc pair		1									1
Other element	1	1									2
Line set	2	1									3
Simple design k1b			1								1
Simple design k3			1								1
Arc set		1	1								2
Band		1	1								2
Other apex element		1	2		1						4
Bar set	1		2	2							5
Left hand	1	35	4	45	6	14	2		1		108
Unknown hand		47	11	37	5	9	2	2			113
Right hand		24	8	22	3	8	3	2	1	1	72
Spray area		34	1		2						37
Variant hand		17	1	1		1					20
Simple design k1a				1							1
Unknown					1						1
Total	7	163	33	108	18	32	7	4	2	1	375
Fragments	1	62	10	3	1						77

Table 4 Motif types by form.

Motif type	Preforms Object stencil	Hand stencil	Hand print	Freeforms Linear	Solid	Outline +infill	Total
	b	h	t	l	s	oi	
Unknown	1						1
Variant hand		11	9				20
Right hand		62	10				72
Unknown hand		99	14				113
Left hand		103	4	1			108
V shape				1			1
Other apex element				4			4
Arc set				2			2
Arc pair				1			1
Bar set				5			5
Fragments				2			2
Line single				3			3
Line pair				1			1
Simple design k1a				1			1
Simple design k1b				1			1
Other element				1	1		2
Band					2		2
Spray area					37		37
Simple design k3						1	1
Total	1	275	37	23	40	1	377
%	<1	73	10	6	11	<1	

Table 5 Knuckle size statistics for stencils and prints (mm).

	Stencils	Prints
min	50	70
max	90	90
mean	80	80
median	80	75
sd	7.0	7.0
n	106	11

shape offers few clues to its identification. It could be a spear, a piece of ceremonial paraphernalia, a thin digging stick, or simply a straight stick.

Motif size

The width at the knuckles of stencilled and printed hands was recorded as an indication of the stature and possible age of the hand's owner (Table 5, Figures 12 and 13). Hand size can therefore indicate the population range that decorated the site. The stencils range in size from 50 mm to 90 mm with a mean of 80 mm. The prints range from 70 mm to 90 mm, but also with a mean of 80 mm. In general, the knuckle measurements of stencils are 5 mm larger than the knuckles of the hand stencilled, and printed knuckles 5 mm smaller. Hence, the two techniques represented in Mulka's Cave seem to represent the same population group. The presence of two very small hands (knuckle sizes 50 mm and 55 mm) amongst the stencils suggests that infants

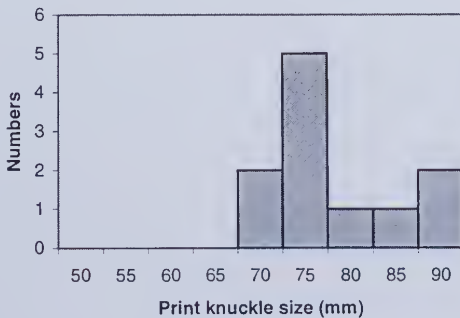


Figure 12 Hand stencil knuckle size frequencies (n=106).

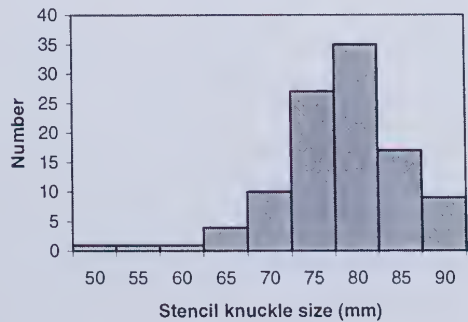


Figure 13 Hand print knuckle size frequencies (n=11).

variant form will doubtless be found in the very varied stencil art of the Carnarvon Range in central Queensland (Walsh 1979), no other suites of this type are known from elsewhere in Australia.

Another variant hand in Mulka's Cave is a white handstencil in which the thumb and index finger are splayed and the other three fingers held together. This stencil is amongst a group of other white handstencils with standard splayed fingers and is likely to be the idiosyncratic work of a particular individual.

A second loose cluster of ten motifs, this time of handprints, occurs on the cusp of the ceiling between the front and main chambers (Figure 8). In nine of these, the fingers are held together and the thumb splayed. The resultant image is suggestive of a trail of macropod tracks. These motifs appear to have been made quite recently and contemporaneously, and are also most probably the work of a single individual.

Three examples of horizontally placed handstencils are noteworthy as they occur within clusters of otherwise vertically orientated hands at widely spaced locales within both chambers.

The yellow stencil placed centrally within the prominent purple nested "C" shapes is the younger of the two. Its placement was clearly deliberate, although whether the association was culturally meaningful is unknown.

The two most distinctive motifs within the shelter are the painted "C" shape just mentioned and an adjacent rambling design in orange-red. They are two of the largest motifs within the cave (830 mm and 1270 mm respectively). Their large size and prominent location immediately inside the front chamber suggests they had considerable significance (cf. Gunn 2003c). The "C" shaped design overlies the rambling design and hence its placement was clearly calculated, to either add to the significance of the earlier motif or, alternatively, to over-ride it. The rambling design is visually comparable to other large maze designs at several shelters elsewhere in the region (Webb and Gunn 2004). They appear to form a distinct stylistic set whose nature has yet to be explored.

Condition

The condition of pigment art is assessed on the basis of the amount of pigment adhering to the

Table 9 Motif condition by colour.

Colour	good	fair	poor	very p	(n)
(%)					
White	7	17	38	38	111
Red-orange	2	14	35	49	43
Red-purple	4	14	20	62	225
White+red		34	34	31	32
Nos					
Cream	3	1	1	2	7
Red-brown	4		2	2	8
Orange	1		1	2	4
Yellow+red	1		1		2
White+yellow			1		1
Yellow		4	2	13	19

rockface. Motifs with a dense coating of pigment are said to be in excellent condition, while those with the merest of traces are allocated a very poor condition. The motifs in Mulka's Cave ranged from good to very poor. No motifs were in excellent condition, although prints and paintings tend to be better preserved than the sprayed motifs (Table 8). This suggests that printing and painting were more favoured over the recent period of the shelter's use.

The data for condition by colour is limited for most colours due to low numbers (Table 9). It appears that cream, brown-red, and white pigments, being among the best preserved colours, represent the most recent colours used at the site. In contrast, purple-red and orange-red have the highest proportion of very poor motifs, suggesting that they were more commonly used in the earlier period of the shelter's use.

Superimposition

Superimposition (the overlying of one motif by another) provides a sequence that can be a guide to chronology, if not age. Underlying motifs must be older than overlying ones. Eighty-seven examples of superimposition were interpreted. Many other examples of overlapping motifs also occur but their sequences could not be reliably elucidated. Not all of the aspects of the sequence (colour, technique and motif type) were clear and consequently the tallies in Tables 9–11 are not the same.

It appears that purple-red was more frequently used during the earlier period of art production, with white, cream and orange used during the latest period (Table 10). Given that white preserves very poorly (Clark 1978), it is again stressed that white may have been used during the earlier period but that the motifs have since deteriorated beyond recognition. The same may be said for cream pigments, which tend to have a white base. The lack of purple-red in the recent layers, however, does seem to be evidence of a real change in pigment preference.

Table 8 Motif condition by technique.

Technique	good	fair	poor	very p	(n)
(%)					
Spray	4	16	25	55	389
Print	11	8	41	41	37
Nos					
Paint	7	4	8	5	23
Draw		2	1		3

Table 10 Colour superimpositioning.

OVERLAYER UNDERLAYER	White	Red- purple	White +red	Cream	Red- orange	Orange	Yellow	Red- brown	Yellow +red	Total
Purple-red	18	15	8	4	6	2	1	1		55
White	9	2	1	1		1			1	15
Yellow	4	1		2						7
Orange-red		4	1	1	1		2			9
White+red									1	1
Total	31	22	10	8	7	3	3	1	2	87

Table 11 Technique superimpositioning.

UNDERLAYER	Spray	OVERLAYER		Draw
		Print	Paint	
Spray	43	17	9	2
Paint			4	2
Print	1			

Table 12 Hand superimpositioning.

UNDERLAYER	OVERLAYER			
	Left	Right	Unknown	Fragment
Left	12	3	6	
Right	7	4	3	
Unknown	8	3	4	2
Fragment	1	1	1	
Variant	2			
Spray area	4			

Age and chronology

Condition by technique and colour suggest that cream, brown-red and white prints, paintings and sprayed motifs are more recent than purple-red sprayed motifs. However, as there is considerable overlap of the two groups, no clear division can be made on the basis of preservation alone. Further, red pigments (ochres) usually preserve better in rock art than white (kaolin or other pipeclays) (e.g., Clarke 1978). Also, it is possible that white pigment was used during the earlier period of shelter use but that these motifs have completely deteriorated, leaving no archaeological evidence of their earlier presence. The picture is further complicated by the unusual situation of the apparent placement of white stencils over a prepared or incidental red ground. On those few of the motifs that retain white pigment, the white appears to be relatively recent. This suggests that some particularly rapid deterioration process is occurring to these motifs, masking their recent production. Consequently, condition here is not a reliable indicator of motif age.

Similarly, superimpositioning of techniques suggests that, of the surviving techniques, spraying was the first used at the site, and that printing, painting and drawing were introduced into the

repertoire at a later time (Table 11). Also, there was no change in the preference for hands over time, with right and left hands occurring in similar proportions in both the earlier and the more recent periods of artwork (Table 12). Taken together, motif condition and superimposition indicate a bipartite art sequence in which purple-red sprayed motifs predate sprays, prints and paintings in cream, brown-red, and white.

The presence of many superimposed motifs indicates that the site has been used for a considerable period of time, most likely a far greater period than is represented by the 500 year old carbon date (Bowdler *et al.* 1989). In common with many other rock art sites throughout Australia, it is likely that the artwork here was produced over the past two or three thousand years (Mulvaney and Kamminga 1999, David 2002). Handstencils are amongst the earliest rock art throughout Australia (Morwood 2002) and excavations around the rim of the Wheatbelt have demonstrated Pleistocene occupation of south-western Australia (Bordes *et al.* 1983; C. Dortch 1979; J. Dortch 1996). However, apart from *walganha*, the few decorated shelters that have been excavated are in broad agreement with the younger age. For example, Frieze Cave, an art site some 200 km to the west of Mulka's Cave and 100 km inland from Perth, produced an occupation phase dating from <3000 BP to the ethnographic present (Hallam 1972). In the Murchison District, 600 km to the north of Mulka's Cave, most decorated shelters have occupation similarly limited to the last 4500 years (Webb in prep.).

The floor deposits and surface scatter

A team from the University of Western Australia excavated a test pit in the floor of the lower shelter in 1989 (Bowler *et al.* 1989). The pit, one metre square and excavated to bedrock at a depth of 1.10 m, was placed about half a metre inside the dripline (Figure 4). A limited stone artefact assemblage was recovered, along with faunal remains representative of several genera native to the region (principally small mammals such as bettong and possums, but no large kangaroos). The artefacts were dominated by rock types of quartz, with small numbers of

dolerite, sedimentary rock, and granite. Red and yellow ochres were also present. Apart from the few dolerite, sedimentary artefacts and the ochres, which would have to have been imported into the site from some distance, the granite and predominant quartz could be obtained locally from outcrops on the hill. The lowest artefact was recovered at 0.7 m, from a pit-like feature interpreted as a drainage channel. Charcoal recovered from a depth of 0.65 m was dated to 420±50 BP.

The excavators concluded that the site had been only briefly or periodically occupied and suggested that the late occupation of the site (c.500 BP) was consistent with the "intensification phenomena" associated with the late Holocene use of marginal resource zones. However, given the disturbed and water-washed nature of the excavated deposits, their conclusions are unlikely to be representative of the site's overall occupation. Consequently, their interpretation of brief or periodic occupation is not seen as definitive. Likewise their c.500 BP date, coming from a refilled drainage line, cannot be taken to represent the initial period of shelter use. Clearly, further excavation at the site would be required if the period of use of the shelter and its outside deposits are to be more precisely dated.

Run-off has eroded a gutter out from the front of the main entrance to the shelter, 100 mm deep, exposing numerous stone artefacts. Artefacts are lightly scattered over an area 100 m N-S and 20 m E-W, following around the base of the rocky outcrop. This distribution suggests that while the cave was a focal point for people coming to the site, most of the occupation occurred on the flat open ground outside the cave; a situation commonly observed in arid areas but also noted in southern woodland areas (cf. Gunn 1997, 2003b).

In a sample of 132 artefacts from the gully analysed during the present project, quartz

Table 13 Artefact stone types.

Stone type	No	%
Milky qz	78	60
Clear (non-crystal) qz	47	36
Silcrete	2	1
Banded ironstone	2	1
Ochre (red)	2	1
Other siliceous	1	>1
Total	132	100

accounted for 96% of the artefacts, with silcrete, banded ironstone, an unidentified siliceous stone and ochre making up the remainder (Table 13). Quartz is readily available from a major outcrop near Captain Roe Rocks, 25 km south-west of The Humps, and in smaller seams on The Humps itself and other granite domes in the region. Banded ironstone outcrops occur in the rises of the Southern Mineral Field north of Lake Cronin, 70 km to the east (Geological Survey of Western Australia 2003). A source for the silcrete is unknown. One of the red ochre nodules is an orange-red and has a flat facet with striation marks, consistent with being ground for use. The other piece is brown-red and unmarked. Both colours are represented in the artwork.

The artefacts were mostly (95%) small: <25 mm. They consisted of debitage fragments (without platform or bulb; 110 or 83%), flakes (with platform and/or bulb; 16 or 12%), backed flakes (3 or 2%), one retouched flake (unifacial and uni-marginal scraper) and two nodules of red ochre (Table 14). Four geometric microliths were located near the main entrance, away from the gutter (Figure 14). These tool types are characteristic of the Australian Small Tool Tradition and are therefore likely to be less than 6000 years old (Mulvaney and Kamminga 1999).

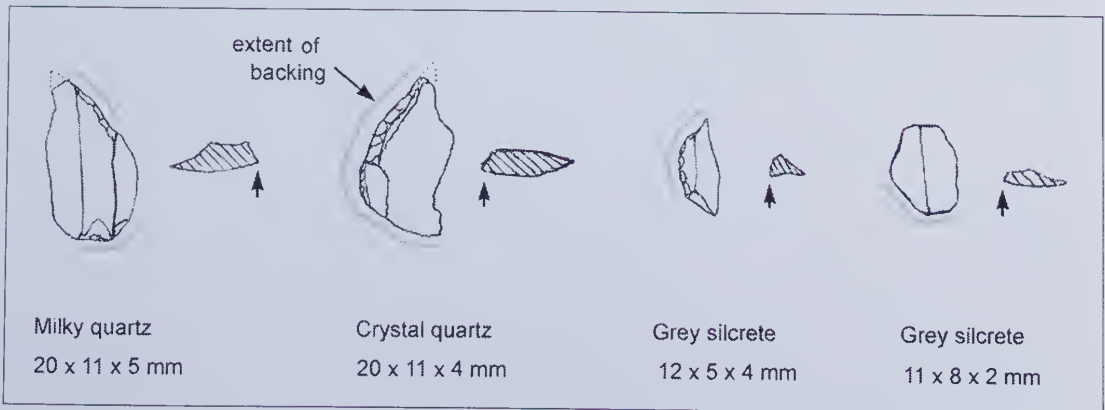


Figure 14 Field drawings of select geometric microliths.

Table 14 Artefact summaries.

Artefact type	Size (mm)	6-10	11-15	16-20	21-25	26-30	31-35	81-85	broken	Total
	Stone type									
Chips	Milky quartz	9	20	29	15	1				74
	Clear quartz	11	19	5						35
	Silcrete	1								1
Flakes	Milky quartz		2						2	4
	Clear quartz	1	4	4					1	10
	Banded iron						1			1
	Other			1						1
Backed flake (geometric microliths)	Clear quartz		2							2
	Silcrete	1								1
Retouched flake	Banded iron							1		1
Ochre nodule					2					2
Total		23	47	39	17	1	1	1	3	132

OTHER ARCHAEOLOGICAL SITES

Lizard traps

Although little documented in the literature (see Webb and Gunn 2004), "lizard traps" are a widely distributed and well-known Aboriginal site-type in south-western Western Australia. Generally they consist of a thin granite slab, around 100 cm square and 10 cm thick (Webb and Gunn 2004), propped on one end to a height of 10 cm, using one or more smaller stones (usually around 10 cm diameter). The trap at The Humps is quite large (240 by 120 by

17 cm). It is raised 13 cm off the pavement at its upslope end by two small rocks (Figure 15). How, indeed if, they were used is unknown. Given the adeptness of traditional desert Aborigines in catching lizards (cf. Gould 1969b, Tonkinson 1978), the raised slab was probably an artificial crevice beneath which the lizards could retreat to when disturbed; only then to be caught with nowhere else to run. There would seem to be no point in dropping the rock onto and crushing any hiding animals, as has been suggested in colloquial discussions.



Figure 15 The Humps lizard trap site with support rock arrowed.

Water reserves

Gnammas, rockholes and pans are different types of depressions in impermeable bedrock that can catch and hold water after rain. Although gnammas and pans are formed by the same geological process (Twidale and Corbin 1963), archaeologically a distinction is made between pit gnammas (gnammas) and pan gnammas (pans) as the former have a good depth relative to their width and hence hold water for a good deal longer than pans, which are broad and relatively shallow (up to 20 cm) and are readily evaporated. Gnammas are essentially rain-fed. In contrast to gnammas, rockholes form along creek lines, usually as plunge pools, and are fed by the creek-flow.

Throughout the Murchison/Wheatbelt area, gnammas were a well-known, well-utilised and highly valued water source for Aborigines and the early settlers (Bowdler *et al.* 1989; Bindon 1997; Webb and Gunn 2004). They provided a reliable reserve that could be targeted by people familiar with the country in which they occur (e.g., Gould 1969a, Myers 1991). Rockholes tend to develop at the base of escarpments, whereas pans develop on top of suitable rock exposures such as granite domes and duricrust surfaces on top of escarpments. Many gnammas, in contrast, occur as nondescript features in a superficially nondescript landscape and would be impossible to intentionally

locate without detailed knowledge of the country (e.g., Gunn and Webb 2003). Many also had granite slab "lids" to prevent animals draining the supply and to reduce evaporation (e.g., Webb and Gunn 2004). Traditionally, rockholes and gnammas would have had Aboriginal names and some associated mythology. Pans, on the other hand, were not regarded as highly because of the more limited life of their reserves due to evaporation.

Five gnammas have been located on and around The Humps (Figure 3). Four occur on the granite pediment to the north of the Mulka's Cave. Two are quite large (e.g., Figure 16); whereas the two adjacent to the lizard trap are very small (Table 15). The fifth occurs on the northern mid-slope of the hill.

A sizeable rockhole has formed within a shallow drainage line that flows off the hill to the north of Mulka's Cave. The ephemeral stream that feeds this rockhole is a prominent feature of the hill. It supports a number of well-vegetated soil patches on an otherwise steep and barren rock slope. The stream flows readily after rain, and continues to trickle for some days after rain (personal observations). The rockhole measures 8.5 by 2.0 by 0.8 m. It has a "V" profile and contains some 650 litres of water when full. As the stream leaves the hill it winds into granite sands that quickly become boggy. It is likely that small sub-surface soaks



Figure 16 The largest gnamma at The Humps.

Table 15 Gnamma dimensions and approximate volumes.

Site	Length (m)	Width (m)	Depth (m)	Capacity (l)
Humps 1	1.40	0.85	0.65	77
Humps 2	4.00	2.50	0.60	300
Humps 3	0.45	0.20	0.30	3
Humps 4	0.20	0.15	0.20	1
Humps 5 upper pan	0.85	0.60	0.20	
Humps 5 lower gnamma	0.25	0.20	0.35	13

would be available along the stream's path for some time after the rockhole had dried.

The pans on top of the hill are numerous and large (around 4.0 by 2.0 by 0.1 m) and together, after rain, would probably hold around 1000 litres of water. With another 1200 litres held over in the gnammas and rockhole, and the possibility of sub-surface soaks along the stream bed, a good minimum supply of around 2000–3000 litres could be ensured: more than enough for an extended family group's transitory stopover or a larger gathering for brief periods. The presence of these reserves may well explain why Mulka's Cave was chosen for decoration.

AN INTERPRETATION OF MULKA'S CAVE

In common with other sites in the Wheatbelt (Davidson 1952; Wolfe-Okongwu 1978; Webb and Gunn 2004; Dept. Indigenous Affairs, Perth, records), the art of Mulka's Cave is dominated by handstencils, but it also includes a small number of large and visually impressive linear paintings. The site also houses a small number of less impressive handprints, small paintings and drawings. Mulka's Cave, with a total of 452 motifs, has a far higher quantity of rock art than most other Wheatbelt rock art sites, which tend to have fewer than 30 motifs. The artwork also utilises a wider range of colours than other regional sites.

As McDonald (1995) inferred for rock art sites in the Sydney Basin, the presence of infant handstencils and others that most likely are those of women and adolescence suggests that at some times family groups camped by and used the cave. The unsuitability of the cave's floor for sleeping suggest that the cave was used as a wet weather retreat and that most camping occurred on the level ground in front of the cave. This is supported by the pattern of surface artefact distribution.

On the other hand, the painting of large geometric designs are almost certainly the work of senior males and most likely refer to the Dreaming tracks of totemic ancestors, as they do in the Western Desert and Central Australia (Spencer and Gillen 1899; Gould 1969b; Bardon 1979; Myers 1991). These paintings and the associated Mulka story

suggest that, at times, the cave was associated with local nearby rituals, at which times it would have been off-limits to women and children. A similar dual-use has been proposed for the densely decorated shelter at *walganha* (Walga Rock), which was known to have been used for ritual in the recent past but was apparently open to women and children at non-ceremonial times (Gunn *et al.* 1997).

Overall then, it is suggested that Mulka's Cave was used by the full age-range of the population, although whether at the same time or at different times for different purposes, is yet to be determined. This view does not support the suggestion that the cave was used as a store-house for ceremonial objects (Serventy 1952), as such store-houses were, and in many areas still are, invariably accessed only by senior males and are always off-limits to women and children (e.g., Gould 1969b, Mountford 1976).

The large area of the campsite in front of the shelter along with the higher number of stone artefacts relative to other art sites in the region suggests that occupation here was indeed recurrent; but whether through short-term, large gatherings or prolonged occupation by small family groups is likewise unknown. The artefacts were made from a limited array of raw materials, all available locally, suggesting that Mulka's Cave was not a focus for large inter-regional gatherings when materials from well outside the region would be brought in by the visitors.

Most water sources and granite outcrops within the region, particularly those with rock art or stone arrangements, probably had associated myths similar to the Mulka story recorded for this site. This was certainly the case elsewhere in Australia where such information has been collected (e.g., Hallam 1972; Berndt and Berndt 1977: 243–256; Strehlow 1978; Myers 1991). Hence, while it is tempting to give some special credence to Mulka's Cave because of the survival of the Mulka myth, this should not be seen as particularly unusual. On the other hand, some myths were more significant than others, possibly due to the strengths of particular clans or individuals (see Spencer and Gillen 1899). Whether the Mulka story was of regional significance or of only local importance is

unknown. The high quantity of artwork, the wide range of colours used, the size of the campsite and the extensive area encompassed by the myth, suggest that Mulka's Cave had at least a regional significance. In contrast to this, the restricted range of motif types used suggests that the site was not a place of inter-tribal gatherings or "aggregation site" as defined by Conkey (1980) and Galt-Smith (1997). At most, the Mulka's Cave site complex would seem likely to have been a focus for local group ceremonies, such as initiation or maintenance rituals. From what we know of such rituals, they were invariably focused on open areas away from general campsites and that rock art use was generally a tangential, albeit important, component of the main ceremony. It is therefore unlikely that Mulka's Cave itself was the principal focus for these ceremonies. If ceremonies did take place at The Humps, they would have been held nearby, either on the dome or out on the adjacent plains, with visits to the cave just one aspect of the ceremony. A likely location for the performance of the main ceremony has not been located.

CONCLUSION

In keeping with the regional profile, the rock art preserved within Mulka's Cave is dominated by handstencils but with a small number of geometric designs. Typically however, one or two of the latter are the largest and most visually impressive motifs within the site. The suite at Mulka's Cave is the densest concentration of rock art yet recorded within south-western Western Australia and consequently must be seen to be one of the most significant archaeological sites within the region.

Similarly, the artefact scatter in front of the shelter is far denser than those noted at most other rock art complexes in south-western Australia (Webb and Gunn 2004), suggesting that the site was important as a recurrent focus of occupation. The archaeological potential of the deposits here have been tested but have yet to be explored to their full depth. The importance of this potential must be acknowledged in the future management of the site.

The interpretation of the evidence to date, although based on analogies from other areas, suggests that the site was used both for ritual purposes related to broader ceremonies held nearby and, probably at different times, for general occupation.

Today, Mulka's Cave is of great significance to the local Noongar community and also, but for different reasons, to non-Indigenous residents of the region and the local tourist industry. It is one of the most visited rock art sites in Western Australia and hence has a broad potential for positive educational uses.

The main focus of this study was to document the

site and illustrate the importance of its' rock art. It is hoped that this will ensure that Mulka's Cave, and The Humps Reserve in which it lies, continues to be managed and interpreted, in a culturally sensitive manner, to the highest standards are available.

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The leptolepid fish *Cavenderichthys talbragarensis* (Woodward, 1895) from the Talbragar Fish Bed (Late Jurassic) near Gulgong, New South Wales

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Abstract – *Leptolepis* *talbragarensis* Woodward, 1895, is the most common fish species in the Talbragar Fish Bed near Gulgong, New South Wales. The genus *Cavenderichthys* Arratia, 1997, has this species as its type. The three species originally proposed by Woodward (1895) for "*Leptolepis*" are a single species. A detailed comparison of *Cavenderichthys talbragarensis* with members of the genus *Leptolepis*, and also with the Late Jurassic forms *Tharsis dubius* and *Leptolepides sprattiformis*, indicates that *Cavenderichthys talbragarensis* is most closely related to Late Jurassic members of the Family Leptolepididae. Analysis of zircons for geochronology showed that the sediment just below the richest fish layer has a youngest component of 151.55 ± 4.27 Ma, corresponding to the Kimmeridgian Stage of the Late Jurassic. Thin sections of the upper prolific fish layer show preservation in tuffaceous sediments, indicating that the fish population was killed by ash falls of felsic tuff that filled the pond they inhabited.

INTRODUCTION

Fossil fishes were first discovered at Talbragar about 30 km northeast of Gulgong by Arthur Lowe of Wilbertree, NSW in 1889 (Woodward 1895). Later, many specimens were collected by Charles Cullen, the collector of fossils for the NSW Mines Department. This material is now in the Australian Museum, Sydney, and the NSW Department of Mineral Resources. Associated with the fishes is abundant plant material, first described by Walkom (1921), then re-examined and classified by White (1981). Some undescribed insect remains are also housed in the Australian Museum, Sydney.

Woodward (1895) described a representative selection of different fossil fishes that had been sent to London in 1890. He considered that the assemblage was of Jurassic age, despite an original field assessment of the age as Triassic, made by W. Anderson of the Geological Survey of NSW. The vast majority of the fishes in the material belong to *Leptolepis talbragarensis* Woodward, 1895, which was cited by Long (1991) as "the first appearance of the teleosteans in the Australian fossil record". Other fishes include one species of palaeoniscid, *Coccolepis australis* (Woodward, 1895), and the holosteans *Archaeomaene tenui* Woodward, 1895, *Madariscus robustus* Wade, 1941, *Aphnelepis australis* Woodward, 1895, *Aetheolepis mirabilis* Woodward, 1895, and *Uarbryichthys latus* Wade, 1941. Interest in *Leptolepis talbragarensis* is due largely to its early teleostean features. Nybelin (1974) suggested that *L. talbragarensis* should be excluded from the family Leptolepididae Agassiz, 1833–44. This was based

partly on his own observations, but also on the work of Cavender (1970) who compared coregonines and other salmonids with some of the earliest known teleosts, including *L. talbragarensis*. Arratia (1997) erected a new genus, *Cavenderichthys*, with *talbragarensis* as the type species, on the basis of material from the Natural History Museum, London, the Field Museum of Natural History, Chicago, and the Swedish Museum of Natural History, but she did not have access to the vast amount of material available in Australia.

The Talbragar site has revealed the best-preserved Jurassic fish in Australia. The outcrop now is very poor, as so much material has been removed in the past and it is now in a paddock used for grazing. The age has been difficult to confirm because there is no control of stratigraphy as the relationship to surrounding rocks is unclear. Previously, no volcanic rocks had been identified to be dated, and palynology is impossible because of the highly oxidised nature of the rocks.

The assemblage of fossil fishes has been thought to indicate an Upper Jurassic age (Long 1991), but early workers suggested a Middle Jurassic age, for example Hind and Helby (1969) who suggested Early to Middle Jurassic based on palynology of the Purlawaugh Formation, within which the Fossil Fish Bed occurs. The site is interpreted as a mass kill site with a longitudinal extent of possibly 200 metres. The upper layer contains a high concentration of extremely well preserved fossil fish, while the layer below, probably less than one metre thick, has scattered fish throughout,

indicating a lacustrine environment. Until now evidence for the cause of death has been sparse, although Percival (1979), and White (1981), have made suggestions.

The purpose of this paper is to reassess the description and classification of *Cavenderichthys talbragarensis*, and to discuss the environment of deposition, the age of the fossil bed, and the nature of preservation. To do this the type material in the Australian Museum, as well as about 250 other specimens from the Australian Museum, the N.S.W. Geological Survey and the Australian National University have been examined. The sediment has been studied in thin section, as has its geochemistry, and plant content. Zircon dating was carried out using the SHRIMP method.

GEOLOGY

The Talbragar Fossil Fish Bed is the informal name given by Dulhunty and Eadie (1969) to the outcrop found on the northeastern side of Farris Hill, about 5 km south of the Talbragar River. The location is GR 753090 6437910, Dubbo 1:250 000 Geological Sheet (Pogson and Cameron 1999). The site is now a geological reserve administered by the National Parks and Wildlife Service, Mudgee Office. The strike is generally north-south, and the dip of adjacent beds is about 10° west. The Fish Bed is thin, forming part of a non-marine sequence. Just below the fossil bed are layers that contain tuffaceous sections. Unweathered samples are grey, very fine grained, and contain angular fragments of minerals such as quartz, some of which is detrital and some of which appears to be igneous in origin. There is no evidence of sedimentary flow structure.

Stratigraphically below this unit are quartz sandstones of the Purlawaugh Formation, which show sedimentary structures such as cross-bedding, pebble layers and washouts. This sandstone unit is comparable to the nearest units of the Purlawaugh Formation that outcrop about 50 km away. The Fish Bed is probably the upper unit of the Purlawaugh Formation, but no equivalent outcrop to the Fish Beds is exposed in New South Wales.

SHRIMP (Sensitive High mass Resolution Ion MicroProbe) analysis of zircons was carried out using the SHRIMP RG machine in the ANU Research School of Earth Sciences. The age of the youngest population was 151.55 ± 4.27 Ma, corresponding to the Late Jurassic (Veevers 2000), indicating that the sediment must be this age, or younger if the zircons were all of sedimentary origin. The morphology of the youngest grains does not show any evidence of transportation by water. Examination of the zircons shows that the rock contains a small tuffaceous component. The range of different types of zircons was quite large, and many of them showed clear evidence of a

sedimentary history (Dr I Williams, personal communication).

Dulhunty and Eadie (1969) described the "Fish Bed Chert" as a hard, fine limonitic cherty-shale, and Pogson and Cameron (1999) stated "In thin section the unit is a red-brown silty mudstone with compaction bedding features and chips of ?tuffaceous quartz, clayey patches after feldspar and/or lithic fragments, magnetite, ankeritic cement and manganese oxide dendrites." Thin section and chemical analysis shows that the fossil-bearing rocks are largely tuff and sediments derived from the underlying sandstones, some of the tuffs representing one or more very fine-grained ash falls (Prof. R. Arculus, personal communication). EDXA (Energy Dispersive X-ray Analysis) has not shown any evidence of carbonate or calcium ions being present, excluding an ankerite [$\text{FeCa}(\text{CO}_3)_2$] cement (Dr A Christy, personal communication). There is evidence of fine bedding and subsequent compaction. The red-brown colour is post depositional because each block has concentric bands of varying intensity of colour as the iron oxide has penetrated from the joint block boundaries. Manganese dioxide is often found infilling the fossil fish cavities and is generally close to the edge of a block, forming dendrites. Many of the fish and most of the plant fossils are white, having not taken up the red iron oxides. EDXA shows the composition of the infilling of plants and animals is not the same. The plants have been replaced by very fine-grained opalised quartz, whereas kaolin is present with the opalised quartz in the infilling of the fish (Dr A Christy, personal communication).

The Talbragar Fossil Fish Bed is probably no more than 60 cm thick (Percival 1979). The current state of the outcrop is poor as the bed occurs as small blocks of fossil-bearing rock scattered through the soil of a paddock. It is impossible to measure the precise thickness or the boundaries of the bed without excavation. The layers of fossil-bearing rock vary from about 2 cm to 4 cm thick, but within these layers the fish are scattered in overlapping layers, rather than all being at the top or all at the bottom of the layer. The exception is some large blocks covered with vast numbers of small fish, some available in part and counterpart. There is no evidence of the original location of these blocks, but it is assumed that this very fossiliferous layer is the upper layer of the deposit, and thus represents one mass-kill event. There is no evidence of desiccation in the sediment, such as mud cracks or aerially exposed surfaces, so this is not a mound spring deposit. It is not an overbank deposit either, as these usually have cyclic layers including sands and coarse-grained layers from flooding, interspersed with soil developments from dry times. The layers that contain an abundance of small fish, which are

thought to occur at the top of the bed, are very fine grained and represent a period of slow deposition, or a time when the pond was still and suddenly became anoxic. Lower layers have occasional scattered fish that have been deposited along with sediment. Percival (1979) recorded that "it is now thought to represent the erosional remnant of the margin of a freshwater lake bed deposit". Evidence now points to the destruction of the lake by several eruptions of volcanic ash.

The fossils show no preferred orientation, although most are laterally flattened. Only one of several hundred specimens is dorso-ventrally flattened. Some of the smaller individuals show dorsal flexion. This flexion of the spine could represent greater flexibility of the juvenile individuals, or could possibly be a result of them dying in suddenly anoxic water as the result of an ash fall. The dorsal flexion of the small specimens was also commented upon by Waldman (1971) in his description of the fish in the Cretaceous Koonwarra beds in Victoria. He considered that particular assemblage, which includes a large number of the closely related species, *Leptolepis koonwarri* Waldman, 1971, was due to winterkill and claimed the flexion is due to asphyxia of the individuals when the pond was covered by ice. As is noted later in this paper, many of the fish are preserved with their mouths open, which could support the idea of anoxia.

Plant fossils are commonly associated with the fish. None of these represent plants growing *in situ*, and there is no evidence for any water dwelling plants. The plant material consists of twigs, individual leaves, occasional cones, and very small fragments. Some beds have masses of very finely shredded plant material.

The area surrounding the lake was heavily forested with an araucarian pine, *Agathis jurassica* (White 1981). The fine detail of plants and fishes preserved implies an anaerobic burial environment. Most of the fish are intact with very few examples of disarticulated bones, indicating a lack of post-mortem turbulence, predation and decay. The plant fragments show venation and cell structure, thus showing no signs of decay or transportation.

Etheridge and Olliff (1890) described one example of a cicada named *Cicada? lowei* found in the fish beds, and further examples of insects have since been found. The Australian Museum houses a collection of Talbragar insects that has not been studied in detail. These insects are the only preserved evidence of a food source for the fish. The insects are apparently found in the upper layer where the fish fossils are most concentrated (R. Beattie, personal communication). Since none have been found in the lower layers where the fish are more scattered it may indicate that the insects were trapped by the ash fall that finally filled in the pond.

Materials

The specimens described in this study come from three sources: Australian Museum, Sydney, prefix AMF (30 specimens); NSW Geological Survey, Sydney, prefix MMF (107 specimens); Australian National University, Canberra, prefix ANU (106 specimens).

Where more than one fossil appears on a numbered specimen, the individual fossils have been allocated a letter suffix to distinguish them, eg MMF36743b.

Some material mentioned in text and figures relates to specimens in the Natural History Museum, London, prefix BMNH.

SYSTEMATICS

Subclass Teleostei Muller, 1844

Family Leptolepididae (Agassiz, 1833–44)

Genus *Cavenderichthys* Arratia, 1997

Synonymy

See Arratia (1997:19).

Diagnosis

Small teleosts ranging from about 4 cm to 12 cm; head with short snout; lower jaw projecting anteriorly; fusiform body. Frontal bone short anteriorly. Suborbital bone absent. Quadrate-mandibular articulation below anterior half of orbit. Elongated symplectic and hyomandibular, as well as ventral limb of preoperculum. Lower jaw with deep coronoid process and wide leptolepid notch. Hyomandibular with a preopercular process. No suprapreopercular bone. Infraorbital sensory canal with very few tubules; generally four broad tubules on lower limb of preoperculum, one at the angle, and one on vertical limb. Anterior ceratohyal short and usually not fenestrate; with six thin arcinaciform branchiostegal rays, and three or four spathiform branchiostegal rays associated with the posterior ceratohyal. 35–45 vertebrae with autogenous neural arches in abdominal region and fused neural and haemal arches in caudal region, with 20–26 pairs of ribs. Midcaudal autocentra thin, ring-like, with or without a longitudinal crest on lateral surface. 12 pectoral rays, 12 pelvic rays, 12 dorsal rays + 3 procurrent dorsal rays, and 10 anal rays. Pelvic, dorsal and anal rays branching distally into 4 lepidotrichs. Preural centrum 1 with short neural spine. Three or rarely four epurals; seven hypurals and five uroneurals; 10+9 principal caudal rays. Well-developed dorsal processes on bases of innermost principal caudal rays of dorsal lobe of caudal fin absent. Two "urodermals". Six basal fulcra on upper lobe of caudal fin.

Remarks

This diagnosis is based on Arratia (1997:19). However changes have been made where examination of new material has added information that contradicts the original diagnosis. For example, Arratia cited a deep body, the hyomandibular lacking a preopercular process, the lower jaw lacking a leptolepid notch, 12 or 13 branchiostegal rays, 43–45 vertebrae, 25–27 ribs, nine hypurals, seven uroneurals, and a lack of epipleural bones. These features are discussed later.

Cavenderichthys talbragarensis (Woodward, 1895)

Figures 1–22

Leptolepis talbragarensis Woodward, 1895: pp. 21, 22, pl. 6, figs 1–8.

Leptolepis lowei Woodward, 1895: pp. 22, 23, pl. 6, figs 9, 10.

Leptolepis gregarius Woodward, 1895: pp 23–24, pl. 4, figs 8–10, pl. 5, fig. 5, pl. 6, figs 11, 12.

Material Examined

Holotype

MMF81. This specimen has been examined, but not used in the current description. It was named as the type specimen by Woodward (1895) and appeared as Plate 6, figure 4.

Paratypes

The following specimens, housed in the

Australian Museum, Sydney, are paratypes, described by Woodward (1895). The old numbers have prefix MF, and have been replaced by new numbers with prefix AMF. AMF120525 (MF276), AMF120509 (MF276), AMF120505 (MF276), AMF120498 (MF276), AMF120512 (MF276), AMF120497 (MF276).

Other material

The following specimens have been examined, provided latex casts in most cases, and are quoted as examples in the text.

AMF27069, AMF4133, AMF51899, ANU54916, ANU54940, ANU54946, ANU54956, ANU54962, ANU54968, ANU54970, ANU54975, ANU54976, ANU54977, ANU54980, ANU54982, ANU54983, MMF13555, MMF13561a, MMF13564, MMF13569, MMF13599b, MMF13603k, MMF13606a, MMF13734a, MMF36716, MMF36718, MMF36721, MMF36728, MMF36729, MMF36730, MMF36732, MMF36732a, MMF36733, MMF36735, MMF36737, MMF36743, MMF36743a, MMF36743b, MMF36746, MMF36753a, MMF36758a, MMF36759, MMF36761b, MMF36773, MMF36778.

Description

Olfactory region

The rostral is evident on several specimens, including ANU54956 (Figure 2A) and MMF13555 (Figure 2B), and is small and almost shaped like an isosceles triangle, with the apex anterior. The two lateral margins are slightly concave, and the posterior

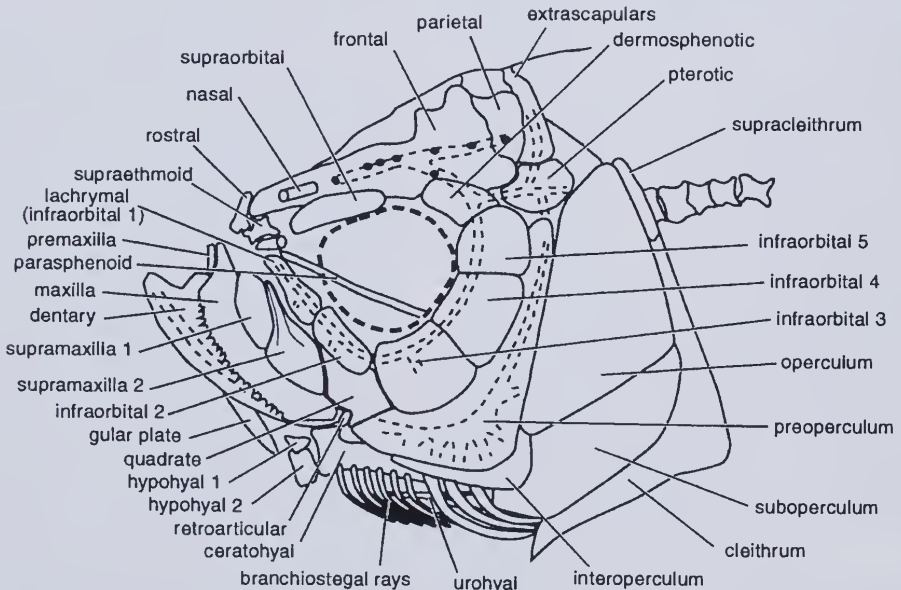


Figure 1 *Cavenderichthys talbragarensis*. Reconstruction of head, lateral view, based on MMF36716.

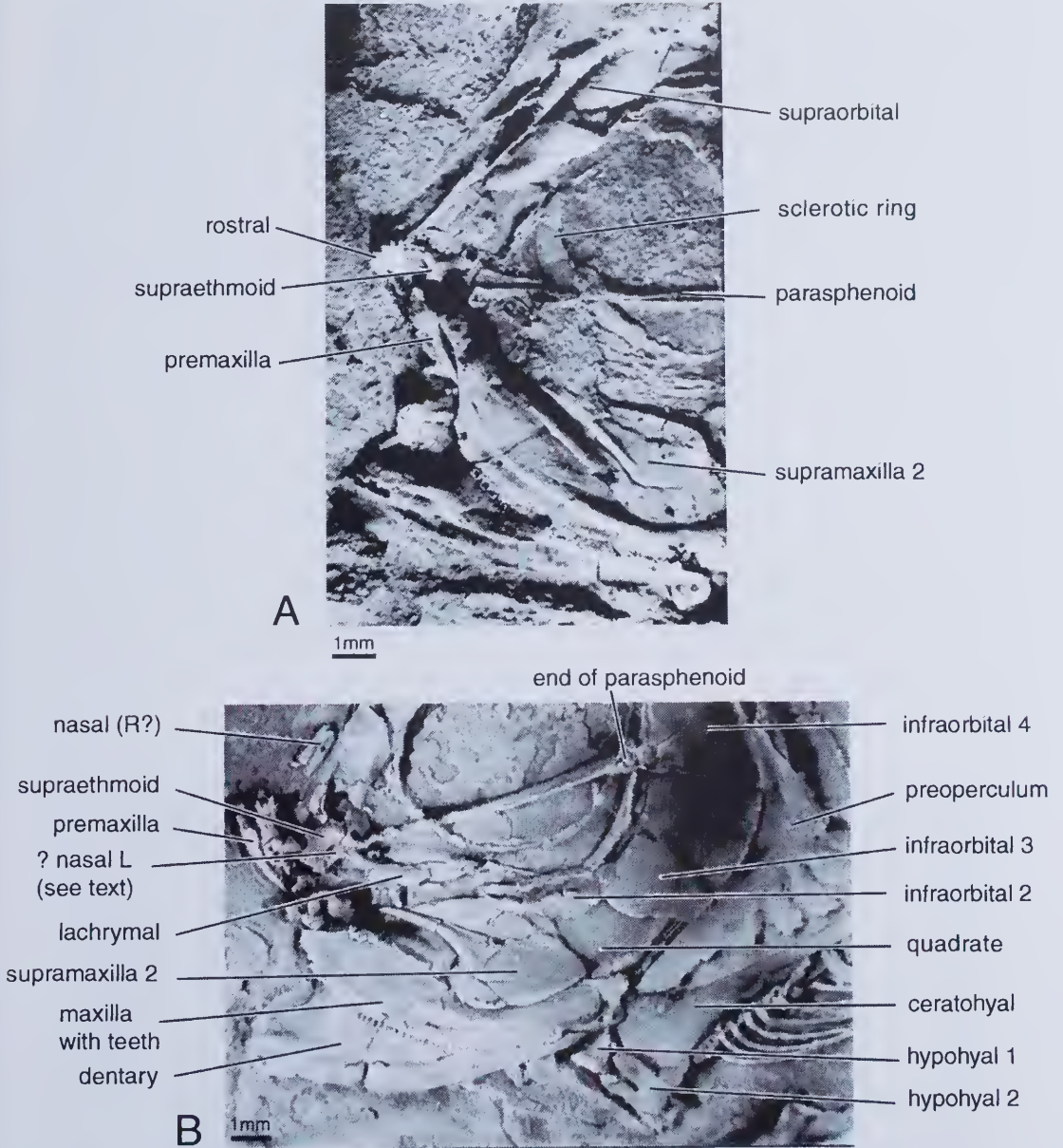


Figure 2 *Cavenderichthys talbragarensis*. Details of anterior head. A, this view of the front of the head of ANU54956 shows unusual detail of the anterior bones. B, the anterior of MMF1355 shows the premaxilla and nasal bones. On the supermaxilla 2 it is possible to see traces of the path of nerves. The preservation of teeth on the maxilla is unusually clear. The posterior of the parasphenoid can be seen to be enlarged.

margin is crenulated where it articulates with the frontal. In ANU54956 it is disarticulated from the frontal, but the posterior margin is clear (Figure 2A). This bone articulates with the maxilla and premaxilla and presumably with the supraethmoid, although this articulation has not been observed. The ethmoid has not been observed in this material.

The supraethmoid is a small median bone that is

under the anterior part of the frontal-rostral and probably is the ossified covering of the ethmoid cartilage. Two specimens, ANU54956 (Figure 2A) and MMF1355 (Figure 2B), show the supraethmoid to be roughly Y-shaped, with the two branches being posterior. The articulation of these branches with other bones cannot be determined in these specimens.

Otic region

The generally poor preservation of the otic region results from it overlying the back of the braincase causing it to be usually crushed, and is only known from one specimen (Figure 7A). The pterotic is roughly rectangular, and located dorsal to the preoperculum and posterior to the dermosphenotic. It carries the sensory canal where it branches off to the preoperculum. The parietals are medial to the pterotic. Only one specimen has an identifiable pterotic (Figure 7A).

Dorsal roofing bones

A small cylindrical bone on MMF13555 (Figure 2B), just ventral to the supraethmoid, has unclear relationships with other bones. It appears to carry a sensory canal, and in the flattened fossil it appears to be adjacent to the anterior end of the parasphenoid. This bone may be the left nasal. The right nasal is well exposed on MMF13555 (Figure 2B), having been detached during fossilization. It is identified on its tubular form and containing the supraorbital sensory canal. It sits adjacent to the anterior part of the frontal, where the sensory canal emerges from under the ridge of covering that protects it in the region above the supraorbital.

Frontals are the largest skull roof bones, almost the same size as the dentary bones. They are narrow at the front and become wider behind the eye. The

suture between them is straight in the narrow region, and then bends back and forth in the wider region. The frontals carry the sensory canal, with pores occurring at the front, above the centre of the supraorbital bone, and at the end of a branch where the canal curves down around the eye. The canal is close to the surface of the bone and is covered by a ridge in some specimens in the anterior narrow part of the frontal, e.g., MMF13564 (Figure 3B). In other cases the delicate ridge has been removed and a canal is visible, e.g., ANU54916, MMF36781, MMF36735, MMF36753a (not figured). About two thirds of the distance from the anterior of the frontals is a prominent pore, behind which the sensory canal branches, with one branch leading into the parietals where it terminates at a pore (MMF36753a, Figure 6A). The other branch turns ventrally and passes into the dermosphenotic. Where the frontal broadens out, it forms the margin of the orbit between the supraorbital and the dermosphenotic.

The parietals are generally rectangular in form and meet medially by an irregular suture. The sensory canal crosses them from the frontals, but does not emerge posteriorly. The parietals occur directly behind the frontals and anterior to the extrascapulars.

The extrascapulars (Figure 6A) are smaller than the parietals and are posterior to them. They carry a

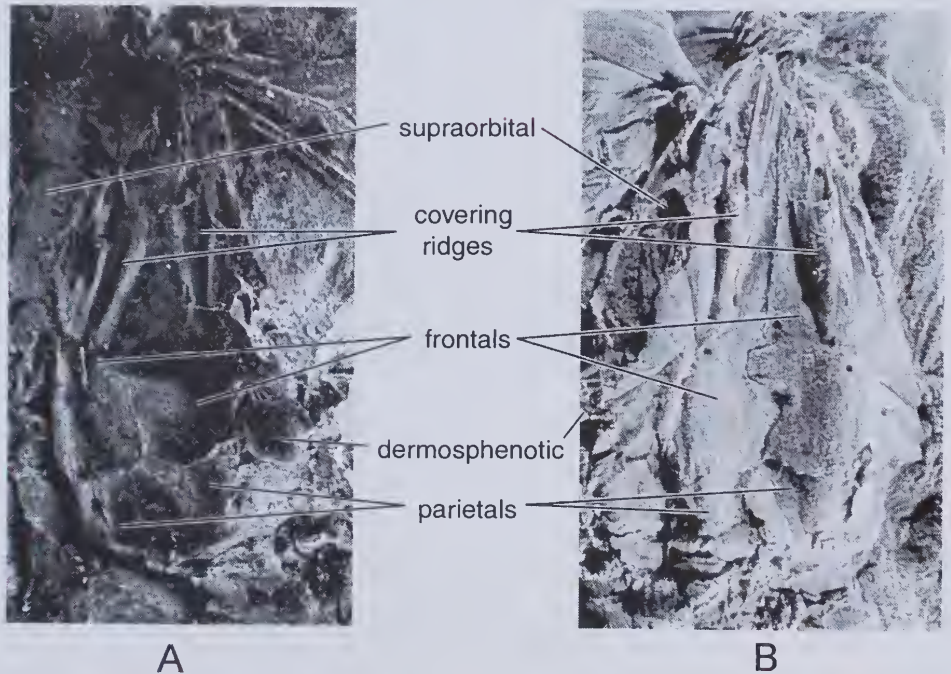


Figure 3 *Cavenderichthys talbragarensis*. Skull roofs. A, this photograph of a latex peel of the skull roof of MMF36728 is a rare example of this view. B, on this peel of MMF13564 it is possible to see even more detail including the mid-line suture and several pores for the emergence of nerves.

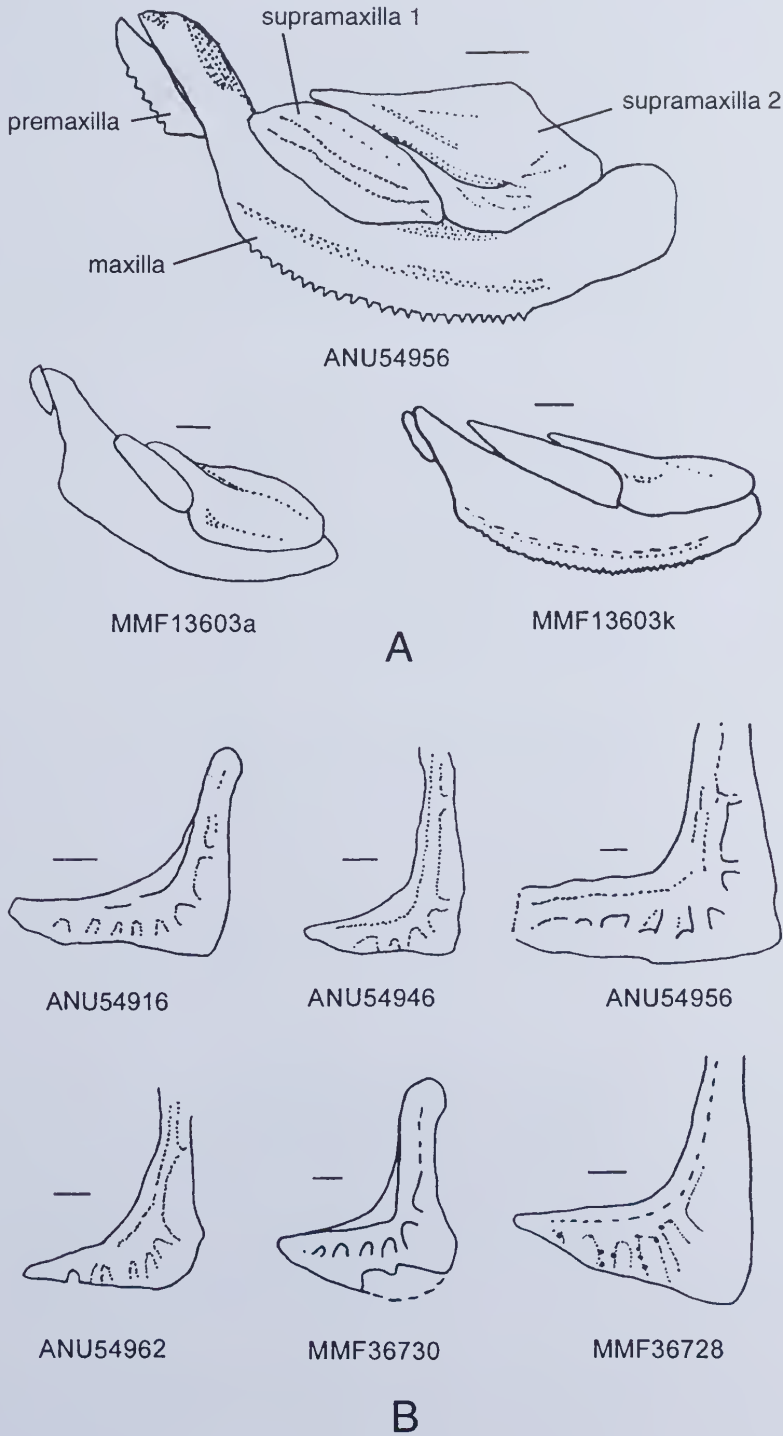


Figure 4 *Cavenderichthys talbragarensis*. A, sketches of the differences in arrangements of bones in the upper jaw. This is natural intra-species variation, and is as much a function of differences in preservation as differences between individuals. B, sketches of the variations in arrangement of the preopercular canal on the preoperculum. Scale bars = 1 mm.

sensory canal with several pores. They are the posterior bones of the roof of the skull, but in many specimens they are crushed and difficult to interpret. Figures 3A and 3B are photos of the skull roofs of MMF36728 and MMF13564 respectively.

Lateral skull bones

The premaxilla (Figures 2A, 2B, 4A and 5A) is small and mobile, and because of this it is often lost due to poor preservation. It fits into a concavity on the front of the maxilla (see below). There are about 6 small teeth on the premaxilla, which lies adjacent to the rostral bone and the supraethmoid, (ANU54956, Figure 2A) but this region is not usually seen clearly. Other non-figured specimens showing the premaxilla include MMF36732a, MMF36778, MMF13555, ANU54916, and ANU54968.

The maxilla has along its ventral margin a row of small, even teeth, which can be seen on specimens ANU54956 (Figure 4A), ANU54976 (Figure 5A), and MMF36729 (not figured). This margin is a smooth gentle convex curve ventrally, with a small arcuate toothless concavity at the front to accommodate the premaxilla. The maxilla and the premaxilla are certainly not fused in any way, as the premaxilla is often detached from the maxilla, but their articulation is not obvious. The posterior end of the maxilla is a smooth semicircular curve and is connected to the coronoid process of the mandible by a flat maxillomandibular ligament (Lauder 1980). The anterior end of the bone has a peg-like process, which enables it to articulate probably with the vomer, ethmoid and palatine in a similar manner to *Amia* (Lauder 1980). This means the maxilla is fixed at the anterior end and free to swing forward and backward from the posterior. When the mouth is agape, the maxilla swings forward, and is often found preserved in this position. Teeth form the margin of the gape when the maxilla is fully protracted. When the mouth is closed the maxilla is pulled backward, and passes outside the dentary, coming to rest on the ridge on the dentary formed by the heavy ossification around the Meckelian cartilage. The outside surface of the maxilla has a ridge running along the middle from the anterior end. Of 142 specimens in which it is possible to distinguish the state of the maxilla, 83 have the maxilla wide open.

There are two supramaxillae, the anterior being a small smooth oval bone that on-laps the anterior part of the dorsal margin of the maxilla (MMF36732a, Figure 6B). The posterior supramaxilla has a generally oval shaped base on-lapping the maxilla, but it also has a long thin slightly curved process extending anteriorly under and above the anterior supramaxilla. This process has a thin ridge and groove that extend from the tip down into the body of the bone. The surface of the

body of the posterior supramaxilla has a radiating pattern of grooves and small ridges, which appear to represent a point of ligament attachment. The maxilla and the two supramaxillae move as a unit and are generally found joined together. Figures 5, 6 and 7 illustrate the various structures of the upper and lower jaws.

Circumorbital series

The system of naming all lower circumorbitals as infraorbitals, as used by Cavender (1970), Nybelin (1974), Patterson (1977) and Arratia (1997) has been used here. Confusion can arise when some bones are not preserved, e.g., infraorbital 1 or lachrymal, and the terminology used by Norden (1961), based on living fish, which clearly identifies specific bones, was used initially by the author to establish relationships. However, the modern terminology has been used to be consistent with contemporary publications.

A single supraorbital bone is the anterodorsal bone of the circumorbital series. It is a long thin oval with a slight upwards curve to follow the dorsal margin of the eye. The ends of the bone are rounded and there is no sensory canal. It forms the anterodorsal margin of the orbit (ANU54956, Figure 2A and MMF36728, Figure 3A).

The infraorbital 1, also called the lachrymal, (MMF13555 Figure 2B) is small, forming the lower anterior rim of the orbit, and contains the terminus of the infraorbital canals (Norden 1961). It is a dermal bone external to the ectopterygoid, fitting into the series around the eye. It is narrow anteriorly and broadens posteriorly and is almost triangular in nature with the apex towards the front. It carries the sensory canal, but due to the state of preservation it is impossible to determine if it is the site of the terminus of the infraorbital canal.

Specimens MMF36728 (Figure 5C), AMF51899 (Figure 7A) and MMF36735 (not figured) show the continuation of the infraorbital series. There are four bones all about the same size and depth around the ventral and posterior part of the eye. They all carry the sensory canal. The first one is the infraorbital 2. In *Cavenderichthys talbragarensis* it has a roughly trapezoid shape. A branch off the canal is directed ventrally. The infraorbital 2 is not as deep as the subsequent ifraorbitals. Its ventral margin is level with the ventral margin of the infraorbital 1 in front, but at the back it is about half as deep as the infraorbital 3.

Infraorbitals 3–5, which are all about the same depth, form the posterior rim of the eye. A suture between infraorbitals 3 and 4 always appears in compressed forms to be adjacent to the posterior end of the parasphenoid. In all the specimens illustrated in this article there is an easily identified bone, infraorbital 3, which occurs anterior to the bend of the preoperculum. Dorsal to this bone is

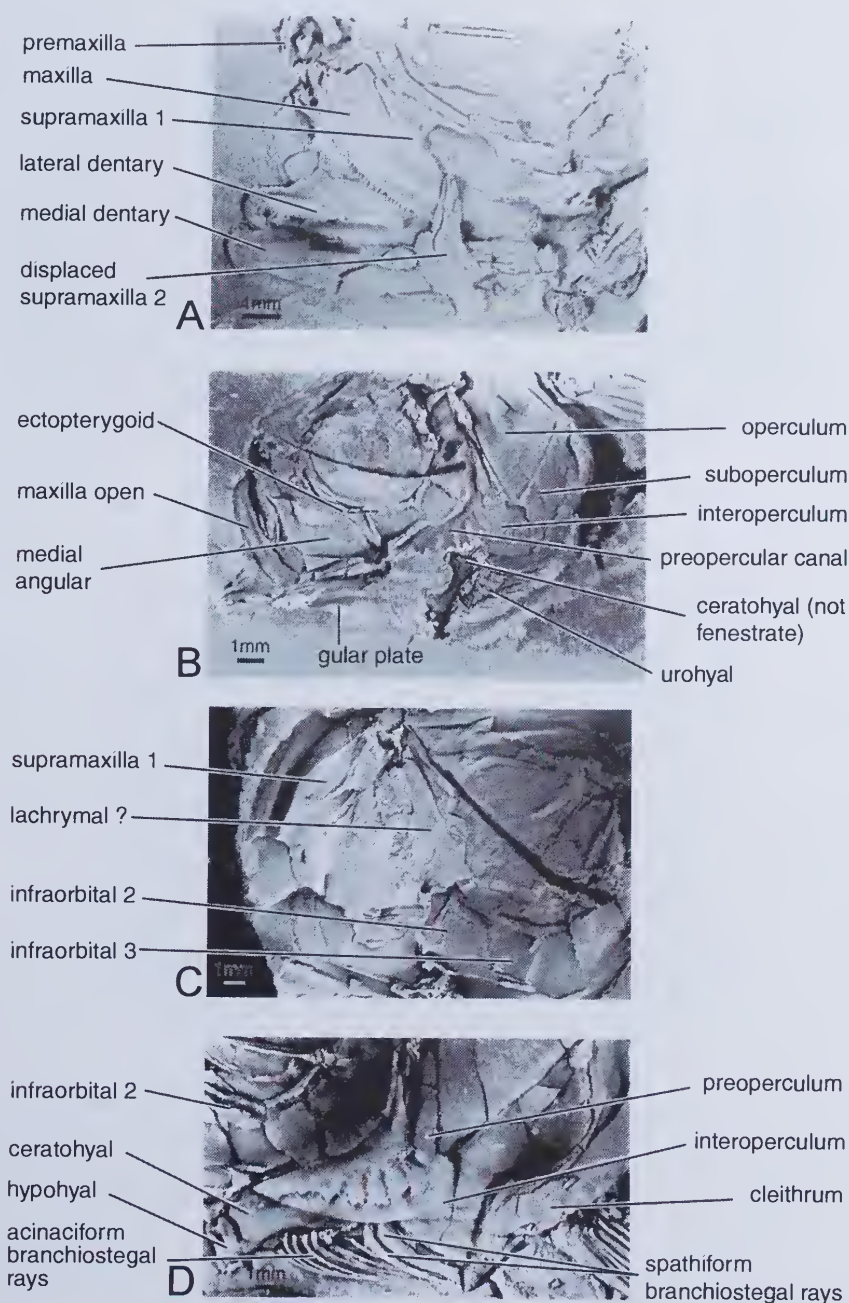


Figure 5 *Cavenderichthys talbragarensis*. A, detail of the jaws of ANU54976. Left and right dentaries are both visible, and well preserved teeth on the maxilla. Supramaxilla 2 has been displaced but its medial ridge is clear. B, medial view of MMF36732a, showing the ectopterygoid and bones of the circumorbital series. In this specimen the ceratohyal is clearly not fenestrate, and the delicate nature of the urohyal is obvious. C, MMF36728 has well preserved bones of the circumorbital series, including the lachrymal. D, in this detail of the posterior ventral region of the head of MMF13555, the ceratohyal is partly covered by the preoperculum, but the relationship of the two forms of branchiostegal rays to the ceratohyal is clear. Two hypohyals are visible at the anterior of the ceratohyal.

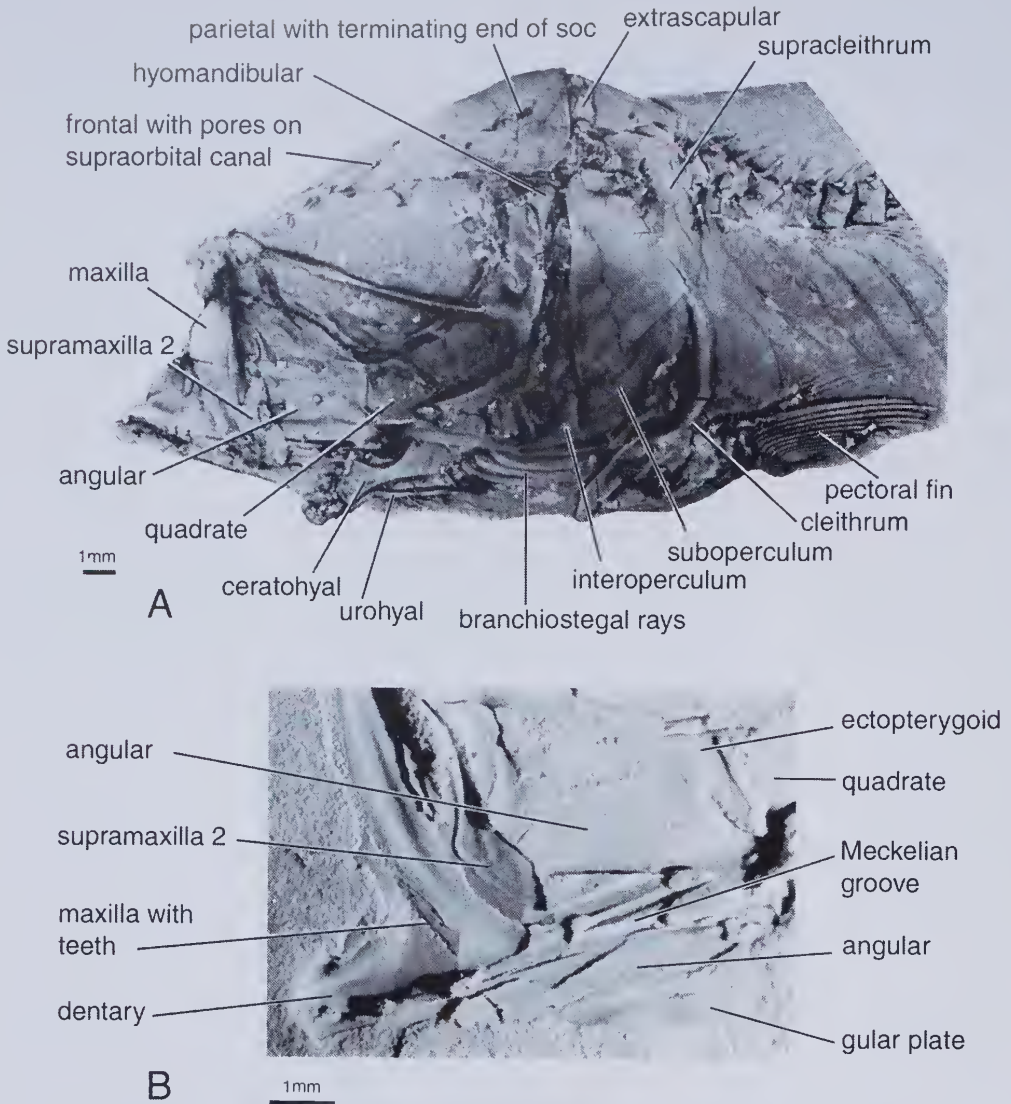


Figure 6 *Cavenderichthys talbragarens*. Heads showing the maxilla in the forward open position. A, this photograph of a peel of MMF36753a includes a ceratohyal that is not fenestrate, and very clear pores on the supraorbital canal. The characteristic position of the parasphenoid appearing to bisect the orbit is well demonstrated. B, the detail of the jaws of MMF36732a is taken directly from the specimen. The location of the Meckelian cartilage present along the interior surface of the dentary is obvious.

infraorbital 4, a squarish bone that in *Cavenderichthys* is as deep as infraorbital 3. The most dorsal infraorbital 5 (Figures 7A, 7B, 8A) is not squarish but roughly triangular with rounded corners, the apex pointing dorsally. These bones lie anterior to the preoperculum and overlap it slightly. Infraorbitals 3 and 4 have approximately rectangular shapes with curved margins. There are no branches of the sensory canal in infraorbitals 4 and 5 (see MMF36761b, Figure 7B, and MMF13599b, Figure 8A).

Dorsal to infraorbital 5 is the dermosphenotic, or infraorbital 6 (AMF51899, Figure 7A). Norden classifies the dermosphenotic as a "small, dermal postorbital bone, which bears a triradiate sensory canal." In many specimens this bone is crushed and difficult to identify, but it is possible to see in several specimens that it carries a junction of the sensory canal where it descends from the frontal, continues into the highest infraorbital, and branches posteriorly towards the pterotic. It makes part of the posterior rim of the orbit.

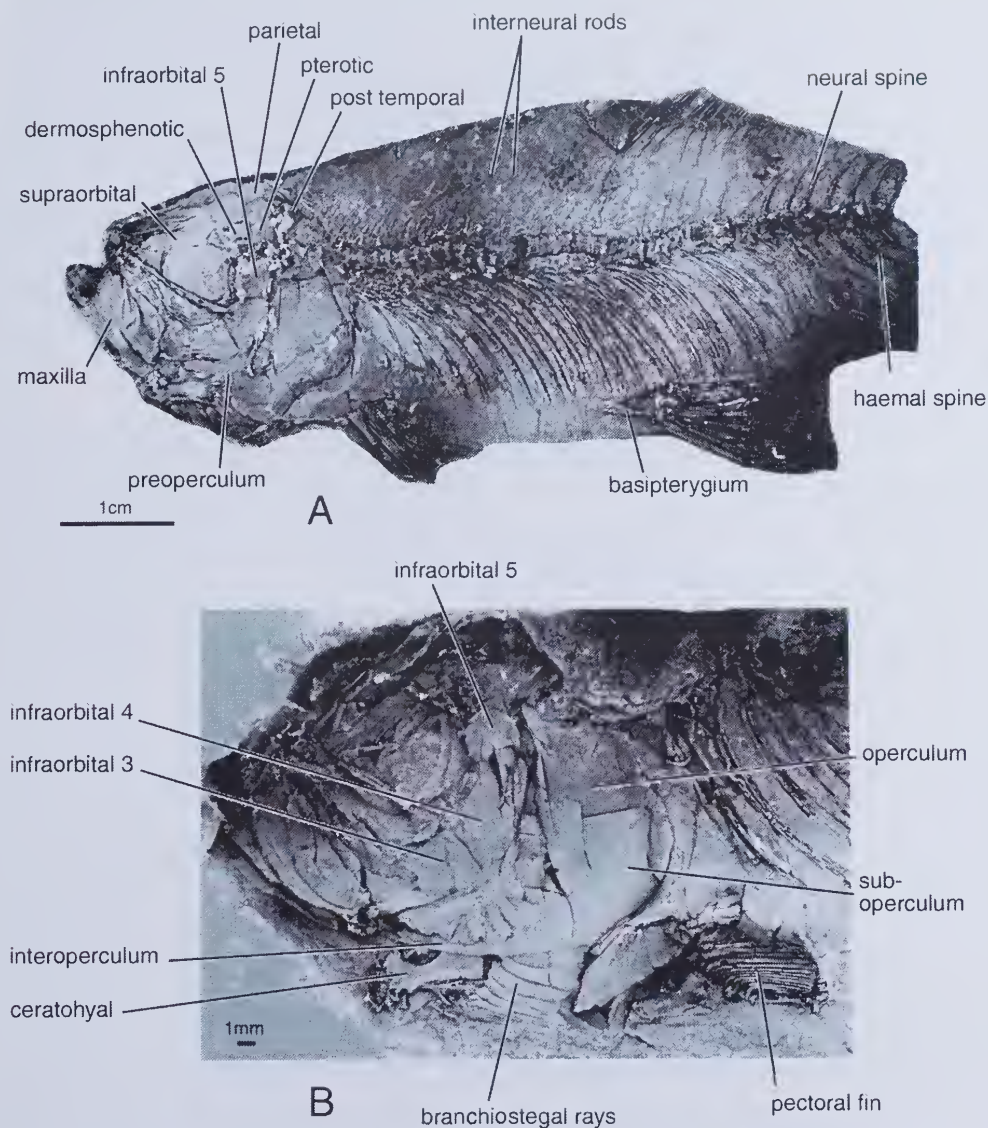


Figure 7 *Cavenderichthys talbragarensis*. Heads showing the jaws closed. A, F51799, infraorbitals 3–5 can be identified as well as the pterotic and dermosphenotic. In the pleural region the vertebral column is well preserved and interneural bones are visible. The basipterygium can be seen supporting the pelvic fin. B, on the specimen MMF36761b the bones of the opercular series and the infraorbital bones can be easily identified. The spathiform branchiostegal rays are seen posterior to the ceratohyal. The path of the preopercular canal clearly shows five branches.

Preoperculum

A commonly preserved bone is the preoperculum, well seen on MMF36730, MMF36759, ANU54916, ANU54968 and ANU54940 (see Figure 4B). It lies behind the infraorbital series, and is not part of the opercular series. The bone is arcuate, with an angle of approximately 110° between the dorsal and ventral limbs, and it carries a prominent branch of the sensory canal. The dorsal margin of the upper limb is often crushed. The postero-ventral margin is smoothly curved, making

a more acute angle than the anterior margin. The anterior margin of the ventral limb extends to a point lateral and just posterior to the articulation of the lower jaw. The sensory canal is carried close to the outer surface of the bone, and continues onto the mandible. When the external surface is preserved it is apparent that the canal makes a ridge on the surface, with small pits at the ends of side branches opening to the surface. Often the canal is preserved by infilling with fine-grained white material, indicating that it was closed at the time of

death and has subsequently been filled with material that is different from the typical matrix. The canal is located closer to the anterior margin than the posterior, with a series of branches running down towards the posterior margin, on average six branches, sometimes seven and occasionally five. There is usually only one branch on the dorsal limb, about halfway up, with the others evenly spaced, three along the ventral limb and two adjacent to the bend. The branches are broad and tend to widen away from the main canal. Illustrated examples of the preoperculum are Figure 4B, MMF13555 (Figure 5D), MMF36732 (Figure 5B), and MMF13599b (Figure 8A).

Suprapreoperculum and suborbital bones are lacking.

Opercular series

The shape of the operculum is roughly triangular with the most acute angle dorsal. The top is sometimes involved in the crushing at the back of the braincase, but when well preserved it can be seen to be smoothly rounded. The anterior margin is approximately perpendicular to the line of the vertebral column. The posterior margin is convex posteriorly. The ventral margin is straight and inclined down towards the front, and overlaps the suboperculum.

The suboperculum has the appearance of being an isolated continuation of the operculum (Figures 6A and 7B). The anterior and posterior margins follow the same lines. The ventral margin of the suboperculum follows the line of the ventral surface of the fish and overlaps the branchiostegal rays. It is adjacent to the cleithrum.

The interoperculum is a triangular bone, ventral to and partly hidden by the preoperculum. It often overlaps the branchiostegal rays, and is adjacent to the suboperculum. It can be seen in specimens MMF13555 (Figure 5D), MMF36732a, MMF36728, ANU54976, ANU54983, MMF36761b (Figure 7B), MMF36753a (Figure 6A), and MMF36735.

Six thin acinaciform branchiostegal rays are regularly associated with the ceratohyal, presumably with a ligamentous connection between them. They leave the ceratohyal ventrally then curve around to point posteriorly (Figure 5D). They extend toward the cleithrum and end as thin points, floating freely. The left and right rays are separated by the Y-shaped urohyal.

There are three or four spathiform branchiostegal rays that also seem to be connected to the epihyal (MMF13555, Figure 5D and MMF36761b, Figure 7B). They are dorsal to the thin rays but curve around in a similar fashion and parallel the base of the suboperculum. This maximum number of 10 branchiostegal rays is less than the 12 or 13 counted by Arratia (1997) in her diagnosis of *Cavenderichthys*. This may be because

sometimes the rays from both the left and right sides are visible.

Palatal bones

The generally poor preservation of the front of the head means that it has not been possible to identify the vomer, which should be a median toothed bone between the two premaxillae. In comparison, the appearance of the parasphenoid bisecting the orbit is one of the typical features of *Cavenderichthys talbragarensis*, e.g., Figures 2A, 2B, 5B, 5C, 6A, 7A, 8A, 8B. The parasphenoid is a median dermal bone that forms the roof of the mouth, so when the fish is laterally compressed it appears across the large eye socket. This bone is thin dorso-ventrally, and it is slightly concave dorsally. The rear of the parasphenoid is generally hidden behind the postorbitals, so details of its relationship with the brain case cannot be determined. One figure of MMF13555 (Figure 2B) shows an expanded posterior end. The anterior end extends to the front of the head and probably articulates with the vomer. The line of the parasphenoid is inclined upwards towards the front, making an angle of about 120° with the line of the spine.

Mandible

The dentary is the major bone of the lower jaw; see Figures 2B, 5A, 9A, 9B and MMF36730, MMF36733, MMF13734a (unfigured). The Meckelian canal which carries the Meckelian cartilage lies close to the internal surface, and adjacent to this on the external surface there is a prominent ossification of the dentary covering the sensory canal, making a ridge along the external surface. This ridge is sometimes removed or damaged, leaving a deep canal. If the surface is preserved there are seen to be two or three pores along the path of the canal, as shown by Arratia (1997: 21). The front of the dentary always protrudes beyond the line of the maxilla, whether the gape is open or closed. The ventral margin of the dentary forms a smooth gentle curve, passing posteriorly into the angular. The anterior margin of the dentary is tightly rounded. The anterior-dorsal margin is slightly inclined and sometimes carries about 6–10 small teeth. These are not commonly seen, even when the maxilla teeth are clearly preserved. They may be just very small, or possibly they are not always present. Posterior to the toothed surface the margin of the dentary forms a downward notch before rising steeply to the coronoid process (Figures 9A, 9B). This notch is equivalent to the "leptolepid notch" referred to by Nybelin (1974), Patterson (1977), and Arratia (1997) (see later comparison with other species). The notch is smoothly curved, is higher on the internal surface and makes a channel down towards the outer

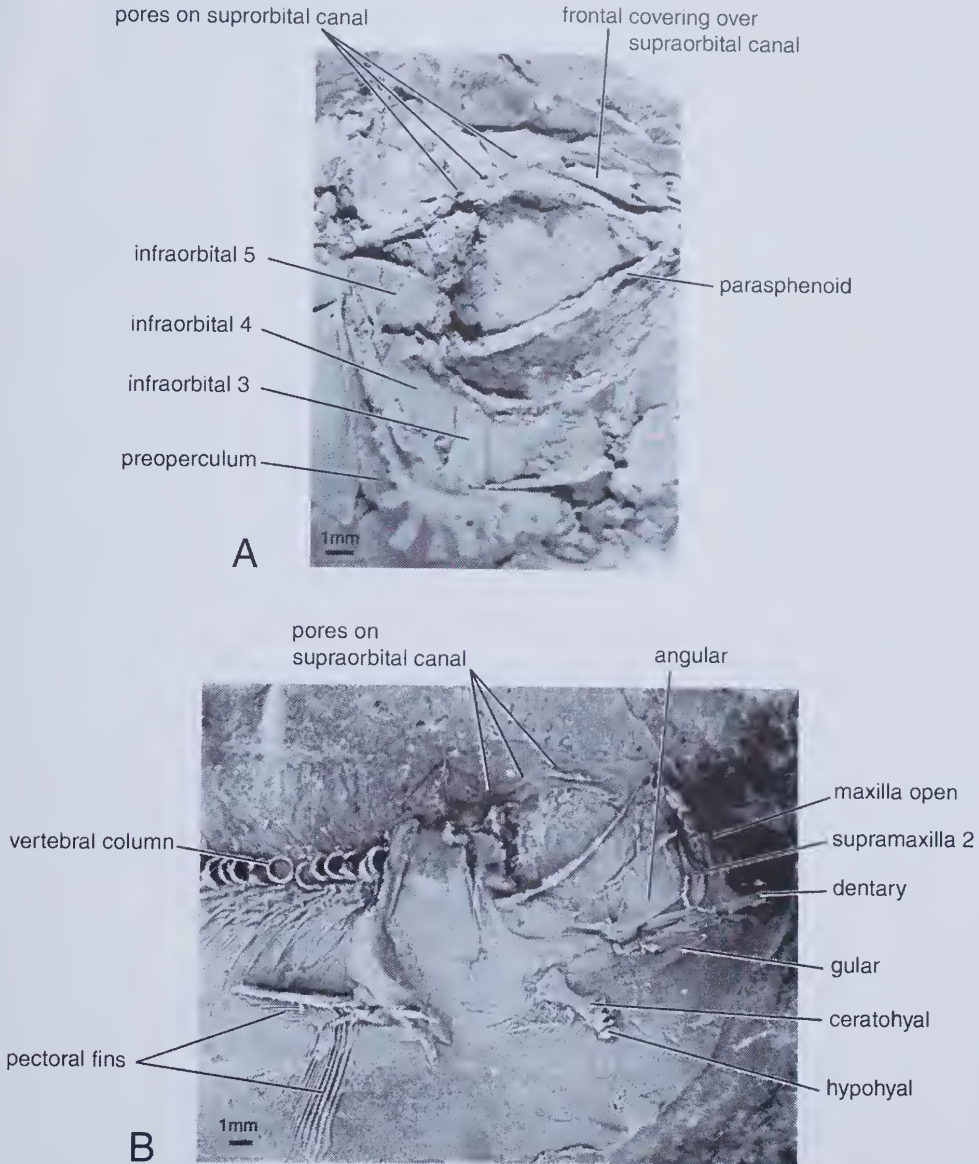


Figure 8 *Cavenderichthys talbragarensis*. A, MMF13599b, some detail of the roof of the skull is seen, including pores on the supraorbital canal. Infraorbitals 3-5 are clear. B, this photograph of a peel of MMF36732a shows uncommon detail of the pectoral fins, the structure and degree of ossification of the anterior vertebrae, and the pores on the supraorbital canal. The gular plate is preserved below the dentary, and the ceratohyal not fenestrate.

surface. It is much wider than the notch illustrated by Nybelin in *Leptolepis coryphaenoides*, but it occurs in the same location. The dorsal margin of the coronoid process is formed anteriorly by the dentary and posteriorly by the angular. The angular and dentary are always found closely associated, together with the retroarticular.

The angular fits into a V-shaped notch on the back of the dentary and can be seen on MMF13734a

(Figures 9A, 9B). It is thin dorsally and thickens ventrally adjacent to the Meckelian canal. The postero-ventral corner, which incorporates the fused articular process, articulates with the quadrate. The angular makes up about the posterior third of the ventral margin of the mandible. There is not sufficient information to determine a true relationship between the angular and articular due to the lack of exposure of this area.

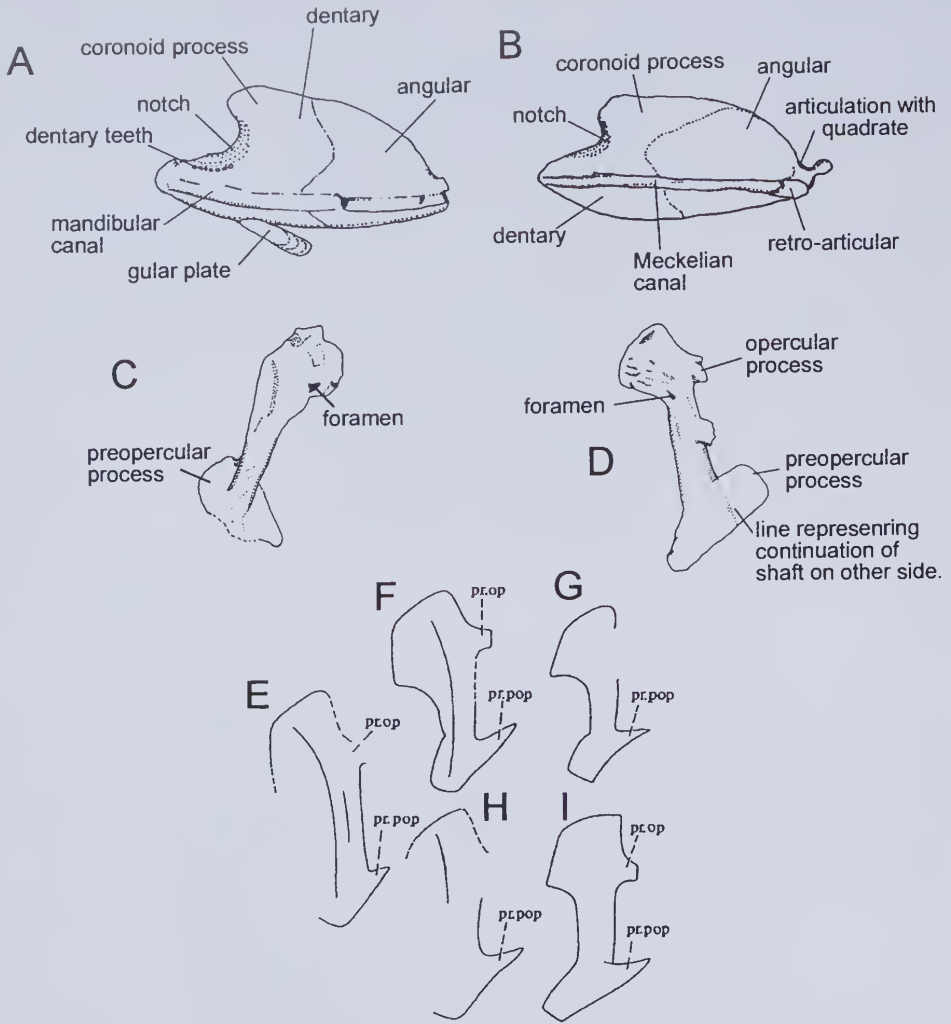


Figure 9 *Cavenderichthys talbragarensis*. A, lateral view of the left mandible of MMF137a, drawn from Figure 21E. B, medial view of the right mandible of MMF13734a, drawn from Figure 21D. C, medial view of the left hyomandibular of MMF13734a, drawn from Figure 21B. D, lateral view of the right hyomandibular of MMF13734a, drawn from Figure 21C. E, F, G, outlines of the hyomandibulars of *Leptolepis normandica*. H, I, *Leptolepis coryphaenoides* [Nybelin (1974) figure 3] included to provide a comparison with the structure of the hyomandibular of *Cavenderichthys talbragarensis* as seen above in D. The presence and location of the opercular process (pr.op) and the preopercular process (pr.pop) are very similar.

The retroarticular is a small bone, possibly fused to the posteroventral margin of the articular and forming part of the articulation of the lower jaw.

Palatoquadrate arch

The ectopterygoid, which can be seen on MMF36732a (Figure 6B) and MMF36732 (Figure 5B), forms the anterior sidewall of the mouth. It is boomerang shaped, thin anteriorly and thickens posteriorly where it articulates with the quadrate.

The dorsal margin is convex while the ventral margin of the ectopterygoid is concave, does not articulate with anything and is usually covered by the upper jaw.

The quadrate can be seen on MMF36753a (Figure 6B), MMF36732a, ANU54962 and ANU54977 and is a fan shaped bone that forms part of the articulation with the mandible. The dorsal part is thin and spreads out like a quarter of a circle. The apex of the bone, which is ventral, thickens into an

articulating post which articulates with the back of the angular-articular and the retroarticular process.

Hyoid arch

Of the hyoid arch, the hyomandibular bone is only rarely visible as it is generally covered by the preoperculum. In ANU54976 the dorsal end of the bone appears in the orbit, but in the dorso-ventrally flattened MMF13734a, both hyomandibulars are visible, see Figures 9C, 9D, and later in text the photographs of Figure 21. The bone is long with a central shaft, a thickened dorsal end and a thin expanded ventral end. The antero-dorsal margin projects anteriorly from the shaft, then curves smoothly to a dorsal point, resembling the shape of an axe head. The postero-dorsal margin curves concavely down to an opercular process. The postero-ventral margin thins out behind the base of the shaft into a thin flattened preopercular process with a curved margin. The ventral margin of this process extends in a straight diagonal line down to a point anterior of the shaft, and then curves back up to meet the shaft just below where the posterior part of the process intersects the shaft. The preopercular process is very thin and not likely to be preserved (or visible) in many cases. It is only due to the dorso-ventral flattening of just one specimen (MMF13734a) that the details of both the left and right hyomandibulars can be seen. A clearly visible foramen on the outer surface of the upper part of the bone allows passage of a branch of the facial nerve (Norden 1961), see Figures 9C, 9D.

It has not been possible to find sufficient evidence to describe the symplectic.

The epiphyal, seen on ANU54976 (not figured), is usually covered by the preoperculum. It is a flat, roughly rectangular bone with a slightly concave anterior margin that articulates with the slightly convex posterior margin of the ceratohyal. The ventral margin is slightly convex. It appears to be associated with 3 or 4 spathiform branchiostegal rays.

The ceratohyal is often preserved and quite clearly visible, for example on MMF13555 (Figure 2B), MMF36732a (Figure 5B), MMF36761b (Figure 7B), MMF36732a peel (Figure 8B) and MMF36735 (not figured). The ends of the bone are flattened and splayed out with curved margins. The ventral margin is smoothly concave, and bears the attachments of the six thin branchiostegal rays. The dorsal margin also has a smooth, deep, sometimes semicircular curve. In this species the ceratohyal does not appear to generally be fenestrate. In several specimens (ANU54980, MMF36743, MMF13606a, MMF36721,) there may be a thin rod connecting the anterior and posterior dorsal margins, but in each case it has been broken. More commonly the ceratohyal resembles the shape of the

archetypal dog's bone, e.g., MMF36732a (Figure 5B), MMF36753a (Figure 6A), MMF36761b (Figure 7B), MMF36781, MMF36743a and MMF36728. Cavender (1970) suggested that the rod-like connection between the dorsal ends of the ceratohyal may be present on the larger specimens. Many small specimens show that the ceratohyal is definitely not fenestrate (*contra* Arratia 1997) as the dorsal margins can be clearly seen and there is no sign of a rod connecting anterior to posterior.

Two very small hypohyal bones can be seen on MMF13555 (Figure 2B), MMF36732a (Figure 8B), MMF36729, and ANU54983, fitting into the slightly concave anterior surface of the ceratohyal. They occur one above the other, and would have been connected to the ceratohyal by cartilage. They appear as if they may be conical, with the upper one fitting over the apex of the lower one. Other forms of fish have only one hypohyal per ceratohyal, but in leptolepids, having two hypohyals is not uncommon. It is also the usual situation in modern Salmonidae.

Branchial arches

No observable articulated branchial arches have been preserved in these specimens, but isolated bones are identified below.

The urohyal is a very delicate median bone (see ANU54982, ANU54983 and MMF13603k) with a Y-shape, where the branches are pointing posteriorly. The urohyal is located between the two sets of branchiostegal rays (MMF36732, Figure 5B and MMF36753a, Figure 6A). Its relationship with other bones, apart from the branchiostegal rays, cannot be determined.

The gular plate, which is seen on MMF36732a (Figures 6B, 8B), ANU54982 and ANU54983, is a small narrow median plate found between the two lower jaws. It is quite often visible with its anterior margin hidden behind the dentary, but its posterior margin pointing downwards. This is the case when the ceratohyal is also visible below the jaw-line. The gular plate has continuous growth lines outlining the elongated oval shape. It probably increases in length, but not greatly in width, as the individual grows.

Vertebral column

The number of centra is highly variable. Of the 48 peels with centra that can be counted reliably, there is a range from 35 to 45 centra (cf. 43–45 recorded by Arratia 1997). The mean value is 40.4 with a standard deviation of 3.5. There is also no relationship between length of the individual and number of centra. Each centrum is a thinly ossified cylinder, constricted in the middle. The centra in the abdominal region have a small process on each side for the attachment of the ribs.

The last two upturned centra in the tail are called

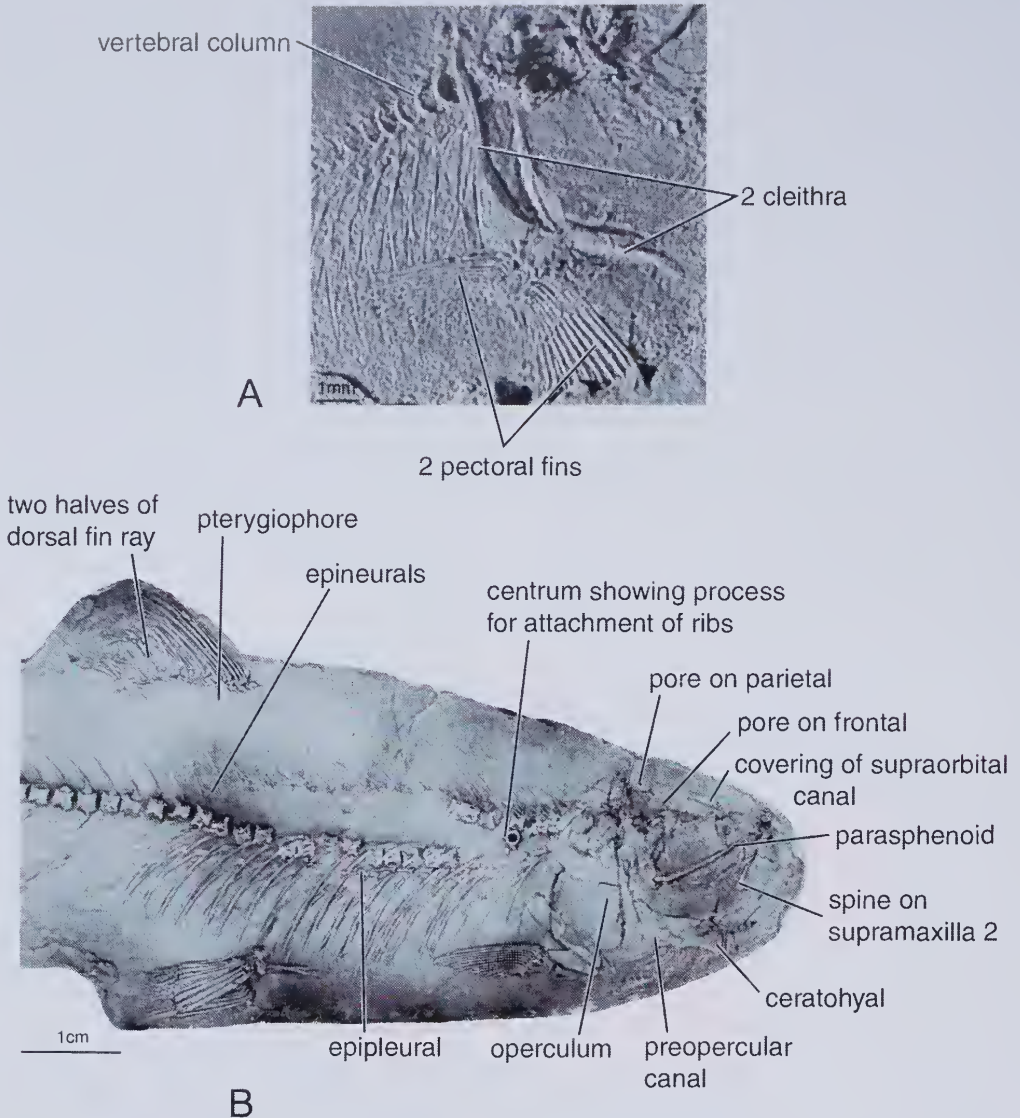


Figure 10 *Cavenderichthys talbragarensis*. A, pectoral fins of ANU54938, ventral view. B, peel of F27069 showing detail of the vertebral column. Vertebra turned on its side shows two small processes for the attachment of the ribs. Just ventral to the spine in the pleural region are small epipleural bones. The epineurals are visible detached from the dorsal side of the spine. On the pelvic fins distal branching of the rays can be seen.

ural centra. Anterior to this the centra that carry haemal arches are called preural centra.

Epineural bones come off the neural arches that carry ribs, anterior to the dorsal fin, see AMF27069 (Figure 10B), MMF36743b (Figure 16B), and AMAMF4133. They point backwards at an angle of about 20° above the column. They occur on each side of the column because they are inter-muscular bones that support the flesh of the fish (Gosline 1971).

Anterior to the dorsal fin are interneural bones,

which are “a series of median supporting rods” (Norden 1961: 689) extending from just below the dorsal surface of the fish to the level of the neural arches, see MMF36743b, AMF4133. They are thin rods whose proximal tips fit between the tips of the bifurcating neural arches (AMF51899, Figure 7A).

The neural arches are paired bones that articulate with the centra and form an arch through which the spinal cord passes. They extend dorsally approximately half way to the dorsal body margin. In the abdominal region it is often possible to see

the two separate bones that form the arch, but behind the dorsal fin the bones of the neural arches are fused, forming neural spines. They are well ossified.

The haemal arches (ANU54970, Figure 16A) are composed of a pair of bones that fuse together to form haemal spines. The junction of the ural and preural centra is marked when the haemal artery is no longer passing through a haemal arch.

The number of ribs is variable as is the number of centra. Of the 49 specimens where ribs can be counted, the mean number is 23 with a standard deviation of 2.3. The range is from 20 to 26 pairs of ribs.

In a couple of specimens there appear to be epipleurals (AMF27069, Figure 10B), which are small fine bony projections originating near the point of attachment of the ribs and extending backwards to the level of the next rib. This has only been seen in the pleural region. Arratia (1997) stated that *Cavenderichthys* lacks epipleurals.

Caudal fin

The caudal centra are 3 upturned vertebrae in the caudal region, comprising preural centrum 1 and the ural centra, which is a characteristic of coregonines, salmonines, and thymallines (Norden 1961). The preural centra are well ossified, each consisting of a ring with a large circular canal in the middle. The haemal and neural arches always appear to be attached to the centra. The first preural centrum is slightly smaller than the subsequent ones. The first ural centrum appears to be fused with the second, as it is longer than other centra but has a smaller diameter. The first and second hypurals, which articulate with U1-2, appear to be fused, or at least closely associated.

The principal rays of the caudal fin form a double series of rays, which sandwich the ends of the hypurals, to which they are attached (Figure 12C). The two outer principal rays are segmented, but do not divide. The inner rays branch progressively earlier toward the centre of the tail. As the rays

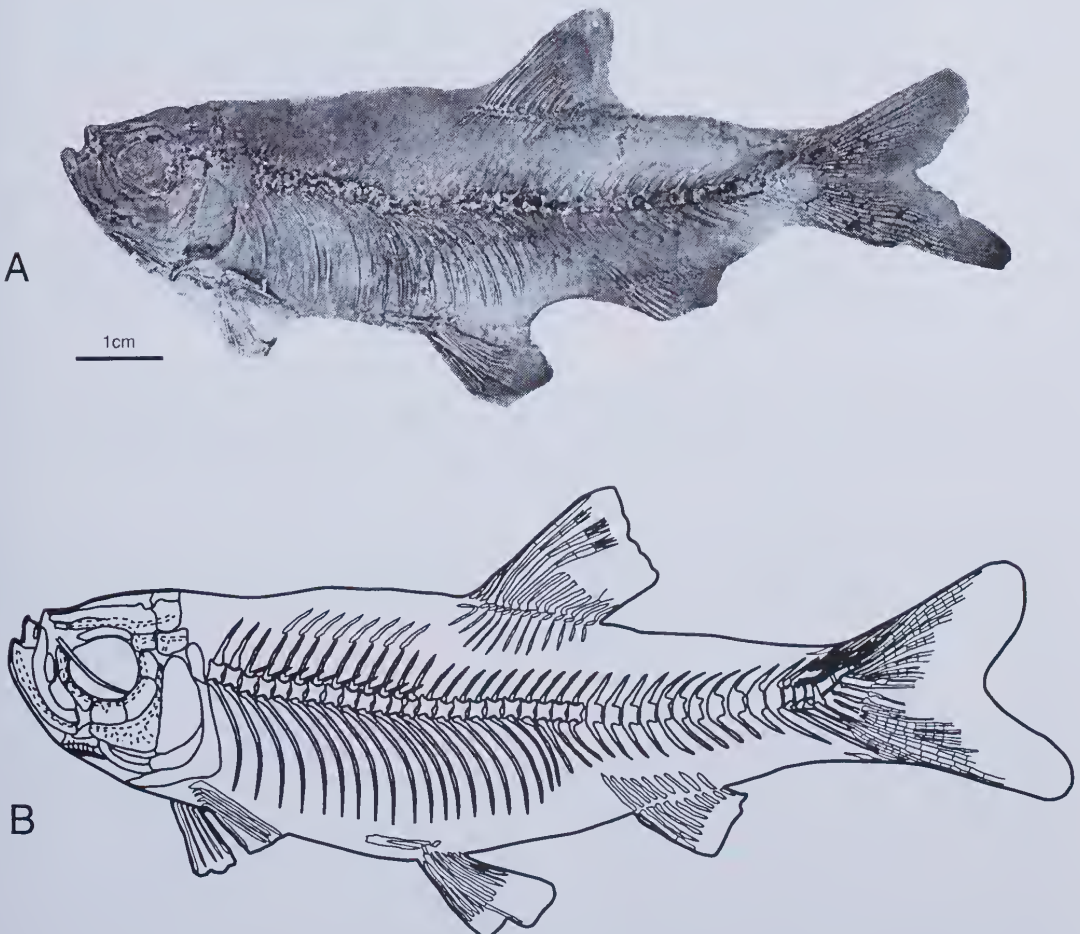


Figure 11 *Cavenderichthys talbragarensis*. A, F4133 used for the reconstruction of the skeleton of the whole fish in B.

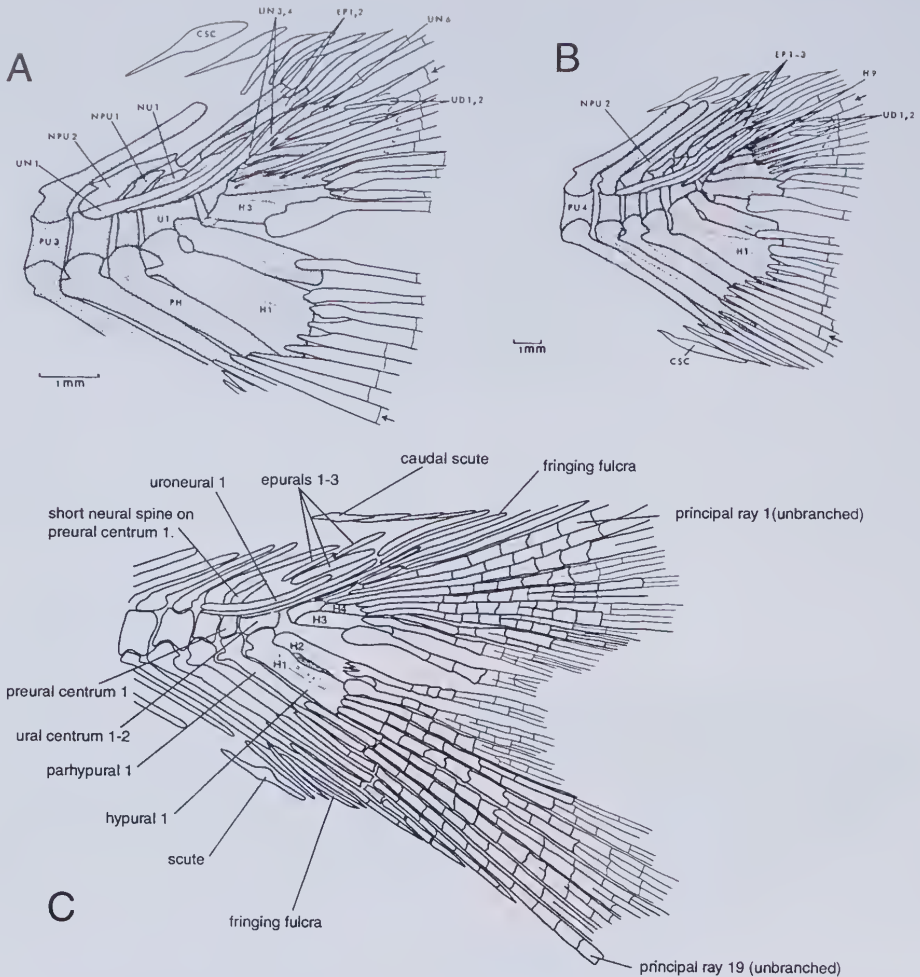


Figure 12 *Cavenderichthys talbragarens*. Comparison of reconstructions of the caudal skeleton. A, Patterson and Rosen (1977) figure 46 reconstructed from BMNH P37973. B, Patterson and Rosen (1977) figure 46 reconstructed from BMNH P12439. C, my reconstruction of MMF13561a, showing species defining similarities, but some small inter-species variation.

branch they become more and more delicate, so the complete fin is preserved in relatively few specimens. They branch up to four times, such that the middle section of the tail, where branching occurs early, is very thin, delicate and flexible. The principal rays articulate with the hypurals in the upper section, and in the lower section PR 19 articulates with pre-hypural haemal spine 2 (parhypurals), PRs 18 and 17 articulate with pre-hypural haemal spine 1, then PRs 16, 15, 14, 13 and 12 articulate with hypural 1-2 (combined unit), and PR 11 articulates with hypural 3. The proximal ends of several PRs are broad where they articulate with the hypurals, e.g., on MMF36746 (Figure 14A) the ends of PRs 8, 9 and 10 are enlarged. In contrast, the proximal ends of PRs 1-6 taper to a point.

The neural spines on the preural centra are narrower than the haemal spines. They also become progressively shorter posteriorly. The neural spines on preural centra 2, 3 and 4 bend back strongly, and they overlie the short neural spine on preural centrum 1.

There are three epurals, rarely four, which extend from the ends of the long neural spines to the bottom of the basal fulcra, covering the dorsal surface between the caudal scute and the first principal ray (Figure 12C and MMF36773, Figure 13B).

Dorsal to the epurals lie the epaxial basal fulcra (MMF36773, Figure 13B), usually about six, which form a series with the three procurrent rays between the principal rays and the anterior caudal scute. Sometimes it is not easy to distinguish

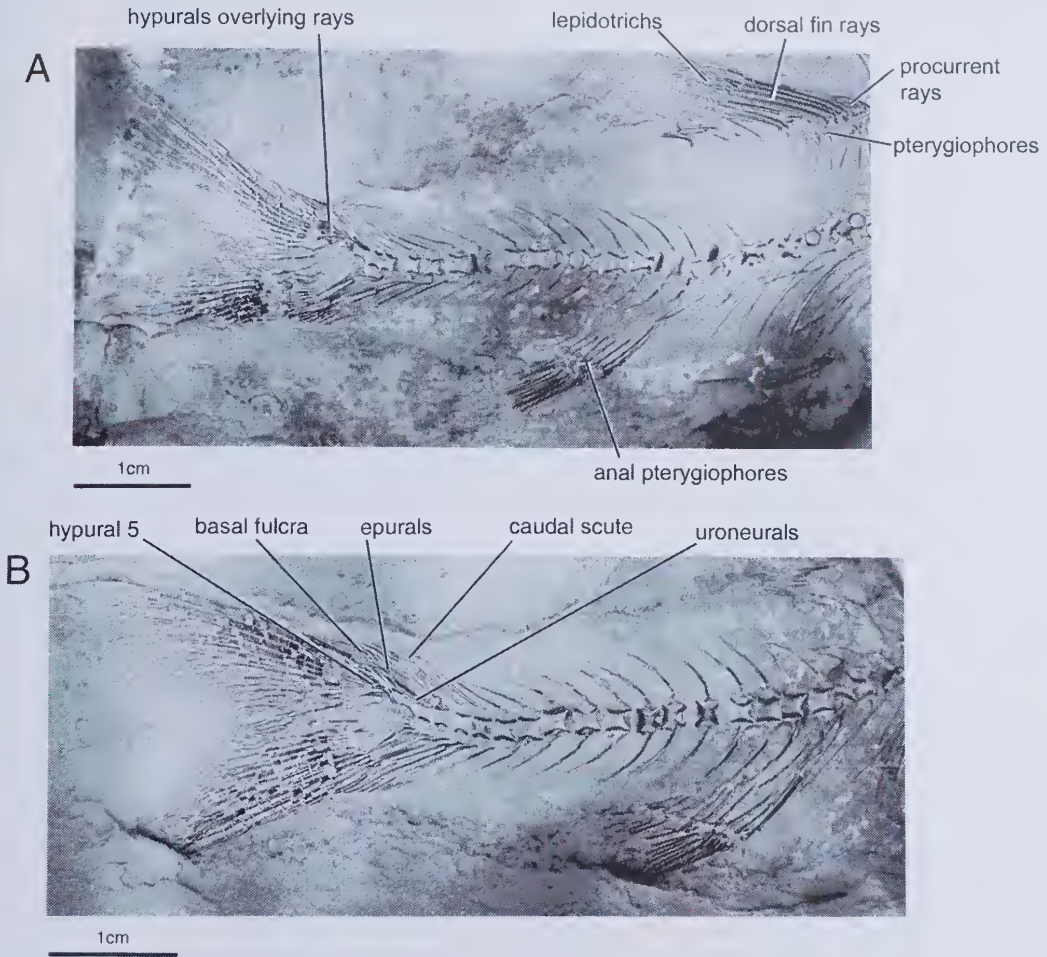


Figure 13 *Cavenderichthys talbragarensis*. Photographs of the original specimens showing the layered nature of the caudal skeleton. Peels were not made due to the risk of destroying some of the delicate overlying structures, especially where the hypurals overlie the rays. A, MMF36718. B, MMF36773.

between the basal fulcra and the unsegmented procurrent rays. There are also several ventral basal fulcra.

The caudal scute marks the junction between the dorsal surface of the fish and its tail (Figure 12C and MMF36773, Figure 13B). It is similar in size to the six dorsal basal fulcra, but slightly sinuous in shape, and broader. The ventral caudal scute is similarly a sinuously shaped bone.

Generally there are three uroneurals that lie down either side of the ural centra. They act as bracing for the thinning end of the vertebral column. They project anteriorly beyond ural centrum 1 and overlap preural centrum 1 and 2, effectively crossing the “chondrostea hinge”. Usually one, sometimes two more, short uroneurals project backwards from the posterior of ural centrum 1–2.

These five uroneurals make a functional continuous series from the epurals through uroneurals to the principal rays in the upper lobe. These can be seen on MMF36773 (Figure 13B), MMF36746 (Figure 14A), MMF36732a (Figure 15B), and ANU54975 (Figure 15A).

There are seven hypurals (MMF13561a, Figure 12C). The lowest two hypurals articulate with the first ural centrum 1–2. They often appear to be fused. Hypural 3, which articulates with ural centrum 3, carries the inner rays of the upper lobe, i.e. principal rays 8, 9, and 10. These rays often have thickened ends where they attach to the hypural. This probably gives strength to the fragile but flexible inner rays. In most cases the upper four, or possibly five, hypurals are covered by the overlapping ends of the upper principal rays.

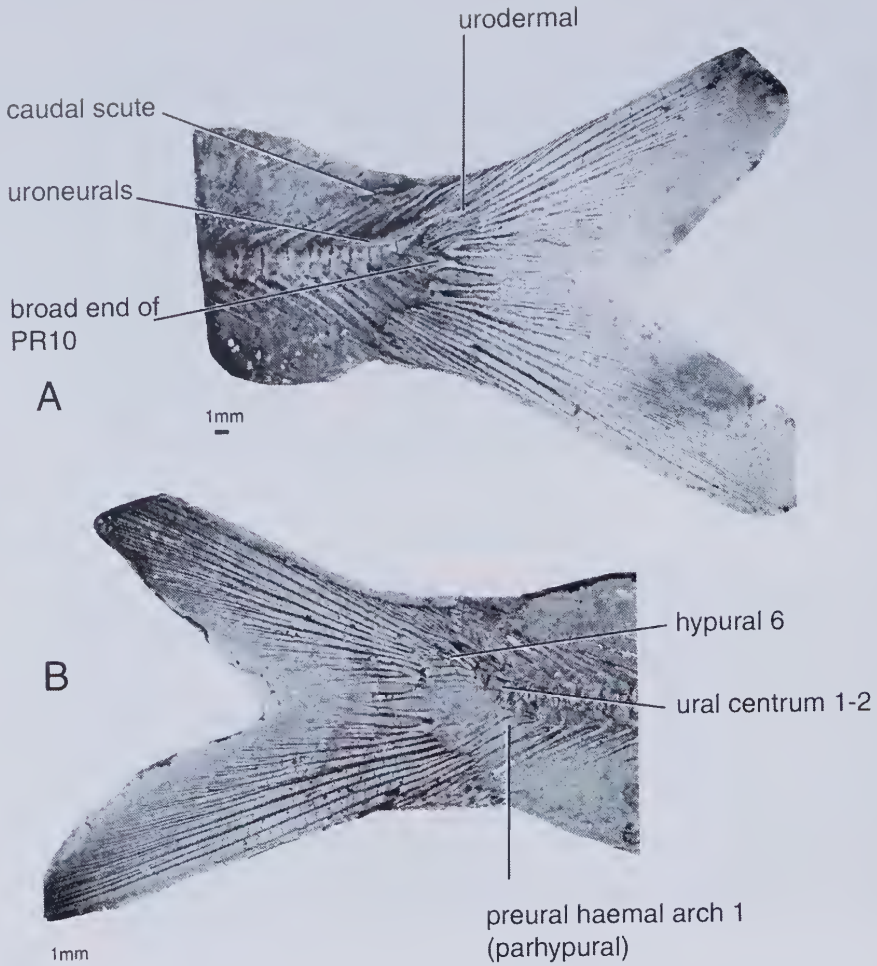


Figure 14 *Cavenderichthys talbragarensis*. These photographs of peels support the caudal skeleton reconstruction in Figure 12 C. A, MMF36746. B, MMF36748.

Urodermal bones are not generally preserved. However in three specimens, AMF4133, MMF13569 and ANU54975 (Figure 15A), there appear to be two small fine bones that are not part of the segmented principal rays in the dorsal part of the fin. They overlap two principal rays, either 2 and 3 or 3 and 4, and may provide extra bracing at the end of the vertebral column. According to Cavender (1970), "they are clearly ossifications at the distal ends of two of the tendons that originate from the superficial epaxial muscle mass in the caudal region and which insert proximally on the dorsal edges of the first and second branched rays respectively." Maybe they are not always ossified, or possibly they are not always preserved because they lie outside the general caudal fin structure (see also MMF36746, Figure 14A).

Median fins

The dorsal fin is positioned over the mid point of the body, see AMF27069 (Figure 10B), MMAMF4133, ANU54946 and MMF36743. The anterior margin of the dorsal fin is about level with the mid-point of the vertebral column. The posterior margin is level with the anterior margin of the anal fin. The length of the fin, measured along the line of the articulation, is 10–12mm. This position in the mid-portion of the fish indicates a role as keel (Gosline 1971).

The dorsal fin consists of 12 to 15 rays, the anterior three being short procurent rays that do not branch, the first principal ray being full length and unbranched, and the rest being full-length rays that branch into lepidotrichs about halfway along their length. The rays are supported by internal

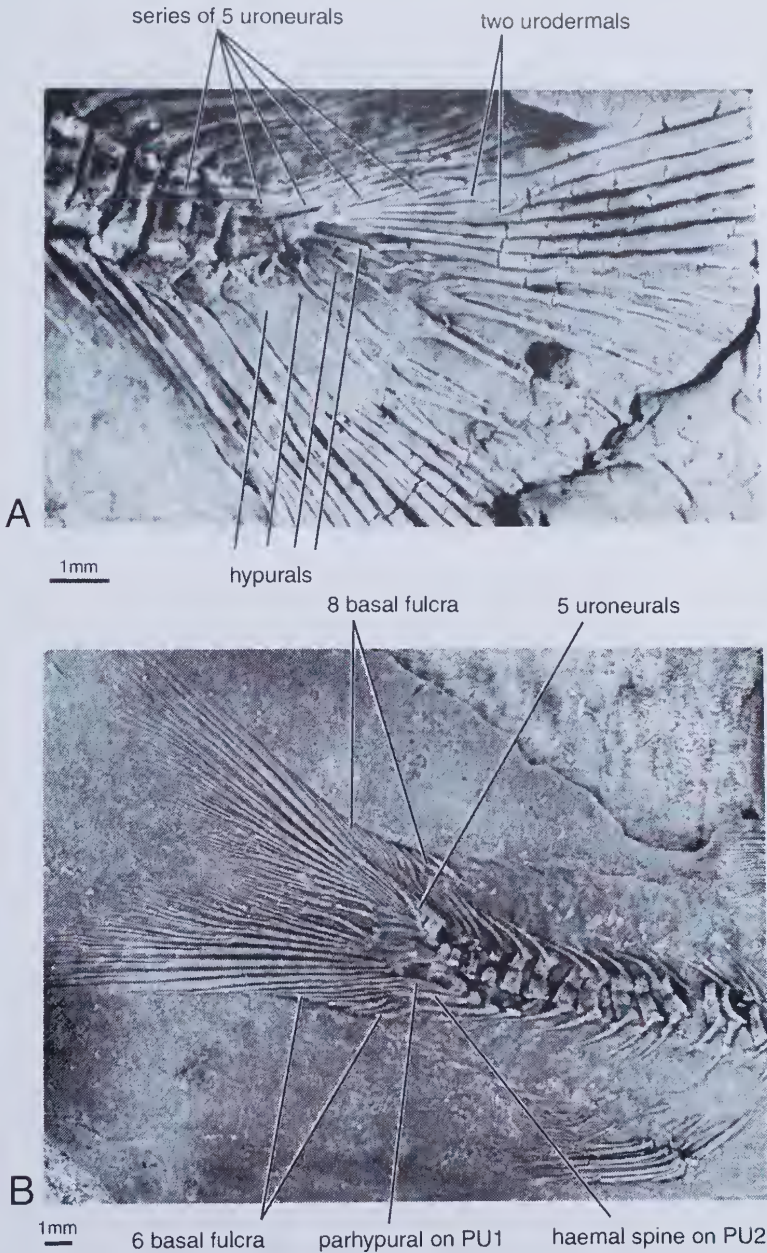


Figure 15 *Cavenderichthys talbragarensis*. A, the peel of ANU54975 shows two urodermals and the series of uroneurals. B, on MMF36732a the dorsal and ventral basal fulcra are clearly preserved.

bones called pterygiophores (MMF36718, Figure 13A), also called radials, which are described by Norden (1961) as being "composed of 3 segments, a small, rounded distal bone, a short, horizontal middle bone and a long, pointed proximal bone." It is possible to see both the proximal and horizontal pterygiophores in AMF27069 (Figure 10B). The anterior proximal pterygiophore points forward, lying at an acute angle to the dorsal surface, and is

forked. It supports the anterior procurent rays. The pterygiophores supporting the middle of the fin are perpendicular to the dorsal surface. They are fine, pointed rods, but they broaden dorsally where they articulate with the horizontal elements. The pterygiophores are single structures, which appear in the mid-line, dorsal to the neural arches.

The fin rays of the dorsal fin, like the pterygiophores, are fine, emerging from the broader

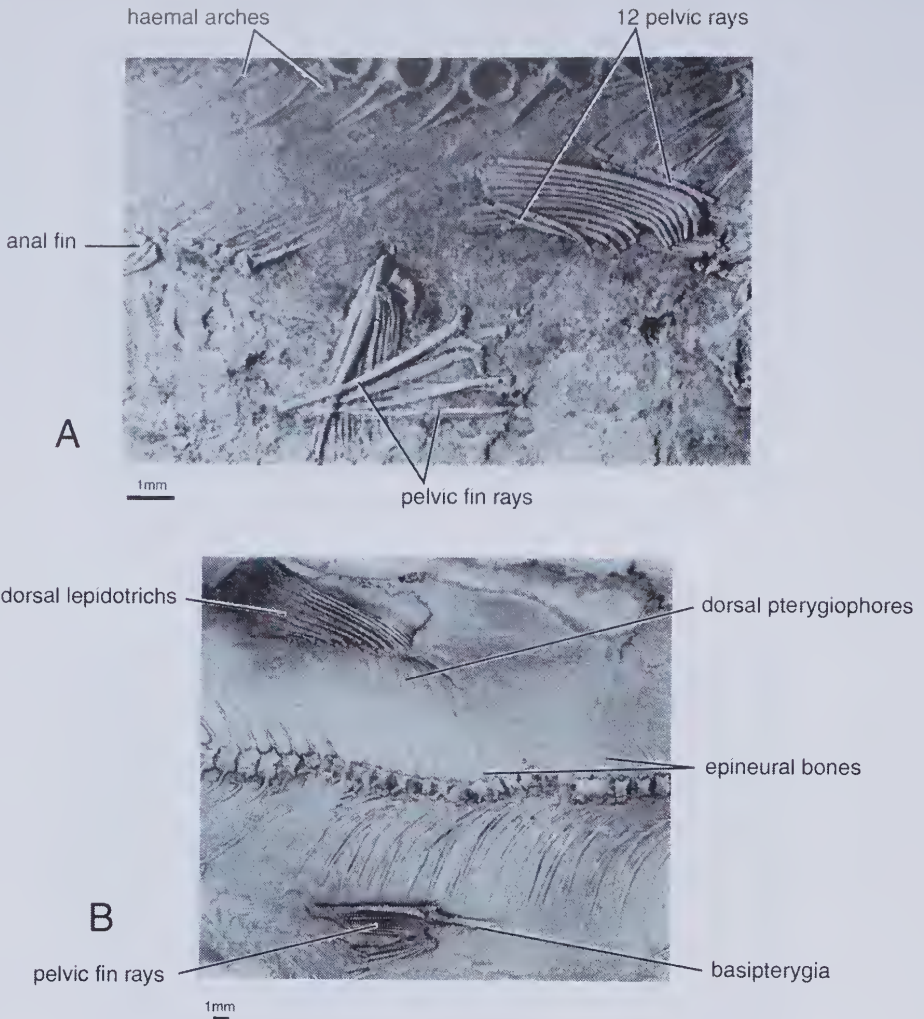


Figure 16 *Cavenderichthys talbragarens*. Pelvic fins. A, in this detail of ANU54970 12 pelvic fin rays can be seen, and the structure of the hemal arches. B, on MMF36743b the pelvic fin is in situ, directly under the position of the dorsal fin.

ball-like articulating surface that fits over the middle horizontal pterygiophore. They are composed of two half cylinders which are held tightly together along their length. The rays gradually expand slightly along their length until they bifurcate about half way along the total length of the fin. Beyond this bifurcation, the lepidotrichs are jointed, and bifurcate once more, so that at the back of the fin there are four lepidotrichs for every ray.

The anal fin is located half way between the pelvic fins and the caudal fin, see Figure 11A and B and MMF36737, MMF36743b (unfigured). Its anterior margin is level with the posterior margin of the dorsal fin. It is always supported by nine pterygiophores, or radials, which are single bones.

They are narrow bones that broaden toward the proximal end. The ten anal fin rays are paired bones that broaden where they articulate with the pterygiophores. With the exception of PR1, which is unbranched, the principal rays also branch into lepidotrichs, which are sometimes preserved, resulting in four lepidotrichs for every original ray. A short unbranched ray is at the anterior margin of the anal fin.

Pectoral girdle

The post-temporal is often not preserved. It has been seen as a squarish bone that comprises the area between the extrascapulars and the scales (Figure 7A). It carries the lateral line canal onto the head,

and in F51799 (not figured) it appears to have a canal running diagonally across the bone. The bone is posterior to the extrascapulars, and dorsal to the supracleithrum.

The supracleithrum is the dorsal bone of the pectoral girdle (Figure 6A). It is a narrow bone that, when fossilized, crosses the position where the vertebral column emerges from the back of the braincase. The dorsal margin is rounded, while the ventral margin abuts or slightly overlaps the top of the cleithrum.

The cleithrum (Figures 6A, 10A) is the largest bone of the pectoral girdle. It extends from just below the level of the vertebral column in a curve, to end at the level of the branchiostegal rays. The bone is quite deep, having a strong ridge on the external surface. The bottom of the operculum and suboperculum are sometimes crushed over the cleithrum, making a deep hollow and a high ridge at the postero-ventral margin of the head.

In the 25 specimens examined for the pectoral girdle no bone could be described as a post-cleithrum.

The scapula is a short stout bone that articulates with the coracoid anteriorly and with the first principal ray of the pectoral fin posteriorly. It is often covered by the ventral margin of the cleithrum.

The coracoid occurs at the antero-ventral margin of the cleithrum. It appears to be a flattish bone, slightly pointed anteriorly and broader posteriorly, which articulates with the cleithrum and the scapula. The articulation with the cleithrum has not been observed clearly, although the coracoid bone is always adjacent to the cleithrum. The articulation with the scapula can be seen in specimen ANU54940 (not figured).

Pectoral fins

There are 12 rays in each of the pectoral fins (Figures 6A, 7B, 8B, 10A). The first ray is more robust than the others and has a broad head that articulates directly with the scapula. The other 11 rays are bent over nearly at right angles at the proximal ends where they form delicate points to enable them to articulate with the three radials. The radials are two or three short straight rods that start near the scapula and extend just far enough to allow the rays to articulate with them. The direction of the radials is the same as the direction of the rays, which explains why the rays have to turn at right angles to be able to attach to the radials. The radials are visible in specimen MMF36758a, but are generally not preserved. The rays themselves are unsegmented for about half their length, after which they become segmented then divide into lepidotrichs. The two pectoral fins originate very close together on the ventral margin of the body, just behind the head. This position is much lower

than some more recent fish, but is similar to other leptolepids.

Pelvic girdle

Norden (1961) described the basipterygia as "a pair of triangular endochondral bones which form the pelvic girdle." In *Cavenderichthys talbragarensis*, each basipterygium seems to widen posteriorly where it articulates with the rays of the pelvic fins (Figure 16B).

Each pelvic fin has 12 rays (Figure 16A). They also turn around at right angles at the proximal end. The rays are unsegmented for the first half of their length, then they become segmented and also divide into lepidotrichs.

Scales are cycloid with concentric growth rings. They are generally only visible near dorsal and ventral body margins, their delicate nature, combined with the well ossified spinal structures, leading to their poor preservation.

DISCUSSION

The early work

Woodward (1895) classified the most common fish in the Talbragar assemblage as a member of the Family Leptolepididae, genus *Leptolepis*. He noted its general characteristics, but commented that no detailed osteological synopsis had been published for the genus. He described many of the features already listed in this paper, such as the narrow roof of skull between the eyes, the wavy suture separating the frontals, the small parietals, the minute premaxilla, and the two elongated supramaxillary bones. He did say that the sclerotic ring is ossified, but this has only been observed in ANU54956 (Figure 2A) and MMF13555 (Figure 2B). In the majority of specimens there is no evidence for a sclerotic ring. He did not describe a gular plate, but it has been now observed in 20 specimens. When describing the ceratohyal he said it has "the ordinary hour-glass form, but is noteworthy for the extension of a supplementary, delicate, straight rod of bone between its extremities on the upper side." (Woodward 1895: 20) This comment is very similar to the description in this paper, and less aligned with the comment by Arratia that the ceratohyal is always fenestrate (Arratia 1997: 19).

Woodward (1895) also described three species of *Leptolepis*: *L. talbragarensis*, *L. lowei* and *L. gregarius*. *Leptolepis talbragarensis* is by far the most common species. Wade (1941:83) wrote "Previously three species have been ascribed to the genus from this locality, but in the view of the uniformity of the structure of the head the writer is convinced that only one species, *Leptolepis talbragarensis*, need be recognised, the specific differences previously relied on being due to individual peculiarities or

mode of preservation or differences in maturity." Further examination during the current study of the bones of *L. gregarius* demonstrates it is just a schooling, juvenile form of *talbragarensis*. Woodward describes *L. gregarius* as having a different proportion of the head, and the anal fin being slightly more anterior, but these characteristics are not supported by a statistical analysis of the dimensions. The two specimens called *L. lowei* are slightly more elongated in the head region than *L. talbragarensis*, but the rest of the skeleton, including the tail, is the same as *talbragarensis*. It is here considered that they belong to the same species, but are differently preserved.

Wade (1941) did not add any detail to the description of *Leptolepis talbragarensis*, but he did reclassify the other genera present in the assemblage. Cavender (1970) used *Leptolepis? talbragarensis* as an example of an early teleost and compared it with genera from the coregonines and other salmonids. His description of *L? talbragarensis* is quite detailed and it has been the reference description for subsequent workers including Arratia (1997), but it formed part of a comparison and was not a systematic description.

Nybelin (1974) reassessed the classification of *L. talbragarensis* noting that it possesses some characteristics "unfamiliar in the true leptolepids. The deep body and the configuration of the head with its short snout are rather unlike the leptolepids. The anterior part of the frontal, anterior to the exit of the supraorbital sensory canal, is strikingly short, much shorter than in the leptolepids, and seemingly ending at the same level as the nasal." (Nybelin 1974: 170) The description of the body as deep is very imprecise, and when compared with truly deep-bodied fish such as *Aethiolepis mirabilis* it is seen as being totally inappropriate. Both Arratia (1997) and Cavender (1970) continued the pattern of describing *Cavenderichthys talbragarensis* as deep bodied, but such a description is misleading, as even the adults are fusiform. The vast majority of examples are small, thin, fusiform fish, with the dorsal and ventral margins being approximately parallel. The fish has a short snout with a protruding lower jaw, a centrally placed short dorsal fin, pectoral fins that are placed low, a centrally placed low pair of pelvic fins, short anal fin positioned just posterior to level of dorsal fin, and a delicate, symmetrical, bifurcated tail.

Nybelin (1974) considered the most significant osteological features of the true leptolepids are the presence of a preopercular process on the hyomandibular and the notch in the ascending anterior margin of the dentary. Neither he nor Cavender (1970) saw these features on *L. talbragarensis*. Nybelin (1974) considered that the most significant difference between *L. talbragarensis*

and the true leptolepids is in the sensory canal system – few branches from the infraorbital sensory canal, and the 6 branches on the preopercular canal is smaller than the number of branches in other leptolepids. There are similarities between *L. talbragarensis* and *Leptolepides sprattiformis*, but the differences in the caudal skeleton were considered to be the most striking difference. "The presence of four epurals, only a single neural arch on U1, all uroneurals mutually free, and two urodermals, separate *talbragarensis* and *sprattiformis* to such a degree that a close relationship between them seems definitely excluded." (Nybelin 1974: 171) Thus the species "*L.*" *talbragarensis* was removed from the family Leptolepididae.

Points of Contention in Understanding the Morphology

The illustrations of *Cavenderichthys talbragarensis* by Arratia (1997) are refinements of those published by Cavender (1970), and I agree with the changes she has made to his description by including a gular plate and an interoperculum. Arratia maintained the pattern developed by Nybelin (1974) and endorsed by Patterson (Patterson and Rosen 1977) of there being no connection between the suborbital canal and the supraorbital canal (*contra* Cavender 1970). This interpretation is disputed for several reasons. Firstly, this part of the skull is notoriously poorly preserved, and few specimens show clear identification of the dermosphenotic. Secondly, the branch of the supraorbital canal that heads ventrally on the frontal seems to be headed directly for the position where the dermosphenotic ought to be in most specimens. Thirdly, in modern teleosts the connection between the supraorbital canal and the suborbital canal is the normal condition. In no specimen in which both canals are visible, are they *not* connected.

Arratia (1997) stated that the ceratohyal is always fenestrate, whereas many specimens studied herein show no sign of a connection between the dorsal projections of the ends of the ceratohyal, neither bone nor cartilage. However, there are also several examples showing evidence of such a connection, such as ANU 54980 and ANU 54976, which have an incomplete link across the dorsal margin of the bone. Thus I presume it is possible for this bone to be fenestrate, as is the common condition in related species, but it is definitely not present in all samples.

Observations of the hyomandibular and the dentary in the dorso-ventrally flattened specimen (MMF13734a) suggest that *C. talbragarensis* does have a preopercular process on the hyomandibular and also has a significant dent on the rising anterior surface of the dentary that corresponds with the

leptolepid notch. The lack of these two characters has been considered significant by other workers, and led Nybelin (1974) to argue that *C. talbragarensis* could not be a member of the family Leptolepididae. The absence of a suborbital bone, which is present in the genus *Leptolepis* but not in later leptolepids, is here considered more significant than the absence of a small process on one bone. On the basis that it has been found that *Cavenderichthys talbragarensis* does have these characteristics, it is now felt that it should be included in the family Leptolepididae.

Description of the caudal skeleton largely agrees with the illustrations provided by Arratia. She showed the intra-species variation in the number of epurals (three and four), and uroneurals (six and seven), but the eighth hypural is doubtful (only seven hypurals have been observed in this study).

The dorsal fin has a range of the number of fin rays and pterygiophores. Considering fin rays, five specimens have 10 principal rays, four have 11, six have 12, and one has 13. Considering pterygiophores, one has 10, one has 11, twelve have 12, and two have 13. Many specimens do not have all rays readily visible. Arratia's diagnosis of *Cavenderichthys* noted 15 dorsal rays, corresponding to 12 principal rays plus three unsegmented rays. This is certainly the most common case in my specimens, but not the only possibility.

The numbers of rays in the fins agree with other descriptions, but wide variation is found in the number of vertebrae (range 34 to 45 centra,

excluding the last two ural centra). The number of vertebrae is not related to the length of the specimen, but it is closely related to the number of pairs of ribs. Thus there is variation both within the abdominal vertebrae and the precaudal vertebrae.

An analysis was made of the structure of the dorsal fin. The angle of elevation of the dorsal fins can vary from 70° to 15°, without any sign of disarticulation or destruction of the joints. Of 43 specimens for which dorsal fins were measured, three had an angle of elevation of >60°, 25 were between 60° and 30°, while 15 were collapsed to less than 30°. This indicates that the fin could be collapsed when travelling fast, and raised like a keel when cornering. According to Gosline (1971) this is a characteristic of teleosts, that "the whole fin can be raised or lowered, more or less like a partially collapsible fan. The soft rays may also be swung from side to side by the contraction of muscles attached to the base." (Gosline 1971: 23). The size of the fin is comparatively small and takes up less than 1/5 the total length of the fish.

Arratia (1997: 19) argued that *C. talbragarensis* is a "deep-bodied" fish. In order to test this, measurements were made of its depth to establish the ratio of depth to length. The ratio of the average depth to average length is about 1:4.8. The results are summarised in the following graph (Figure 17). The straight-line relationship between length and depth suggests that it is determined only by the stage of growth. The graph is based on data from 86 specimens. The regression equation is $y = 0.25x - 0.3$.

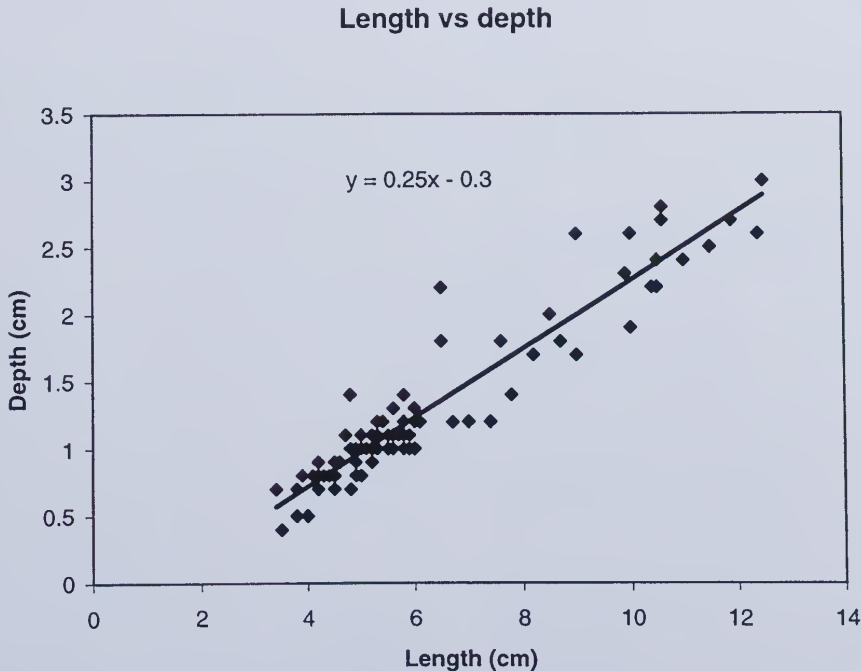


Figure 17 Graph of relationship between length and depth.

The concentration of data in the lower left hand corner represents the large number of small specimens collected on the slabs representing the mass kill. The smaller number of larger fish is due to at least two factors. Firstly fewer individuals survive to be fossilised in their maturity. These individuals occur singularly rather than on mass kill slabs. The other factor is related to the habits of collectors. Large, well-preserved specimens are well regarded in collections, so isolated examples of medium sized fish may be overlooked when faced with the prolific numbers of small individuals on large slabs, and the few excellent large specimens. Thus the distribution on the graph does not necessarily represent the natural distribution in the population.

Comparisons between *Cavenderichthys* and *Leptolepis*

The Head

The type species of *Leptolepis*, which is *Leptolepis coryphaenoides*, and *L. normandica* described by Nybelin (1974), have several significant differences from *C. talbragarensis*, as well as the obvious similarities (see Figure 18). The head of *C. talbragarensis* is shorter than *L. normandica* and *L. coryphaenoides*. Nybelin (1974) suggested that this might be due to the shortness of the frontal bones, but Nybelin's figures 1 and 4 (Figure 18A, 18B) show the rostral is the bone that is significantly shorter in *C. talbragarensis*. Also in these text figures there is a large gap behind the upper jaw, resulting from the large size of the infraorbital 3 bone, which in both *L. coryphaenoides* and *L. normandica* is considerably wider than the other bones in the infraorbital series. In *C. talbragarensis* the posterior infraorbitals are all about the same width, allowing the preopercular to come closer to the orbit. This arrangement is very similar to *Tharsis dubius*, an Upper Jurassic (Kimmeridgian) member of the Family Leptolepididae (Figure 18D). The other significant difference is that *C. talbragarensis* lacks a suborbital bone between the infraorbital series and the preoperculum, and once again this is a point of similarity with *T. dubius*. This is also tied in with the consistent width of the posterior infraorbital bones, leading to an overall shortening of the head in comparison with *L. normandica*. In *C. talbragarensis* the size of the orbit is relatively large, which means that the dermal bones occupy a restricted space, even if the underlying structures of the braincase are very similar in size to other species.

Nybelin (1974) placed a great deal of emphasis for classification on the sensory canal systems, especially on the preoperculum and the infraorbital series. *C. talbragarensis* certainly has fewer branches on both these canal systems. Considering the preopercular canal, *C. talbragarensis* has a maximum

of six undivided branches of this canal. This is far less than *L. coryphaenoides* (19), and less than *L. normandica* (10), but quite similar to *Leptolepides sprattiformis* (5). The latter (Figure 18C) also has a very similar jaw arrangement to *C. talbragarensis*. The suborbital canal system on *C. talbragarensis* has very few branches, possibly a few on the lachrymal, definitely one on the infraorbital, but none or very few on the postorbitals. This is very different to *L. coryphaenoides*, but quite similar to *Leptolepides sprattiformis*.

The supraorbital sensory canal in *C. talbragarensis* also has very few branches. However, Nybelin's (1974) figures 1B and 4B show that on *L. coryphaenoides* and *C. talbragarensis* (Figure 18A, 18B) the presence of pores along the canal is similar. There may be more pores present on *C. talbragarensis* than figured herein, but they are not always consistently placed. The back of the skull is not included in the diagram because it has not been possible to clarify the arrangement of extrascapulars and suprascapulars due to poor preservation. The presence of a branch in the supraorbital canal just above the position of the dermosphenotic is likely since the posterior branch of the canal terminates in the parietal, as shown by Nybelin (1974), and thus the ventrally directed branch should be connected to the infraorbital canal on the dermosphenotic. This is the logical connection, as the lateral line canal system has to be interlinked, and it is the general situation in similar extant forms. Possibly there is no connection between these canals in members of the Leptolepididae, as figured by Nybelin (1974), or possibly it is present but has just not been observed or described.

Comparison of the text-figures from Nybelin (1974) and those from Patterson and Rosen (1977) with the new reconstruction of the head of *C. talbragarensis* indicates that the parasphenoid is a valid point of comparison. Nybelin did not draw the parasphenoid on either *L. normandica* or *L. coryphaenoides* (his figures 1 and 4), however the photographs in his plate 2 figure 2 and plate 4 figure 2 (*L. normandica*) and plate 6 figure 1, plate 7 figure 1 and plate 9 figure 4 (*L. coryphaenoides*) the parasphenoid is quite clearly visible. This omission in the drawings may have led to some confusion because Patterson and Rosen (1977) have included the parasphenoid in diagrams of *Leptolepides sprattiformis* and *Tharsis dubius*. It is certainly an obvious characteristic of *C. talbragarensis* as it bisects the orbit, thus comparing very closely with these other species.

The operculum in *C. talbragarensis* is narrower at the top with its anterior and posterior margins diverging ventrally to form an approximately triangular shape, whereas in *L. coryphaenoides* the anterior and posterior margins are almost parallel.

The skull roof is another region that requires

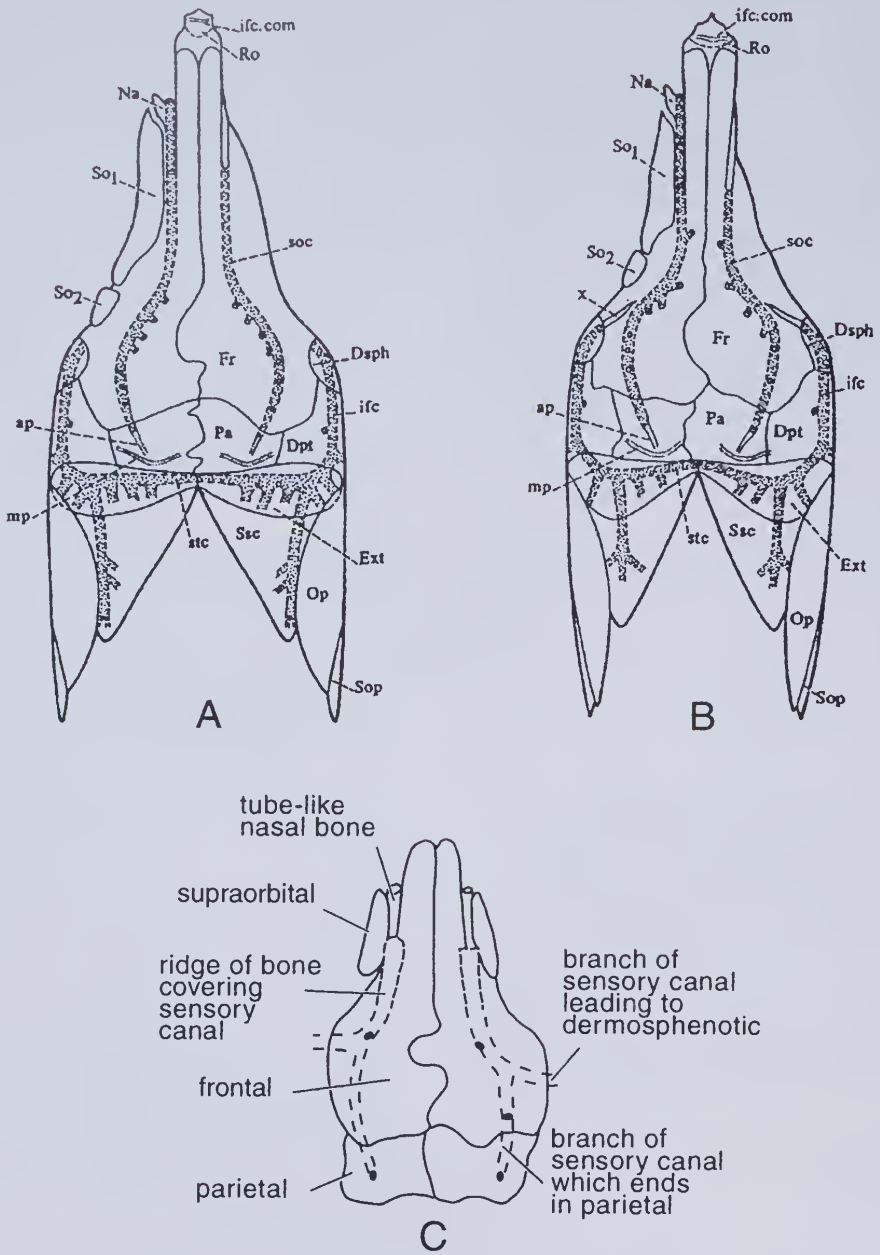


Figure 19 Comparative reconstructions of skull roof. A, *Leptolepis coryphaenoides* from Nybelin (1974, figure 4B). B, *Leptolepis normandica* from Nybelin (1974, figure 1B). C, *Cavenderichthys talbragarensis*, reconstruction based on MMF13564 and MMF36728.

comparison. Neither Woodward (1895) nor Cavender (1970) mention the existence of nasal bones on *C. talbragarensis*, but they are preserved on several of the studied specimens. The nasal bone provides a protective tube for the sensory canal as it leaves the frontal bone. In *C. talbragarensis* there is often a quite prominent protective ridge on the

frontal, above the supraorbital, covering the sensory canal. When this ridge is destroyed during preservation the canal appears as a deep groove. Just behind this covering ridge is a large pore marking the position of the canal. Beyond this pore the canal curves ventrally, sending a branch onwards towards the parietal. It seems to end at the

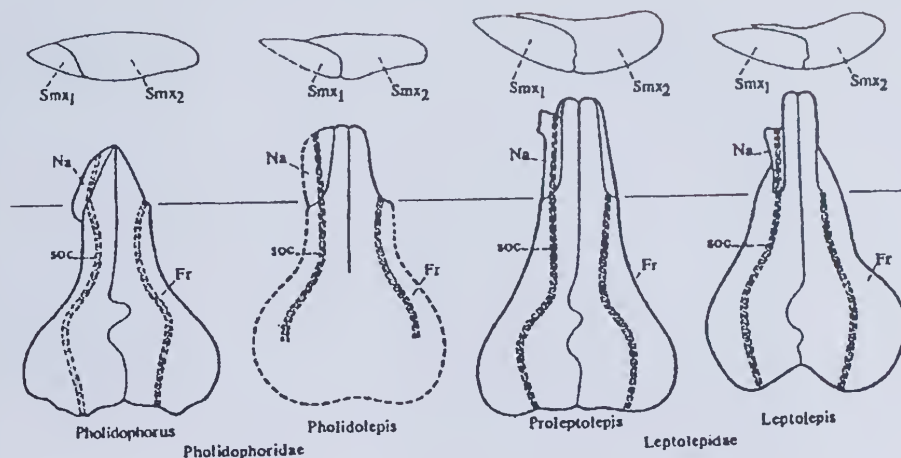


Figure 20 Nybelin (1974, figure 37). Comparison of skull roofs, illustrating the difference between families Pholidophoridae *s. str.* and Leptolepidae *s. str.*, exemplified by differences in relative size of the two supramaxillae and by the nasal relation to the anterior end of the frontal. This figure shows Nybelin's ideas about evolutionary trends in the form of the skull roof. *Cavenderichthys talbragarensis* would fit on the right hand end of this series.

back of the parietal where it surfaces through a pore. The branch of the canal heading in a ventral direction passes into the dermosphenotic. Cavender also noted this connection and went on to comment; "This is a significant point of difference in the cephalic sensory system of *C. talbragarensis*, since the junction of the infraorbital and supraorbital canals is known to be absent in *Leptolepis* (Patterson 1967)." (Cavender 1970: 15)

Another bone of contention is the hyomandibular. Woodward (1895) did not mention it, but Cavender (1970) describes the bone in *C. talbragarensis* in medial aspect. "The upper portion is expanded into a single broad, articulating head that shows a very slight emargination toward the middle of the dorsal margin. The basal half of the opercular arm is partially differentiated from the expanded portion of the hyomandibular and produces a convex posterior margin. The distal (condylar) part of the opercular arm is not ossified. A large opening is visible near the centre of the expanded portion, which is the foramen for the hyomandibular trunk of the VII nerve. The ventral portion of the hyomandibular is constructed like a slender pillar." (Cavender 1970: 21)

He went on to say that he did *not* find "an anterior laminar expansion from the upper part of the hyomandibular which contacts the metapterygoid, or an adductor ridge along the postero-lateral margin where it contacts the vertical limb of the preopercle." (Cavender 1970: 21) Basing her diagnosis on her own observations and Cavender's description, Arratia (1997) described a "hyomandibular without preopercular process, but

with a well developed levator arcus palatini crest" (Arratia 1997: 19). The latter feature has not been observed by the author. It is found that this bone is generally hidden in *C. talbragarensis*. On seeing the dorso-ventrally flattened specimen (MMF13734a) in the NSW Geological Survey collection it became possible to interpret their descriptions. Nybelin's (1974, figure 3) is very instructive (Figures 9C-E).

It seems clear from these comparisons that *C. talbragarensis* does indeed have a preopercular process on the hyomandibular, that it is not pointed as in the *Leptolepis* specimens, but that it is obviously serving the same function. The articulation with the preoperculum will cause that bone to be involved when the gill covering is opened. This occurs when the lower jaw is depressed and the opercular series (operculum, suboperculum and interoperculum) are rotated dorsally (Lauder 1982).

The same dorso-ventrally flattened specimen that shows the hyomandibular (MMF13734a) also exposes two complete lower jaws (Figure 21). They can be seen to have a deep, wide dent on the ascending portion of the anterior margin. This dent is not as constricted as the leptolepid notch shown in Nybelin (1974, plate 5, figure 9) for *L. normandica*, but it occurs in the same position. In many of his plates, dentaries are shown that do not exhibit a leptolepid notch, but Nybelin's (1974, plate 14, figure 2), *Proleptolepis furcata* shows a dentary with a notch in the same place as in *C. talbragarensis*. His description stated "a detached dentary of *Proleptolepis* sp. shows, however, a rather deep notch in its ascending anterior margin

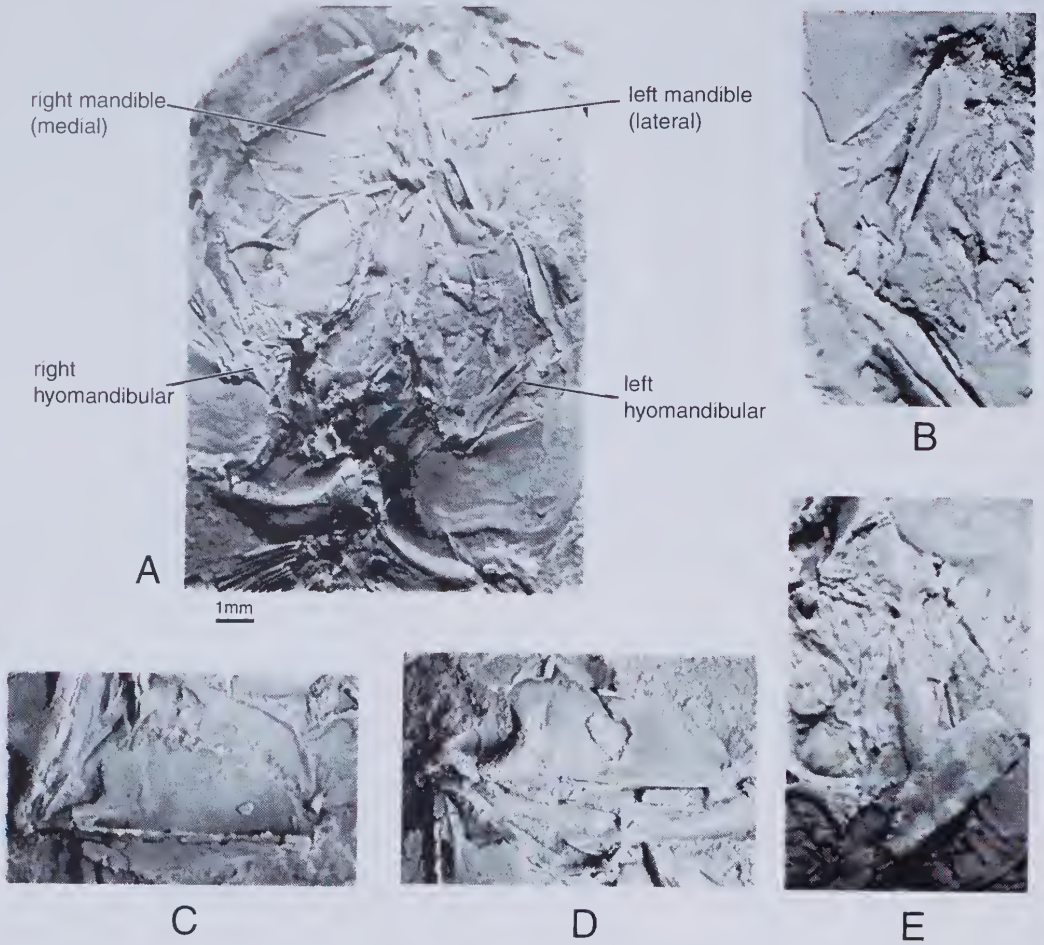


Figure 21 *Cavenderichthys talbragarens*. Dorsally flattened head of MMF13734a. A, ventral view of flattened head. B, medial view of left hyomandibular. C, medial view of right mandible. D, lateral view of right mandible. E, lateral view of right hyomandibular.

and a similar notch is obviously present in the holotype." (Nybelin 1974). This confirms that the notch in the dentary of *C. talbragarens* is equivalent to a leptolepid notch.

The Caudal Skeleton

A caudal reconstruction (Figure 12C) corresponds closely with those of Patterson and Rosen (1977, figures 12A, 12B). The condition of the caudal skeletons of *L. normandica* and *L. coryphaenoides* is not clear, as there were not any well-preserved specimens for Nybelin to describe. However, Patterson and Rosen (1977, figure 22A) figured the caudal skeleton of *L. coryphaenoides*. This shows a caudal fin with three epurals, seven uroneurals, and short neural spines on both preural centra 1 and 2. It looks more similar to *C. talbragarens* than the caudal region of *Tharsis dubius* (Patterson and

Rosen 1977, figure 22B), despite the numbers of bones being the same in *T. dubius* and *C. talbragarens*. The other "leptolepid" with a similar caudal arrangement is *Leptolepides sprattiformis*, with three epurals, five uroneurals, seven hypurals and one urodermal, see Figure 22C.

Patterson was also able to examine some specimens of *C. talbragarens* kept in the Natural History Museum and comments (Patterson and Rosen 1977: 144) that they only have three epurals, not four as noted by Cavender. He saw six uroneurals arranged as four long strap-like bones and a posterior group of three shorter ones, as well as two urodermals (Figures 12A, 12B).

EVOLUTION

The rise of the teleosts began in the Triassic but they flourished in the Early Jurassic when they

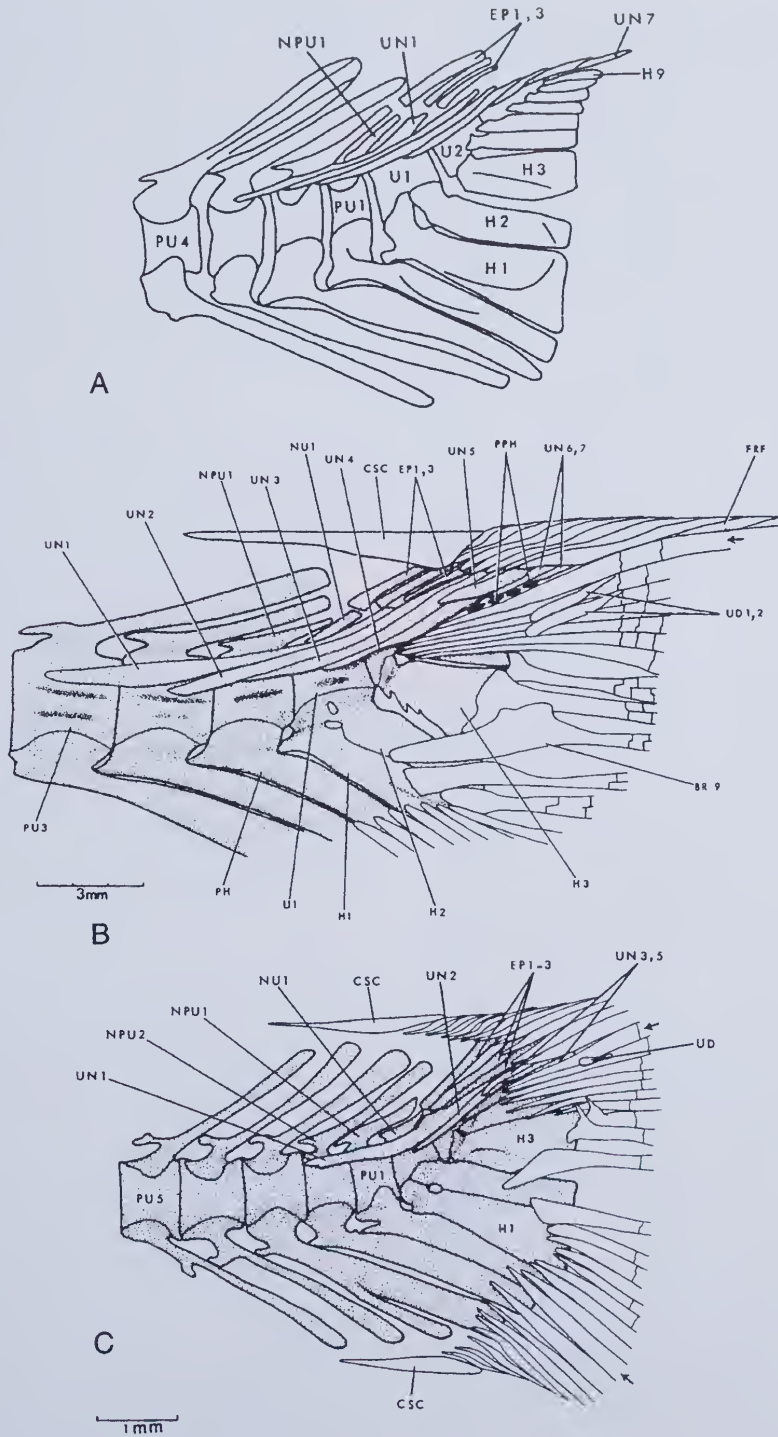


Figure 22 Comparative reconstructions of the caudal skeleton. A, *Leptolepis coryphaenoides* from Patterson and Rosen (1977, figure 33B), based on BMNH 32456, 32467, P42857 and P7622. B, *Tharsis dubius* from Patterson and Rosen (1977, figure 35), based on BMNH P.927. C, *Leptolepides sprattiiformis* from Patterson and Rosen (1977, figure 50), based on BMNH P926.

rapidly achieved a worldwide distribution. Today the Teleostei is the most abundant and diverse group of vertebrate animal (about 29,000 species.). The earliest teleost has been a matter of conjecture over the years, with the leptolepids long being considered one of the oldest representative groups of teleosts. The pholidophorids arose in the Triassic, a group that has more in common with the holosteans than do the leptolepids. Gardiner (1960) described a possible leptolepid from the Upper Triassic of Tanzania, which he called *Leptolepis africana*. This would have been the oldest leptolepid, except that Nybelin's (1974: 168) re-examination of the specimen led to its inclusion in the genus *Pholidolepis*, a member of the Pholidophoridae. This family was considered to be more primitive than the Leptolepididae, but it is still a member of the teleosts (Patterson 1982).

The teleosts arose from the holosteans grade group, and replaced them as the dominant actinopterygians during the Jurassic. Some characters that are considered primitive in teleosts by Arratia (1997) include the following: the parietals suturing with each other; dentition on the parasphenoid; the possession of a suborbital bone; the absence of a preopercular process on the hyomandibular; premaxilla being a slightly triangular bone; absence of supramaxillae; position of quadrate-mandibular articulation located below the posterior of the orbit; having a leptolepid notch; having epineural bones but not epipleural bones; having four epurals; having a high number of hypurals e.g., 10; 10 or more principal caudal rays in the lower lobe; ganoid scales.

Cavenderichthys talbragarensis certainly has many of the characteristics of an early teleost. It has a small, mobile premaxilla, which is free from the maxilla. This is an early teleost characteristic (Rosen 1982), as in later teleosts the premaxilla becomes the dominant bone of the upper jaw, bearing all the teeth. The maxilla is hinged in the ethmoid region and swings anteriorly as the mouth opens. This helps to prevent water spilling from the corners of the mouth so encouraging food to be drawn into the mouth. As the mandible is depressed the operculum rises and rotates outwards, also encouraging the through flow of water and food (Lauder 1982).

The roof of the skull has a continuous suture between the frontals and the parietals. This is characteristic of early teleosts (Arratia 1985), but the later trend is for separation of the parietals to allow insertion of muscles. There also seems to be a trend to a reduced number of tubules branching from the sensory canals, certainly within the leptolepids if not within all teleosts. In this respect *C. talbragarensis* shows an advanced feature.

Actinopterygian locomotion involves two styles, firstly caudal propulsion which is used for cruising

and sprint swimming, acceleration and fast turns, and secondly median and paired fin propulsion used for slow swimming and in precise manoeuvres (Webb 1982). *C. talbragarensis* makes use of both these modes of swimming, with an emphasis on caudal propulsion. The well-ossified axial skeleton gives it strength, its homocercal tail outline gives it a balanced force from the caudal area, while the scooped out centre of the tail improves flexibility and steady swimming. The low position of the pectoral fin and the middle position of the pelvic fins are early teleost characteristics (Gosline 1971) as the trend is for the pectoral fins to rise while the pelvic fins become placed in a forward position. The collapsible dorsal fin can reduce drag during fast swimming but can also be raised to act like a keel, especially during tight turns. The light scales have reduced resistance in unsteady swimming, and they help to reduce the mass of the body (Webb 1982).

C. talbragarensis has a primitive location of the pectoral and pelvic fins, and yet the arrangement of the premaxilla and maxilla is one stage advanced from primitive. Rosen (1982) commented, "changes in jaw mechanics first arose, and in some cases proliferated, in teleosts with a primitive fin arrangement and morphology" (Rosen 1982: 269). There is no inherent reason why characters should evolve at the same pace. It is possible that the advanced placement of paired fins did not become a selective advantage until the jaw structure had been modified significantly. The change in feeding style allowed by the more advanced mouth may have been aided by the forward placement of the paired pelvic fins, closer to the centre of gravity of the fish.

Considering Arratia's (1997) list of primitive characters, *C. talbragarensis* has parietals with a suture between them, the quadrate-mandibular articulation appears to be below the middle of the orbit, the leptolepid notch is wide, and it has epineural bones. In these characteristics it is primitive. However, many of its features are more advanced than primitive as it has no dentition on the parasphenoid, does not have a suborbital bone, does possess a preopercular process on the hyomandibular, has two supramaxillae, has epipleural bones, has commonly three epurals, seven or eight hypurals, nine principal rays in the lower lobe of caudal fin, and has cycloid scales.

One of the major advantages of this study over previous work is the large amount of material included, namely approximately 240 specimens. Thus it has been possible to assess the internal variation and whether there is more than one species in the population. The material includes a range of sizes of the specimens and a range of states of preservation, including at least one good example of all the cephalic dermal bones and many

examples of well-preserved fins and axial skeleton. The major conclusion is that there is only one species of fish originally called *Leptolepis* by Woodward, not three as he proposed. This is supported by a statistical analysis of the range of dimensions of the specimens. There are certainly other genera present in the population, but they will be described in another paper. The leptolepids represent a population with a preponderance of young individuals, but also with a representative sample of older individuals. Woodward's *Leptolepis gregarius* is the juvenile form of *C. talbragarensis*, while *L. lowei*, in which the head appears to be elongated, is an artefact of preservation.

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A bioarchaeological investigation of a multiple burial associated with the *Batavia* mutiny of 1629

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Abstract – On 29 October 1628, the *Verenigde Oostindische Compagnie* (VOC) *Retourschip Batavia* embarked on a voyage into infamy. Originally sailing as part of a fleet of six other ships, the *Batavia* was subsequently separated, and wrecked on Morning Reef in the Houtman Abrolhos on 4 June 1629. The ship's Commander, Francisco Pelsaert, had survivors landed on nearby Beacon Island, and then embarked on a rescue voyage to Batavia (modern day Jakarta). During Pelsaert's absence, an ultimately unsuccessful mutiny attempt resulted in the murder of at least 125 people.

Human skeletal material has been recovered from excavations of the *Batavia* land sites since the 1960s. Four individual burials were discovered between 1960 and 1964. A further six individuals were recovered from a multiple burial between 1994 and 2001. Characteristics of the multiple burial, such as the age, sex, positioning of individuals interred and evidence of trauma are analysed and compared for any similarity to individuals listed, and events outlined and historically recorded. The results of this analysis suggest that four of the interred are probably the sick individuals who were amongst the massacre's early victims; two sub-adults were also included in the burial, at least one of which can also be directly accounted for.

INTRODUCTION

The *Verenigde Oostindische Compagnie* (VOC) ship *Retourschip Batavia* was one of the largest and finest armed vessels of the time. Carrying a complement of approximately 316 people, the *Batavia* embarked from Amsterdam on 29 October 1628, destined for Batavia (modern day Jakarta). Cramped on board were men, women and children of various socio-economic backgrounds and nationalities, including VOC officers and crew, in addition to naval cadets, passengers and soldiers (Drake-Brockman 1963; Tyler 1970). Originally sailing alongside a fleet of six other ships, the *Batavia* was subsequently separated, and wrecked on Morning Reef in the Houtman Abrolhos off Australia's west coast on 4 June 1629 (Figure 1) (Drake-Brockman 1963; van Huystee 1998). According to historical records, the exact events leading to the separation of the *Batavia* from the fleet and her subsequent grounding remain somewhat speculative.

Unable to free the *Batavia* from Morning Reef, the ship's Commander, Francisco Pelsaert had 180 survivors landed on nearby Beacon Island, a small coral island lacking freshwater (Figure 1). About another 40 people (Pelsaert included) were landed on one of the smaller islands early the following morning, leaving approximately 70 to 80 survivors on the ship (Tyler 1970). Of those people still aboard, approximately 40 were reported to have

drowned attempting to swim from the wreck to land (van Huystee 1998). The exact figures are unclear, but Drake-Brockman (1963: 50) puts the total number finally landed at 268. Knowing that their situation was dire, Pelsaert decided to take a group in search of water on nearby islands and the main 'Southland' (Drake-Brockman 1963: 126–127). Failing in their search, Pelsaert resolved to attempt the hazardous voyage of more than 1 900 kilometres to Batavia (Drake-Brockman 1963).

Prior to the wrecking of the *Batavia*, trouble between the ship's skipper, Adriaen Jacobsz, the undermerchant, Jeronimus Cornelisz and Pelsaert had sowed the seeds of dissent, which escalated on the island into a plan for mutiny (see Drake-Brockman 1963: 35–60). So, while Pelsaert attempted the perilous rescue voyage to Batavia, Cornelisz remained on Beacon Island and managed to establish his own 'ruling council', and with the aid of his followers began to murder all who opposed him. Cornelisz planned to reduce the total number of survivors to 40, with whom he planned to hijack the anticipated rescue ship. Before Pelsaert's return, Cornelisz and his accomplices had murdered at least 125 men, women and children. Upon Pelsaert's return on September 17th, Cornelisz and his accomplices were captured, tried and most were duly executed on purpose-built gallows erected on Seals Island (present day Long Island) (Drake-Brockman 1963).

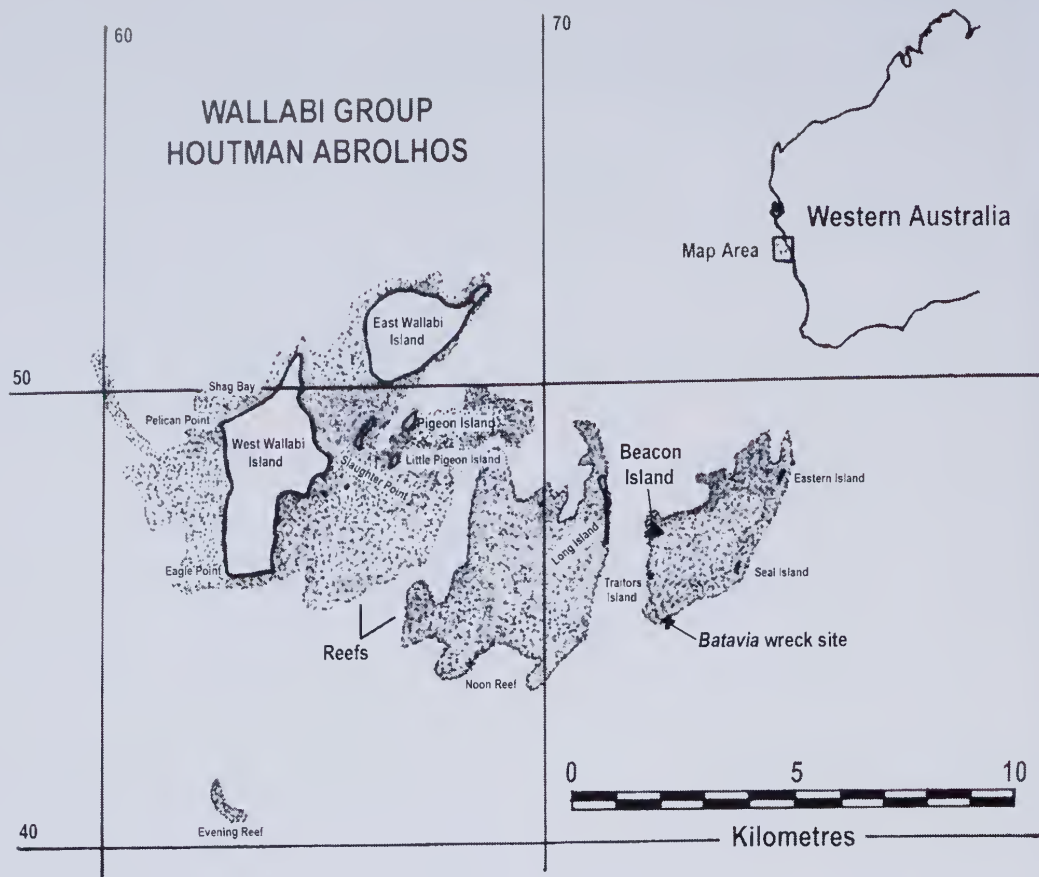


Figure 1 Wallabi Group, Houtman Abrolhos Islands, showing locations of East and West Wallabi Islands, Beacon Island (▲) and the *Batavia* shipwreck (+) location (adapted from Green 1989).

So far, the skeletal remains of ten individuals have been found on Beacon Island. Four individual burials were discovered between 1960 and 1964 (Stanbury 1998). A further six individuals were recovered from a multiple grave between 1994 and 2001. All are believed to be victims of the slaughter. Some brief descriptions of the multiple grave material have been made by Hunneybun (1995), Pasveer *et al.* (1998) and Pasveer (2000). The purpose of this paper is to present a description and interpretation (using forensic, archaeological and historical sources) of the human skeletal material recovered from the multiple burial. Age, sex, stature, general state of health and trauma will be assessed and an attempt made to identify the recovered individuals.

The primary source of information documenting the epic voyage of the *Batavia*, the wrecking of the ship and the trials of the mutineers is the manuscript 'Droevige daghaenteyckeningh int verliesen van ons schip *Batavia*', usually known as the 'Pelsaert Journal' (van Huystee 1998).

THE SITE

The Houtman Abrolhos lie approximately 65 km off the west coast of Australia, between latitudes 28° and 29° south (Figure 1). The Abrolhos are four well-distinguished geographical units: North Island and the Wallabi, Easter and Pelsaert Island Groups (Teichert 1946). The Wallabi Group is the northernmost in the Abrolhos, consisting of 32 islands scattered over an extensive system of coral reefs. The elevation of the islands is generally low, mostly approximately 2.5 metres above sea level (Dakin 1919). The eastern islands, such as Beacon and Long, are considerably smaller and consist of accumulations of coral boulders and shingles (Storr 1965). Beacon Island, with an approximate area of 5.25 hectares, is sparsely vegetated and without a source of fresh water (Bevacqua 1974; Green and Stanbury 1988).

EXCAVATION

A review of the research directly concerning the

discovery of the multiple burials on Beacon Island follows.

1994 Field Season

In 1993, Philippe Godard reported John Gliddon's discovery of a skeleton while digging a hole for a 'septic tank' near his house in 1990 (Figure 2) (Godard 1993: 237). The concern for further damage by souvenir hunters, due to the relatively precise location provided by Godard, supported by Gliddon's declaration under the Commonwealth Historic Shipwrecks Amnesty (1993–1994), provided the impetus for the 1994 field season by the Western Australian Maritime Museum. This season aimed to investigate the nature and extent of the disturbance to the burial site based upon interviews with residents of Beacon Island and to

make a physical investigation of the area (Gibbs 1994).

Gibbs established that the trench dug for piping associated with a nearby toilet (leach drain) had been constructed possibly six years earlier (around 1988) and that at least two or three skeletons were found. One of the workers removed at least one skull and mandible (Gibbs 1994). New sites were identified along the southern edge of the house and excavation in 1 m squares followed (Figure 2). In the absence of detectable stratigraphic changes, arbitrary levels of 5 or 10 cm were removed. Bulk samples were collected, pH and Munsell soil colours recorded and all material sieved through three and five millimetre nested screens (Gibbs 1994).

The excavation area was extended in the hope of

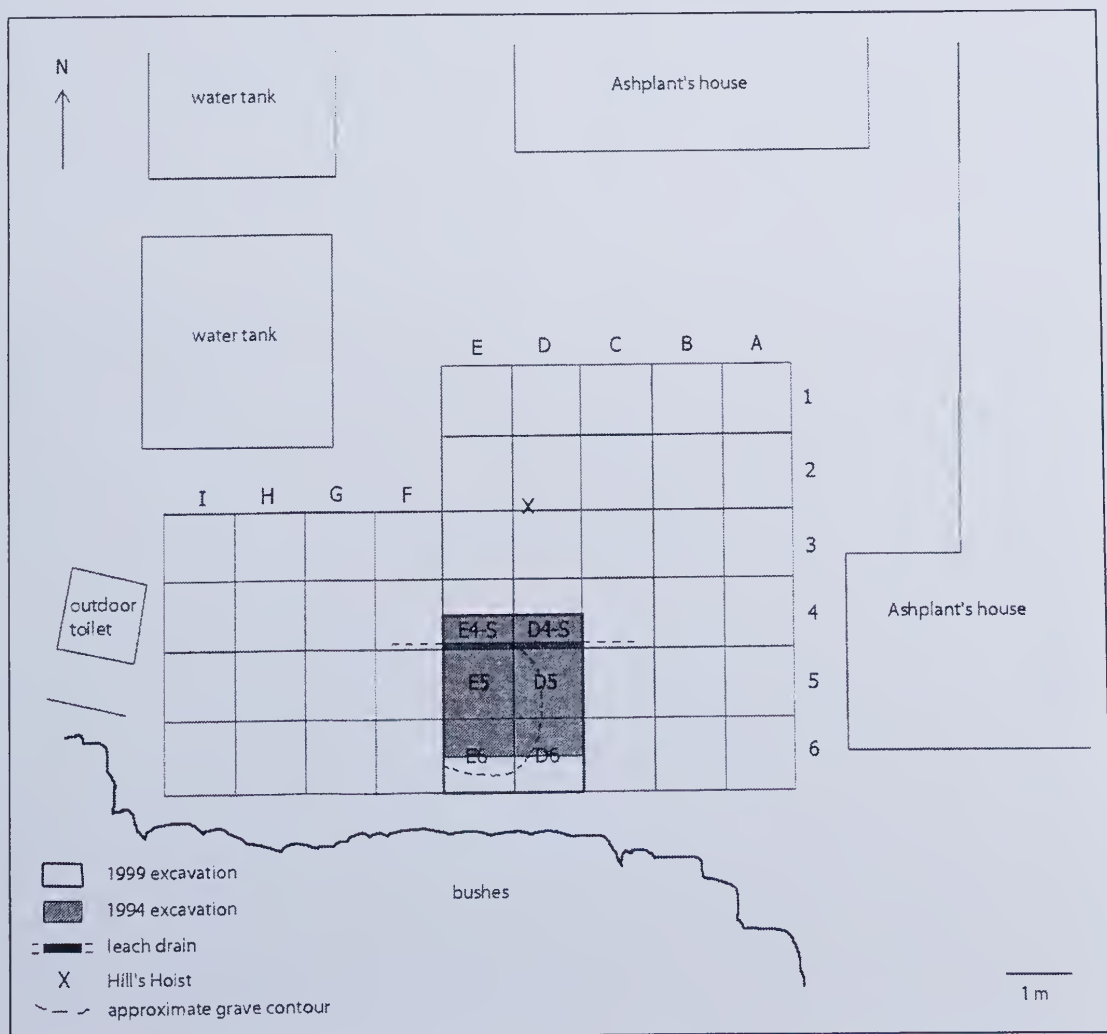


Figure 2 Site map showing the excavated area (from Pasveer 2000). The house currently occupied by the Ashplant family was formerly occupied by John Gliddon.

finding more bone fragments, leading to the location of the remaining *in-situ* skeletal remains. The two squares chosen for detailed examination (E5 and D5 – Figure 2) were found to contain two skulls (one of which was significantly damaged) situated side by side with several other large adult bone fragments (Gibbs 1994). The skeletons appeared to extend south from the region of the skulls. During excavation there were no discernable stratigraphic changes and the soil pH ranged between 8.5 and 10. Bone fragments were evident from the first level and a maximum depth of 35 cm was reached during excavation (Gibbs 1994; Hunneybun 1995).

It was concluded that two skeletons were present in the site and were disturbed during the toilet sump and leach drain construction (Pasveer 2000: 5). Two adult crania (SK5 and SK6) were identified; fragments of SK5 were recovered for analysis and SK6 was left *in situ* (Stanbury 1998; Pasveer 2000). The stratigraphy of the test pits was highly disturbed as a result of both the trenching and subsequent nesting activities of burrowing birds. Gibbs (1994) made recommendations for future systematic investigation on Beacon Island because the sites had been seriously disturbed and their locations were then well known.

1999 and 2001 Field Seasons

The degree of prior human and ongoing disturbance by burrowing birds, together with the risk of future vandalism, led to the decision to fully excavate the burial site in 1999 (Pasveer 2000: 5). An excavation grid was set up and Gibbs' 1994 squares were reopened and extended 0.5 m south (Figure 2) (Pasveer 2000). Squares were excavated in 5 cm levels and all material was sieved with nested 3 and 5 mm screens. Bulk soil samples were collected and Munsell soil colour and pH readings were taken for most levels. The pH levels recorded in the field ranged between 5 and 6, but these measures were subsequently found to be erroneous; reanalysis of the bulk soil samples showed that the pH actually ranged between 8.5 and 10 (Franklin 2001). The soil's high calcium carbonate content favours bone preservation and reflects this level of alkalinity (Hunt and Gilkes 1992).

The excavated area was now found to include five individuals (three adults and two children) who had been laid against each other within a circular pit (Figure 2). These individuals were designated SK7, SK8, SK9, SK10 and SK11 (Figure 3). The bones of the five individuals were in various stages of preservation and some (particularly SK10) were in very poor condition. The crania identified in 1994

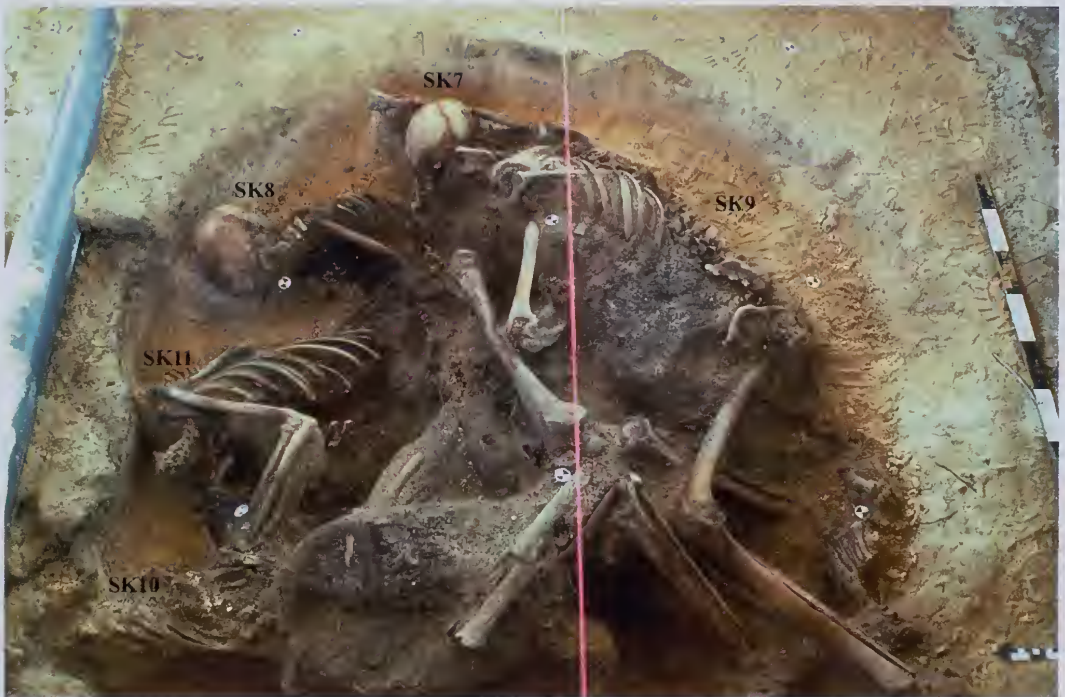


Figure 3 Four of the individuals uncovered *in situ* during the 1999 excavations; the bones of SK9 were removed at an earlier stage of excavation. (Photo courtesy of the Western Australian Maritime Museum).

Table 1 Outlines and descriptions of the *Batavia* multiple burial skeletal material.

Individual	General Description
*SK5 / SK11	Adult: damaged cranium + partially incomplete postcranial skeleton
*SK6 / SK10	Adult: damaged cranium + partially incomplete postcranial skeleton
SK7	Adult: reconstructed skull and fragmentary postcranial skeleton
SK8	Child: reconstructed skull and largely incomplete postcranial skeleton
SK9	Child: reconstructed skull and largely incomplete postcranial skeleton
SK12	Infant: deciduous and permanent teeth only

* Crania and postcranial skeletons recovered and catalogued separately

(SK5 and SK6) were believed to be associated with these individuals, bringing the total sample to five skeletons (Pasveer 2000). The skeletal remains were found over, under, or in, a large deposit of black dense matter possibly of organic origin. The bones embedded in this deposit were left *in situ* and those removed were poorly preserved (Pasveer 2000). Later in 2001, the black deposit was excavated (see Paterson and Franklin 2004) and 16 deciduous and 2 permanent teeth were discovered underneath. This, the sixth individual recovered from the multiple burial, was designated SK12.

MATERIALS AND METHODS

The present study examines the human skeletal material recovered from the single multiple burial excavated during expeditions to Beacon Island in 1994, 1999 and 2001. One of the objects of this study has been to try and refer particular materials to known individuals in the burial. To this end age, sex and stature have been computed even when the material has been limited. The material is briefly listed in Table 1; the methods used for aging, sexing, stature estimation and pathology are described below.

A multifactorial technique of documenting age changes in dental development, eruption (Ubelaker 1999) and attrition, and also epiphyseal union and suture closure, was used for assigning individuals into one of the following categories: Child (deciduous teeth present), Sub-Adult (< 20 years – aged by dentition), Young Adult (20 – 34 years), Middle Adult (35 – 49 years) and Old Adult (50 + years). Sex determination was largely based on Giles and Elliot (1963), the 'Workshop of European Anthropologists' (WEA 1980), and Buikstra and Ubelaker (1994). Both cranial and postcranial metrical and non-metrical sexual characteristics were examined; however the paucity of os coxae bones meant that the cranium was the skeletal element mainly used for sex and age diagnoses.

The stature of adult individuals was assessed using the tables devised for 'Whites' by Trotter (1970). Due to the broken and incomplete condition of many of the long bones, original lengths of the tibia, humerus and radius are reconstructed and

estimated according to the method outlined by Muller (1935). Statures are calculated from all available long bones and only the most reliable estimates are listed (e.g., lower before the upper limb bones). Stature ranges are estimated after consideration of variation in both reconstructions of fragmentary bones and stature regression equations. Palaeopathological diagnoses were made according to the criteria outlined in Ortner and Putscher (1981), Iscan and Kennedy (1989), and Buikstra and Ubelaker (1994). Each bone from the *Batavia* sample was examined macroscopically, with a hand lens and from radiographs of selected bones.

RESULTS

The basic description of the bones, estimated personal age, assigned sex, estimated stature, and any observed pathology and trauma of the skeletal material recovered from the multiple burial are outlined in this section.

The crania and postcranial skeletons of SK5/SK11, and SK6/SK10 were recovered at different times. The crania and postcranial skeletons were thus only able to be tentatively associated on the basis of morphological assessment (size and development of muscle attachments and metrical dimensions). On this basis, the cranium of SK5, which has weak development of muscle attachments, has been associated with the slender postcranial skeleton of SK11; the cranium of SK6, which has large areas of muscle attachment (mastoid processes and nuchal region of occipital bone), and is metrically larger than SK5, has been associated with the larger, more robust postcranial skeleton of SK10.

SK5 / SK11

This cranium (SK5) and incomplete postcranial skeleton (SK11) is significantly damaged. Two of the larger parts of the cranium are the frontal and parietal bones and there are fragments of the occipital and temporal bones. Most of the sphenoid bone is missing, as is the basilar part of the occipital region. The facial bones are significantly damaged and fragmented. There is no palate and only two small pieces of the maxilla are present. Fragments of both clavicles and scapulae were recovered. The

right humerus, radius and ulna are missing. The left humerus, radius and ulna are in good condition with only slight damage to the proximal and distal ends. Ribs 1–11 of the left side are relatively well preserved. Parts of most vertebrae were recovered although their bodies are missing. The left femur, tibia and fibula are in good condition but have some damage to the proximal and distal ends. Only a few small pieces of the right tibia were recovered. Nearly all of the hand and foot bones were recovered.

Dental attrition and sutural closure suggest a middle adult, c. 35 to 49 years of age. The form and size of the nuchal crest, mastoid process and the glabella indicate indeterminate sex (Buikstra and Ubelaker 1994). Although damaged, discriminant function sexing of the cranium was possible, and implied male sex (Giles and Elliot 1963). The radial head diameter (25 mm) is characteristically male (Berrizbeitia 1989), and the long bones are large but with relatively weak muscle attachments, overall they are more masculine than feminine. On balance, cranial and postcranial morphology indicate a probable male sex. Stature was assessed as approximately 1.74 m (range 1.67 m – 1.82 m) from the reconstructed length of the left tibia.

The dentition presents no apparent macroscopic evidence of enamel hypoplasia or caries, but there appears to be some abnormal loss of the alveolar bone of the right maxilla. This resorption may have resulted from periapical abscesses or tooth loss (Ortner and Putschar 1981). The postcranial skeleton presents evidence of traumatic episodes. The shaft of the left ninth rib was broken near the costal angle. This injury appears to have occurred a significant time before death as the rib has healed, but at an obviously abnormally acute angle. The shaft of the left ulna has an area of abnormal bone thickening (periostitis) just superior to the level of the nutrient foramen. The abnormality was initially thought to be a healing or healed mal-aligned fracture, but radiographs show no evidence of a fracture healed or otherwise. The damage to the ulna could be the result of an injury not sufficient to actually break the bone, but enough to have caused blood vessel haemorrhaging, resulting in a subperiosteal haematoma (inter-membrane bleeding and abnormal calcification between the periosteum and endosteum).

On the basis of the osteological assessment, there is no evidence of trauma, which could have contributed to death.

SK6 / SK10

This skeleton is also significantly damaged and largely incomplete. The largest pieces of the cranium (SK6) include most of the facial region, the zygomatic and sphenoid bones, the mastoid and parts of the temporal bone of the left side (Figure

4). Other cranial fragments include parts of the right orbit, occipital and zygomatic bones. The maxilla and palate are complete, but there is no mandible. Only a small proportion of the fragmented postcranial skeleton (SK10) was recovered. The left and right humeri are both fragmented and incomplete. The right radius and ulna are well preserved and mostly complete. There is some damage to the distal regions of the left radius and ulna. A few ribs, lumbar vertebrae and sacral fragments were recovered, but there are no pelvic bones. The lower limb bones are largely fragmented and incomplete. Most of the hand and foot bones were recovered.

Dental attrition and sutural closure suggest a middle adult, c. 35–49 years of age. The form of the mastoid process and the glabella indicate male sex (Buikstra and Ubelaker 1994) and discriminant function sexing of the cranium also suggests male sex (Giles and Elliot 1963). The radial head diameter (23.25 mm) is characteristically male (Berrizbeitia 1989), and the right radius and ulna are large and robust with well-developed muscle attachments, traits that typify a male individual. Cranial and postcranial morphology imply male sex. Stature was assessed as approximately 1.79 m (range 1.75 m – 1.83 m) from the length of the right radius.

The dentition presents no apparent macroscopic evidence of enamel hypoplasia, caries or dental disease. However, apparently before death, the upper right central incisor appears to have been



Figure 4 The damaged cranium of SK6: arrow indicates impacted upper right central incisor. (Photo by Patrick Baker, Western Australian Maritime Museum).

forced through the alveolar process into the nasal cavity (Figure 4). Other than the localised area of intrusion, neither the incisor nor the surrounding maxillary bone appears to be significantly damaged. There is no apparent evidence of postcranial trauma, but there is some disparity between the left and right ulnae and radii, particularly in areas of muscle or ligament attachments and shaft circumference and tuberosity diameters. The right radial tuberosity is better developed and larger than on the opposing side. This asymmetrical development may be the result of adaptations associated with the favoured use of the right side. The terminal and middle phalanges of the fourth digit of the right foot are fused. The aetiology of this is uncertain, but it could be congenital, or the result of trauma or occupational activities.

Although the osteological assessment indicates some evidence of trauma in the cranium, it appears unlikely to have contributed to death.

SK7

This is the most complete skeleton recovered from the 1999 excavation (Figure 5). The skull is largely complete and well preserved. The maxillary region inferior to the right infraorbital foramen is damaged and there is no palatine bone. There is also some damage to the left sphenoid bone. Although fragmentary, most postcranial skeletal elements are represented, but the proximal and distal ends of most of the long bones are damaged to some degree. Of the pelvis only small fragments of the

left acetabulum and greater sciatic notch were found. The bodies of all vertebrae are missing and only the arches were found.

Dental development, attrition and sutural closure suggest a young adult, c. 20–34 years of age. The form of the nuchal crest, mastoid process and mental eminence all indicate male sex (Buikstra and Ubelaker 1994). Discriminant function sexing of the cranium also indicated male sex (Giles and Elliot 1963). The left femoral head is mostly complete and the diameter (49.75 mm) is characteristically male (Stewart 1979). The shape of the greater sciatic notch indicates a probable male morphology (Buikstra and Ubelaker 1994). Cranial and postcranial morphology clearly indicate male sex. Stature was assessed as approximately 1.76 m (range 1.71 m – 1.83 m) from the reconstructed length of the right tibia. The dentition presents no apparent macroscopic evidence of enamel hypoplasia or dental disease and the only carious tooth appears to be the lower right second premolar, which is also broken midway through the mesial cusp.

Evidence of trauma is not apparent, but there is some disparity present between the left and right clavicle and humeri, particularly in areas of muscle or ligament attachment and shaft circumference and diameters. The conoid tubercle of the left clavicle is more developed and larger than the opposing side. The mid-shaft diameter and least circumference of the left humerus are larger than the right side. This asymmetrical development



Figure 5 Reconstructed skull and postcranial skeleton of SK7. (Skull photo by Patrick Baker, Western Australian Maritime Museum).

might be the result of mechanical changes associated with the favoured use of the left side. Radiographs of the right tibia revealed the presence of at least three Harris lines approximately 20 to 25 mm from the distal articular surface. One of the three lines is faint and very short, approximately 15 mm. The remaining two lines are clearly visible and extend at least halfway across the tibial shaft.

Approximately one-quarter of the distal end of the left tibial shaft is markedly roughened and porous, a pattern indicating a deficiency in osteoid production and calcium deposition (Figure 6) (Collins 1966; Aufderheide and Rodriguez-Martin 1998). The shell of lamellar new bone on the surface appears to be attached to the original cortex by a web of more porous bone, which has completely obliterated the nutrient foramen. This implies some metabolic disturbance affecting the individual in the immediate antemortem period and this has been tentatively identified as possibly being scurvy, a condition caused by a deficiency of vitamin C (Aufderheide and Rodriguez-Martin 1998).

Scurvy was common in sailors of the period, and is suggested because scorbutic individuals are susceptible to subperiosteal haemorrhaging due to aberrant blood capillary formation. When the haemorrhage is of a substantial size the bone often has a more porous structure (Aufderheide and Rodriguez-Martin 1998: 311; Ortner *et al.* 1999; Buckley 2000). Since bleeding and the resulting changes to surrounding bone tissue tend to occur in

regions under mechanical stress (Ortner *et al.* 1999: 322), the obliteration of the tibial nutrient foramen is probably not unusual. Similar scorbutic changes in the lower long bones have been reported in individuals from a 17th century Dutch whaling station at Spitsbergen (Maat 1981) and the 14th century Crow Creek massacre site in South Dakota (Willey and Emerson 1993).

The osteological assessment does not reveal any evidence of trauma, which could have contributed to death.

SK8

The skull and some of the postcranial skeleton of this individual were recovered. The skull is significantly damaged, although largely complete, and was reconstructed by Dr Stephen Knott. There is some damage to the right facial bones, particularly the right vomer and maxilla. There is no palate. Most internal bones are missing and parts of the right lateral body and condyle of the mandible are damaged. Fragments of the atlas and cervical vertebrae are present. Fragments of both clavicles, parts of the right scapula and many rib fragments are present. Both the proximal and distal end regions of the left and right humeri are missing and only the shaft remains. The distal regions of the left radius and ulna are also damaged. Some of the phalanges of the left hand were recovered. No postcranial skeletal elements below the pelvis were examined as they are embedded in a dense soil



Figure 6 Distal left tibia of SK7 displaying marked porosity.

feature which has only recently been excavated in a solid block (Paterson and Franklin 2004).

Dental development and sutural closure suggest a sub-adult, < 20 years (c. 15–16 years) of age. It was not possible to conclusively determine the sex of this immature and fragmented skeleton, but the base of the symphysis and the body shape of the mandible display some features noted by Loth and Henneberg (2001) to be male characteristics. The chin region of SK8 extends abruptly downwards and squares off at the base of the symphysis and the transition to the lateral body is sharply angled. These features are typical male characteristics, but more definitive sex determination would require contemporary metrical data from a juvenile Dutch population or DNA analysis. Stature was assessed as approximately 1.51 m (range 1.49 m – 1.53 m) from the reconstructed length of the left radius. The dentition presents no apparent macroscopic evidence of enamel hypoplasia, caries or dental disease.

No apparent evidence of abnormalities was detected in the skeleton. On the basis of the osteological assessment there is no evidence of trauma, which might have contributed to death.

SK9

The skull of this juvenile individual was crushed by the weight of overlying soil and the postcranial skeleton is largely incomplete (Figure 7). The skull, reconstructed by Dr Stephen Knott, is fairly complete, but parts of the right orbit and nasal cavity, lacrimal bone and maxilla are missing or damaged. Most internal bones are also missing and the mandible is fractured through the middle of the symphysis. Dental development suggest a child; c. 5–6 years of age. It was not possible to conclusively determine the sex or reconstruct stature from the

immature skeleton. The dentition presents no apparent macroscopic evidence of enamel hypoplasia, caries or dental disease.

There was no evidence of trauma in the skeletal remains, which might have contributed to death.

SK12

The only remains of this individual that were recovered are the permanent left first molars and all of the deciduous teeth, except for the lower incisors and left canine. Dental development is of a child, c. 8–9 months of age, notably because initial cusp formation of the first permanent molars has occurred and their coalescence is nearly complete. Sex determination was not possible. There is no evidence of enamel hypoplasia in any of the teeth, although there is some noticeable developmental disparity with the left side slightly less developed than the right. This is within a normal range of variation and is not pathological. There is no evidence of occlusal function.

DISCUSSION

The demographics and health status of the individuals recovered from the multiple burial are summarised (Table 2) and discussed below.

Demographics

All of the adults recovered from the multiple burial were assessed as probable males. The sub-adult individual (SK8) is also tentatively classified as male, but the sex of the one child (SK9) and infant (SK12) remain unknown. The bias towards males is expected, given that approximately five men for every woman were murdered by Cornelisz and his accomplices (Drake-Brockman 1963: 50). The *Batavia's* complement comprised mostly males,



Figure 7 Reconstructed skull and postcranial skeleton of SK9. (Skull photo by Patrick Baker, Western Australian Maritime Museum).

Table 2 Main features of the *Batavia* skeletal material including proposed associations (/) of cranial and postcranial skeletons.

Individual	Description	Assigned Sex	Age Range	Mean Stature	Trauma/Abnormalities
SK5 / SK11	Damaged cranium + postcranial skeleton	Male	35-49 yrs	1.74 m	Healed rib fracture and subperiosteal haematoma (ulna)
SK6 / SK10	Damaged cranium + postcranial skeleton	Male	35-49 yrs	1.79 m	Facial damage and skeletal asymmetry (upper limb)
SK7	Skull + postcranial skeleton	Male	20-34 yrs	1.76 m	Harris lines and pathological tibia (scurvy?)
SK8	Skull + postcranial skeleton	Male	15-16 yrs	1.51 m	No evidence of trauma or abnormalities
SK9	Skull + postcranial skeleton	?	5-6 yrs	N/A	No evidence of trauma or abnormalities
SK12	Deciduous + permanent teeth	?	8-9 mo	N/A	Some left/right disparity in dental development

*yrs = years; mo = months

who were regarded by the mutineers to be the greatest threat. As such, males were the primary targets in the initial murders. In contrast, women were perceived as a lesser threat and many were kept alive to serve as unwilling concubines for the mutineers (van Huystee 1998). The age at death of the sample appears to range from approximately 8 months to no older than 49 years of age. Even though only a small sample was available for study, the age demographics, in particular the apparent lack of older adults (50+ years of age), is not unusual given the shorter life expectancy in 17th century Europe (Jacobs 1991). Furthermore, the chances of a career sailor serving aboard a VOC vessel past 50 years of age would be slim, especially considering shipboard conditions of the early 17th century (see Bruijn *et al.* 1987).

Dental health

Even taking the small sample size into consideration, the dental health of the *Batavia* sample as a whole is assessed as generally good. There were relatively few examples of dental diseases such as caries, periodontal disease or calculus accumulation. Some of the older adults in the *Batavia* sample displayed evidence of antemortem tooth loss, often of the first molar. This may have been the result of caries or severe wear exposing the pulp cavity, leading to an infection of the supporting tissue (Ortner and Putschar 1981).

Trauma

Of the multiple burial individuals, the postcranial skeleton of SK11 displays evidence of a healed fracture of the left ninth rib and a subperiosteal haematoma of the left ulna. The relatively poor alignment of the rib fracture may attest to low quality or no medical attention to the injury, although the bone has healed well, which is a

general indicator of good health (Webb 1989). The subperiosteal haematoma of the left ulna most probably resulted from a fall or a blow to that arm. The interpretation of traumatic markers often affords some insight into certain factors concerning the lifestyle of the afflicted individuals (Roberts and Manchester 1995). For SK5/SK11 it was only possible to infer that this individual may have led a physical lifestyle where occupational injuries were common. Other samples of 17th century mariners also reputedly display similar evidence of having led physical lifestyles (cf. Maat 1981: 169). The upper right central incisor of the cranium of SK6 has been forced through the alveolar process into the nasal cavity. This likely resulted from a heavy blow against the teeth, but it is not possible to ascertain whether the trauma is the result of violence or accident. It is important to note that the prevalence of trauma in the *Batavia* sample as a whole may be under-represented due to the small and fragmented nature of the skeletal assemblage.

Nutritional related deficiencies

The tentative diagnosis of scurvy in SK7 is the only possible nutrition-related deficiency in the sample. One of the primary causes of a high mortality rate aboard VOC vessels was disease, particularly scurvy, which could take a high toll on a crew already undernourished on departure (Gaastra and Bruijn 1993: 203). Efforts were made to combat the illness by sending along less perishable fruits or fruit extracts, and the Cape of Good Hope was officially founded as a supply base for fresh food and water in 1652 (Bruijn *et al.* 1987). The little or no evidence of scurvy in this sample may indicate that the provisioning of less perishable foods and the stop over at the Cape (which the *Batavia* made) was helping to combat the disease, although the sample is only a small fraction of the

ship's complement, and much of the recovered material is poorly preserved.

Non-specific stress indicators

No enamel hypoplasia was detected in the dentition of the sample. Relatively small and faint Harris lines were present on SK7, which may indicate a period of childhood nutritional deficiency, stress or illness (Rathbun 1987; Hughes *et al.* 1996). This was not uncommon in 17th century Europe (see Maat's 1984 analysis of 17th to 18th century Dutch whalers). The relatively fragmented, incomplete and poor condition of a large proportion of the postcranial skeletons in the multiple burial may be a factor in the possible under representation of the frequency of Harris lines. A lack of Harris lines does not indicate an absence of disease; the aetiology and multiple factors contributing to the appearance of these skeletal markers is unclear and should not be regarded as the sole indication of a population's health (Hughes *et al.* 1996: 129).

Occupational stressors

Modern clinical data has established that certain activities can cause osteoarthritis and other skeletal changes (Roberts and Manchester 1995). Mechanical factors are obviously important in the production of pathological skeletal changes, but to assume that these changes are indicative of occupational stressors is probably an oversimplified view (Waldron 1993: 73). On SK7 and SK10 some asymmetry was observed in shaft diameters and the size of muscle or ligament attachment sites between the left and right sides of the upper skeleton. Any habitual activity performed with a side-preference can place extra stress on that specific proportion of the anatomy and can contribute to asymmetrical skeletal development (Wienlar and Wood 1988; Capasso *et al.* 1999). Some bending of the spinous processes of the vertebrae of SK7 and SK11 was observed, but this is not considered to be pathological and might be an occupational change related to side-preference.

Interpretation of the multiple burial

From Pelsaert's Journal it is apparent that there are at least two groups of murder victims buried in multiple graves on Beacon Island; the first was a group of sick individuals, the second the Predicant's family (Drake-Brockman 1963: 175, 186). There are, however, many other instances where multiple burials might have been made, among them the large number of people reported to have drowned attempting to swim from the wreck to land (van Huystee 1998). Below we describe two possible interpretations of the Beacon Island multiple burial. The first is that they were drowning

victims, and second that they were the family of the Predicant (the *Batavia*'s official minister) (Pasveer 2000). We conclude that both interpretations appear to be improbable from the evidence of this research. We then outline another more probable theory backed by what we offer as supportive evidence (Franklin and Freedman 2003).

Drowning victims following the wrecking

Could this multiple grave hold the remains of individuals who had died by drowning in the immediate period following the wrecking of the *Batavia*? The skeletal remains in the multiple burial were clearly 'roughly' thrown into the burial pit (Figure 3). It would seem most unlikely that the *Batavia* survivors would have abandoned their religious or social values so soon after the wrecking. While the situation was dire, it was not without hope of rescue. The VOC would soon become aware of their non-appearance and there was also the option to sail for help in the salvaged sloop (as Pelsaert did).

If the survivors were to bury their dead at that time in a multiple grave, one would certainly expect more care to have been taken in the burials rather than the clearly hasty and disrespectful interments they received. For example, a traditional Christian burial style would at the very least have the bodies orientated east-west, which the individuals buried in the multiple grave are not (Figure 3) (Gerven *et al.* 1981). Even when people were faced with lethal epidemics such as the 'Black Death', there are examples of burials that were organised methodically and with care (Royal Mint site, London; Margerison and Knusel 2002). A modern equivalent to the multiple burial on Beacon Island (but on a larger scale) are crude, hasty multiple graves associated with the murder of civilians in the former Yugoslavia (see Stover and Ryan 2001). The conclusion is that it would seem most unlikely that the multiple burial represents a deliberate interment of those who died by drowning or illness following soon after the wrecking of the *Batavia*.

The Predicant's family

The Predicant's family included his wife, maid and six of their seven children; two girls, three boys and a baby. The historical accounts of the murder of the Predicant's family describe 'the beating in of the skull of the wife and that of one of the children' (Drake-Brockman 1963: 174–186). The individual burials discovered in the 1960s all display evidence of cranial damage (sharp weapon trauma and depressed fractures). On the other hand, in the Beacon Island multiple burial there is no apparent evidence of these types of trauma. Also, the number of individuals in the Predicant's family and their stated ages and sexes clearly do not match those individuals from the burial pit (see Table 2)

A likely interpretation: early 'sick' victims of the massacre

On July 10th or 12th (the dates are inconsistent in Pelsaert's Journal) the early 'sick' murders occurred. The victims were Passchier van den Eenden (a gunner), Jacob (Jacop) Hendricxsz (a carpenter), Jan Pinten (an English soldier) and a cabin boy, all of whom were ill and could offer little resistance. They had their throats cut by Cornelisz's accomplices. At least one body (Jacob Hendricxsz) was dragged into a pit 'which had been made ready' (Drake-Brockman 1963: 183–199). It would be reasonable to assume that all four bodies were disposed of in the ready-made pit simultaneously.

The three adult individuals killed by Jan Hendricxsz (the gunner, soldier and carpenter) would all have been adult males. There are what appear to be three male adults (SK5/SK11, SK6/SK10 and SK7) interred in the burial pit. The apparent lack of violent trauma on all of the skeletons is consistent with historical accounts of the throats of these victims being cut rather than having their heads beaten in, but does not rule out other sorts of injuries undetectable in the absence of soft tissue. The poor preservation of the skeletal material recovered from the Beacon Island multiple burial could explain the absence of markers indicative of someone having their throat cut. Interestingly, the mutineers asked to spare the carpenter's life, but Cornelisz reportedly replied, "...that he was half lame and that he must go" (Drake-Brockman 1963: 183). If by 'lame' Cornelisz meant that the carpenter was physically disabled in some manner, it is worth considering that SK7 very likely had some degree of pain and/or movement impediment due to the pathological condition of his left tibia (Maat 1981; Aufderheide and Rodriguez-Martin 1998).

Skeleton SK8 was estimated to be less than 20 years old (probably between 15 and 16 years of age), close to the typical age of a cabin boy. The sex of this individual is uncertain, but the skeleton does display some male characteristics that offer some credibility to assigning male sex. After reconciling historical accounts with biological evidence, it would seem reasonable to postulate that the four individuals described above were those recovered from the multiple burial pit.

There are two other individuals (SK9 and SK12) represented in the multiple burial. SK9 is of a child of unknown sex, approximately 5 to 6 years of age. Approximately two days earlier than the murder of the gunner, carpenter and soldier (July 8th), Jan Hendricxsz strangled the six-year-old daughter of Hans Hardens (Drake-Brockman 1963: 183). SK9 is approximately the same age and does not display any visible evidence of trauma. There is no mention of how the body was disposed, but with the pit available the body might well have been buried

there as well. This murder took place before the first 'public' murder on July 14th (Drake-Brockman 1963: 115), so the body would have to have been concealed until it could be permanently disposed. SK12 is an infant approximately 8 to 9 months of age. This individual cannot be directly accounted for from historical accounts, but there were several children of unspecified ages murdered and how their bodies were disposed of is not always recorded. It is possible that the infant could be the 'suckling' child of Maijken Cardoes, who was strangled by Salomon Deschamps on 20 July; but this seems unlikely because the infant was recovered from the bottom of the burial, and we would have expected it to have died before 10–12 July (cf van Huystee 2000; Paterson and Franklin 2004).

CONCLUSIONS

This study describes the age, sex, stature, trauma and pathology of the six individuals recovered from a multiple burial related to the *Batavia* mutiny on Beacon Island. The burial of those individuals was not systematic, and instead represents a hasty interment in the early part of the mutiny. We postulate that the remains of four of the interred can be reconciled with historical accounts and could be those of a group of sick individuals who were amongst the early victims of the massacre. In addition, two sub-adult skeletons were recovered. The six year old may be the child strangled two days before the other individuals were killed. The infant could not be directly reconciled with historical accounts, but a number of infants are known to have been killed at various times during the mutiny.

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Structure and function of the tooth plates of the Devonian lungfish *Dipterus valenciennesi* from Caithness and the Orkney Islands

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Abstract – The teeth of the Middle Devonian Dipnoan *Dipterus valenciennesi* are described from new material from Caithness and the Orkney Islands, Scotland. The biostratigraphy of the Old Red Sandstone in these two areas is described on the basis of new information. The pallial dentine is made up of groups of hard clusters of material. The core dentine in the tooth plates is now understood in terms of the development of individual elements making up the structure of the dentine. The first deposited material is interstitial dentine, and the second is transparent dentine which is deposited on the pulp canals against the interstitial dentine. All the core dentine is perforate. Dentine continues to the tip of the tooth, and dentine tubules run from the pulp canals through the transparent dentine to the pallial dentine. The structure is not that of petrodentine. The difficulties of using living material for the understanding of dentine in remote structures in time are outlined. The relationships of organisms after the development of new palatal biting in gnathostomes is discussed.

INTRODUCTION

Dipterus valenciennesi Sedgwick and Murchison, 1829 from the Middle Old Red Sandstone of Scotland was studied by White (1965). References to previous work can be obtained from his paper. Later work by Schultze (1975) and Ahlberg and Trewin (1995) is available.

The solid-snouted, cosmine-coated specimens from the Thurso Flagstones, described by Agassiz in 1844 as *Polyphractus platycephalus*, was one of the reasons for Pander (1858) and Watson and Day (1916) to use the specific name *Dipterus platycephalus*. More recently Westoll (1949) described the skull roof patterns of specimens from Banniskirk (Caithness) and found them sufficiently aberrant to separate them into a new species, *Dipterus brachypygopterus*, and he revived Agassiz's specific name *platycephalus* for all other Scottish specimens of *Dipterus*. He advocated the abandonment of the name *Dipterus valenciennesi*. White (1965) concluded that the *brachypygopterus* pattern was a variation on other specimens that occurred at Banniskirk and elsewhere. The only other genus comparable with *Dipterus* is a new genus to be described by Newman and den Blaauwen from the Middle Old Red Sandstone of Caithness and Sutherland, formerly included in either *Pentlandia* or *Dipterus*. It has a different postcranial morphology and skull-roof pattern.

Following White (1965) we consider *Dipterus valenciennesi* as a valid name.

STRATIGRAPHY

A stratigraphic table showing the distribution of the Middle Old Red Sandstone is attached (Figure 1).

D. valenciennesi is well known from Eifelian or Givetian cyclic sequences in the Orcadian Basin. The species is common in the fish-bearing laminites of Achanarras (Forster-Cooper 1937; Trewin 1986) and the equivalent laminites on Orkney, the Sandwick fishbed (Trewin 1976). These laminites were deposited in deep water in an extended lake in the Orcadian Basin. Small specimens lack cosmine on the scales and dermal plates, but specimens 20 cm or over in length, have cosmine on part of the scales on the ventral side and part of the dermal bones. Fully grown ones have a complete cosmine cover. *Dipterus* is also found in the calcitic nodules from the Moray Firth area where the sediments show fluvial domination in a southward extension of the Achanarras fishbed (Trewin and Thirlwall 2002).

Research in museum collections in the U.K. has shown that it is not possible to identify *D. valenciennesi* positively in sediments older than the Achanarras-Sandwick fishbed horizon.

G I V E R T I A N	CAITHNESS/ SUTHERLAND	Fauna ost---arthr---dipn.	ORKNEY	Fauna ost---arthr---dipn.
		John o' Groat Subgr.	Ta. Wf. Pm.	Eday Flags
	Mey Subgr.	Mm.	Rousay Flags	Mm.
E I F E L I A N	Latheron Subgr./ Ham-Scarfsk.Subg.	Tp. Op. Dt.	Upper Stromness Flags	Tp. Op. Dt.
	Achanarras Horizon	Gm.	Sandwick Fishbed	Gm.
	Robbery Head Subgr.	Om. Dv. Ps.	Lower Stromness Flags	Ga. Om. Dv.
	Lybster Subgr.	Cc.		ost. Cc.
		Tm.		

Figure 1 Biostratigraphic table of Caithness, Sutherland and Orkney indicating faunal elements which are of importance for correlation. Bars indicate the approximate range. Abbrev.: arthr. arthrodire; Cc. *Cocosteus cuspidatus*; dipn. dipnoan; Dt. *Dickosteus threiplandi*; Dv. *Dipterus valenciennesi*; Ga. *Gyroptychius agassizi*; Gm. *Gyroptychius milleri*; Mm. *Millerosteus minor*; Pm. *Pentlandia macroptera*; Ps. New Dipnoan Genus; Om. *Osteolepis macrolepidotus*; *Osteolepis panderi*; ost. osteolepid; Ta. *Tristichopterus alatus*; Tm. *Thursius macrolepidotus*; Wf. *Watsonosteus*.

Specimens from the Lybster Subgroup which belong to the osteolepid *Thursius macrolepidotus* are often misidentified as *D. valenciennesi*. The specimens from the Robbery Head Subgroup include a new genus being described by Newman and den Blaauwen, and those from the John o' Groat Subgroup belong to *Pentlandia macroptera*.

The lacustrine sediments above the Achanarras-Sandwick fishbed show climatically controlled cycles resulting from long-term rise and fall of lake levels in an enclosed basin (Crampton and Carruthers 1914; Donovan *et al.* 1974; Donovan 1980; Trewin and Thirlwall 2002). These beds show playa-lake conditions, though in places the water may have been sufficiently deep to allow articulated fish skeletons to accumulate. The cyclicity of the sediments probably results from Milankovitch periodicities. Some of the sediments deposited in shallow water have polygonal mudcracks and shrinkage cracks. Many sediments show structures the shape of gypsum crystals or pseudomorphs showing gypsum crystal solution. These sedimentary structures are often preserved by sand infill, introduced by wind transport across

the dried up lake floors (Astin and Rogers 1991; Rogers and Astin 1991). Sediments indicating very shallow lake deposits produce only disarticulated fish remains, sometimes locally concentrated in 'bonebeds'.

From extensive field work and mapping of fish remains a biostratigraphic pattern has been distilled. Naturally there are some difficulties in correlation of fresh water sequences in the Orcadian Basin, where drying of parts of the lake and the prevalence of desiccation features occur in contrast with widespread lake extension conditions in which laminites were deposited. Details of the issues will be discussed elsewhere by den Blaauwen *et al.*, but from the point of view of the dipnoans, *D. valenciennesi* has been identified from the base of the Achanarras Horizon to the top of the Mey Subgroup on the mainland, and the equivalent Sandwick fishbed to the top of the Rousay Flags in Orkney.

Specimens used in this study come from the units indicated in the Figure 1, above the Achanarras and Sandwick fishbeds. They are common in the Latheron Subgroup and the Mey Subgroup in Caithness and in the Upper Stromness Flags and

the Rousay Flags of Orkney. Also specimens from Tynet Burn, one of the fishbeds from the nodule localities in the Moray Firth area, have been studied. Specimens of *D. valenciennesi* sampled in sediments indicating shallow lake conditions, are disarticulated and are mostly mature or even fully grown. Most specimens possess a well developed cosmine coating.

SPECIMENS EXAMINED

All the specimens examined have come from Caithness and the Orkneys. They have been taken from the collections of den Blaauwen, Michael Newman and Jack Saxon, and they have been placed in the National Museum of Scotland (NMS) collections. The new numbers are as follows:

G2004.10.1 From Clardon Haven, Caithness. Latheron Subgroup. Posterior end eroded *in situ*. Palatal tooth plates well developed.

G2004.10.2 From Clardon Haven, Caithness. Latheron Subgroup. Palate sectioned to show the 'cosmine' between the teeth.

G2004.10.3 From Clardon Haven, Caithness. Latheron Subgroup. Mandible with tooth plates.

G2004.10.4 From Thurso East, (the slates), Caithness. Latheron Subgroup. Mandible with left tooth plate lost.

G2004.10.5 From Thurso East, Caithness. Latheron Subgroup. Right palatal tooth plate. Sectioned horizontally, and vertically.

G2004.10.6 From Clardon Haven, Caithness. Latheron Subgroup. Pectoral girdle.

G2004. 10.7 From Thurso East, Caithness, Latheron Subgroup.

G2004.10.8 From Clardon Haven, Caithness, Latheron Subgroup.

G2004.10.9 From Buckquoy west of Aikerness, Mainland Orkney, Rousay Flags.

G2004.10.10 Same as 2004.10.9.

G2004.10.11 From Thurso East, Caithness, Latheron Subgroup.

G2004.10.12 to G2004.10.16 From Clardon Haven, Caithness, Latheron Subgroup.

GROSS FEATURES OF THE DENTAL SYSTEM

The Palatal Tooth Plates

New rows of teeth are introduced between the anterior sets of rows as spaces become available (Figures 2, 8A). Some specimens show symmetrical insertions of the two plates of the one specimen, but others do not. The specimen figured by White (1965, plate 1, figure 1) shows small teeth inserted between the first and second rows, and in places these teeth are more closely spaced. Specimen G2004.10.8 (Figure 2A) is remarkable in that it has a new irregular row of teeth anteromedially inserted,

and part of the original median row resorbed. The same specimen shows gaps for the occlusion with the mandibular teeth. Irregularity of rows is shown by G2004.10.5 which leaves spaces for the insertion of new rows on the mediolateral parts of the teeth. Obviously the new rows were formed wherever a space exists because of irregular growth in old rows, and we conclude that genetic control on the precise position of new teeth was limited. New rows occupy only a small part of the length of the head.

The parasphenoid is well defined, is up to three times the length of the tooth plates, and has a well-defined buccohypophysial foramen. The nasal capsules occupy about two thirds of the length of the plates. Most of the posterior buccal cavity is therefore not roofed by the dental plates. This point is emphasized by the mandible in which the dental plates are relatively small in relation to the whole structure.

Structure of the Mandible

The best specimens we have are of individuals which are a little above half grown, and show features which we consider significant. The tooth plates are 0.33–0.40 the length of the jaw (Figures 3 A,B), and the distance between the two tooth plates is large in comparison with the Early Devonian genera *Dipnorhynchus* and *Speonesydrion* (Campbell and Barwick 1984). The ratio of the median length to the total length of the mandible, is only about one third. Note also that the mandibular dental plates have a short median length in comparison with the posterior length. This is different from the shape of the palatal dental plates, suggesting that the contact between the mandibular and palatal plates was not one-to-one. This interpretation is supported by the fact that the inner face of the mandibular plate is turned ventrally, and could not have met the palatal plate on full closure of the jaw. This is standard for the assembled Late Devonian species (Barwick and Campbell 1996; Campbell and Barwick 1998).

A second point is that the anterior gap between the two mandibular plates is very large, and the unencumbered space for the tongue pad would be not only wide but also long and deep. The point of origin of the tooth rows have been resorbed, and on G2004.10.3 restorative dentine has been added to the anteromedian side of the tooth plate. The tooth plates of *Dipterus platycephalus* from a Scottish specimen in the Manchester Museum, and figured by Watson and Gill (1923, figure 34), also shows the reduced tooth plates similar to those described above. The cavities for the cartilage forming the articulation with the quadrate are deep and slightly doubled (Figure 3C), thus limiting the lateral movement of the mandible.

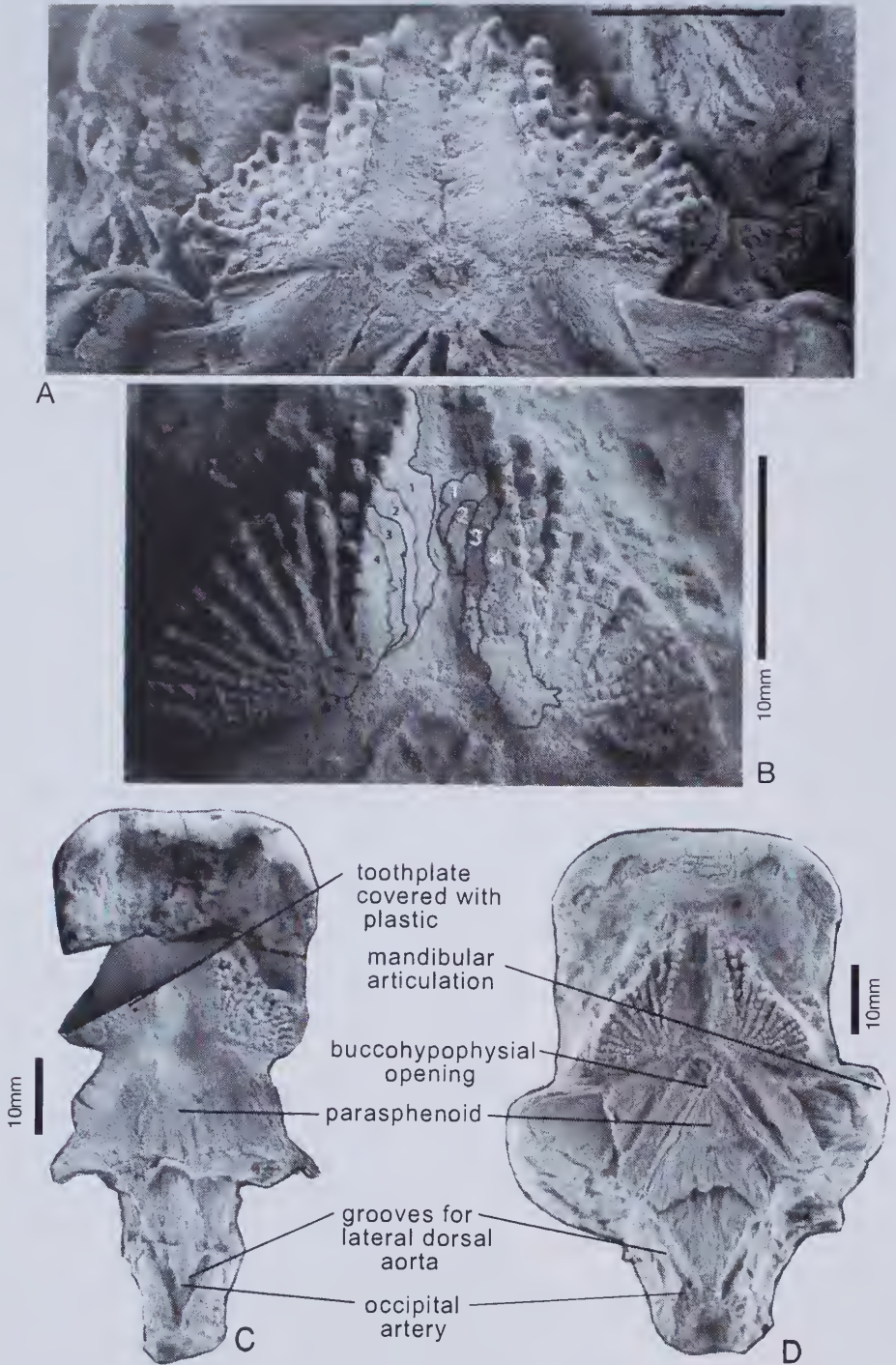


Figure 2 A, palate of G4004.10.8. Specimen antero-posteriorly compressed, 'cosmine' removed; bone on the posterior of the tooth plates. B, G2004.10.1, 'cosmine' on the palate; first row of teeth partly covered by 'cosmine'. C, palatal view of the specimen G2004.10.2; 'cosmine' sectioned from right palatal tooth plate. D, the specimen from which Figure 2B was prepared; squashed antero-posteriorly. Scale = 10mm.

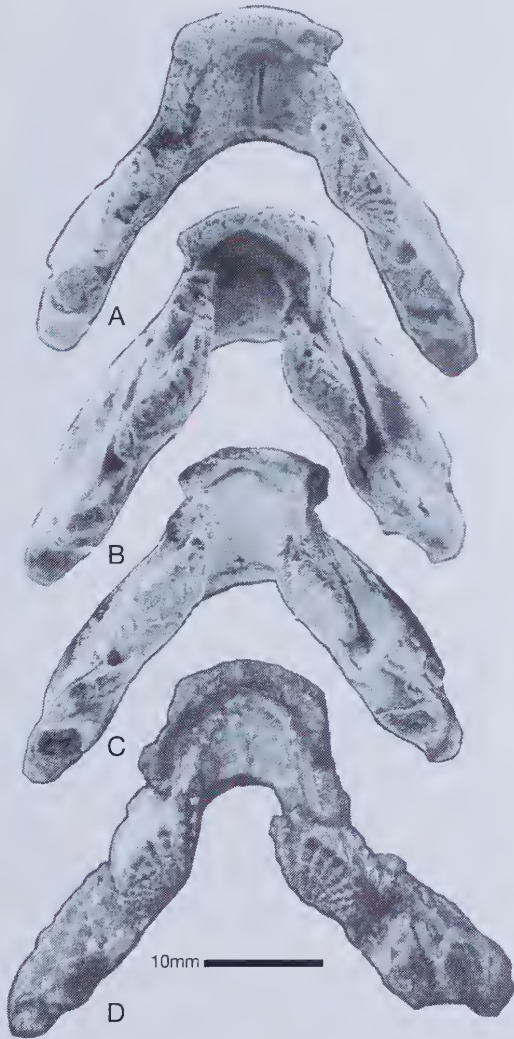


Figure 3 A–C, two small mandibles G2004.10.3 and G2004.10.4; A and B are dorsal views showing tooth-plates. C is a more posterior view of B showing the articulation cavities and the position of the adductor fossae. D, G2004.10.7 showing both tooth plates.

'Cosmine' on the Medial Parts of the Palatal Tooth

White (1965, plate 2) and Denison (1974, figure 4) figured a thin layer of tissue occupying the space between the two palatal tooth plates. It was termed 'cosmine' by both the above authors, because this layer has a shiny surface, it often contains a large number of pores, and superficially it has a resemblance to cosmine. But pores are not always present, and where pores are present, no pore canals can be found beneath them. This point and

the reality of Westoll lines will be considered later in this paper. The presence of enamel on the surface of this tissue is the most important point to be considered here.

Significance of These Gross Features

The functional significance of these features is largely related to air breathing. We consider these points under the following headings: extant air breathers; palatal plates and parasphenoid; tongue pad space; and brachial laminae

Extant air breathers

Extant dipnoans fall into two groups – *Lepidosiren* and *Protopterus* which are obligate air breathers, and *Neoceratodus* which is a facultative air breather. These two groups have been discussed by Thomson (1969), who has also compared them with the Middle Devonian *Dipterus*.

In *Lepidosiren* and *Protopterus* (Bishop and Foxon 1968) the tongue fits between the pterygoid tooth plates and makes a closing valve when air is depressed into the lungs. This is done by the anterior rotation of both the ceratohyal and the pectoral girdles. The air is stored in the parabronchial cavity partly roofed by the elongate parasphenoid, the teeth are small with respect to the size of the head and they are separated to leave a space for the tongue to close off the buccal cavity when air is forced into the lungs. Associated with this procedure is the increase in space between the mandibular tooth plates which allows the tongue pad to expand forwards. The ventral surface of the head is also able to expand the buccal cavity to permit more space for the retention of air. *Neoceratodus* has a different arrangement based on an opercular pump, and Thomson (1969, figure 5) shows the movement of the opercular fold during a breathing phase. In addition *Neoceratodus* has a massive ceratohyal which takes part in breathing movements.

Palatal Plates and Parasphenoid

The palatal plates in *Dipterus* are situated well anterior in the mouth, and they are well separated from each other. In comparison with such Early Devonian genera as *Dipnorhynchus* or the Late Devonian *Chirodipterus* the plates are very short. The parasphenoid has a long posterior projection, and extends back over a long distance behind the pterygoids. Both these features make for long orobranchial and parabronchial cavities.

Space for the Tongue Pad

The gap left for the tongue between the prearticulars is large and deep in comparison with that of Early Devonian genera *Dipnorhynchus* and *Speonesydrium*. The gap between the palatal tooth

plates is covered with 'cosmine', and this shows that the large tongue pad had ample room to lie between these plates when the mouth is closed. The enamel surface on the 'cosmine' shows that the epidermis was in contact with this surface. This is the ideal arrangement for the stop valve when the air was being forced into the lungs from the orobranchial and parabranchial cavities.

Pectoral Girdle of D. valenciennesi

We have access to several specimens of *D. valenciennesi* which are better preserved than any specimens previously described. The four specimens are now labeled G2004.10.6, G2004.10.13, G2004.10.14 and G2004.10.15. We will describe this material in a separate paper. The pattern of the branchial laminae and the scapulocoracoid are very similar to those on *Chirodipterus australis* (Campbell and Barwick, 1987) a marine form from the Late Devonian Gogo Formation, Western Australia. The branchial laminae would have operated in the same way in the two species.

Summary

Dipterus has a large opercular plate as well as small suboperculars, the movement of which would have produced a large expansion and contraction of the parabranchial chamber as detailed by Thomson (1969). We note that *Neoceratodus* uses an opercular parabranchial pump when breathing air, and uses the very large ceratohyals to push the air from the orobranchial and parabranchial chambers into the lung. On the other hand, the branchial laminae are so large and the ceratohyal so short, that *Dipterus* could not have used the methods of breathing adopted by *Lepidosiren* and *Protopterus*. We have concluded that *Dipterus* was a facultative air breather, though the structures could not have been as efficient as those of *Neoceratodus*.

We note that Schultze and Chorn (1997) consider that lungs were a feature of primitive osteichthyans, quoting the fact that lungs are present in primitive actinopterygians (e.g., *Polypterus*), actinistians, lungfish, and tetrapods. Campbell and Barwick (1999: 137–138) have commented on their arguments, and these will not be repeated here. Incidentally they offer no mechanism supporting their views. *Neoceratodus* is also gill breathing, and spends most of its life submerged. Comparison with *Dipterus valenciennesi* suggests that this Devonian form also had the capacity to use gill respiration as well as aerial respiration.

Our arguments are based on morphology of *Dipterus* and the extant dipnoans, and not on cladistics or the range of air breathing in some extant animals. Contrary to the argument of Schultze and Chorn (1997), we still maintain the marine Devonian dipnoans lacked the

morphological features which would indicate that they were air breathers.

DESCRIBED HISTOLOGY OF THE TOOTH PLATES

The histological structure of *D. valenciennesi* was not described from Scottish material until recently, because like all the bones at the fossiliferous localities, the teeth were deeply stained by organic carbon. White (1966, plate 1, figure 2) published a figure of a section of a tooth plate in which the end tooth was sectioned medially and showed a translucent core. The figured adjacent teeth apparently showed a bony core, presumably because they were from marginal sections of the teeth. Denison (1974: 39) commented on these structures, but his work has not been confirmed.

Smith (1984) described teeth from the specimens described by White (BMNH P44691), and later another specimen, BMNH P53537, from Caithness (Smith 1989). These papers give no details of the pallial dentine, and their structure of the tooth core is obscure. Comments will be made on this work later in this paper.

Kemp (2001) in her paper on petrodentine does not describe the histological structure of *D. valenciennesi*, and most ancient forms dealt with are of Carboniferous age. Because of this lack of direct analysis of *Dipterus valenciennesi* tooth plates, the discovery of well-preserved specimens now gives us an opportunity to place these plates in the primitive position which their stratigraphic position accords them.

INTERPRETATION OF DENTINE IN NEW MATERIAL

There is nothing more contentious than the terminology of dentine in dipnoan teeth. For present purposes Smith (1984, 1985, Table 1) has provided the basis on which subsequent work has developed. Further work on this topic can be found in Lison (1941), Barwick *et al.* (1997), Campbell and Smith (1987), Lund *et al.* (1992), Kemp (2001) and Reisz *et al.* (2004).

Vertical Sections of Teeth

The considerable advantage we have is the availability of growth stages of the teeth. Growth of the layers in the dentine can be outlined by a number of specimens. In the first instance we describe a number of teeth from a single section.

Sections through sediment with placoderm plates

Some specimens have structures sufficiently well preserved to show histological detail throughout the teeth. Section G2004.10.9 shows the best vertical

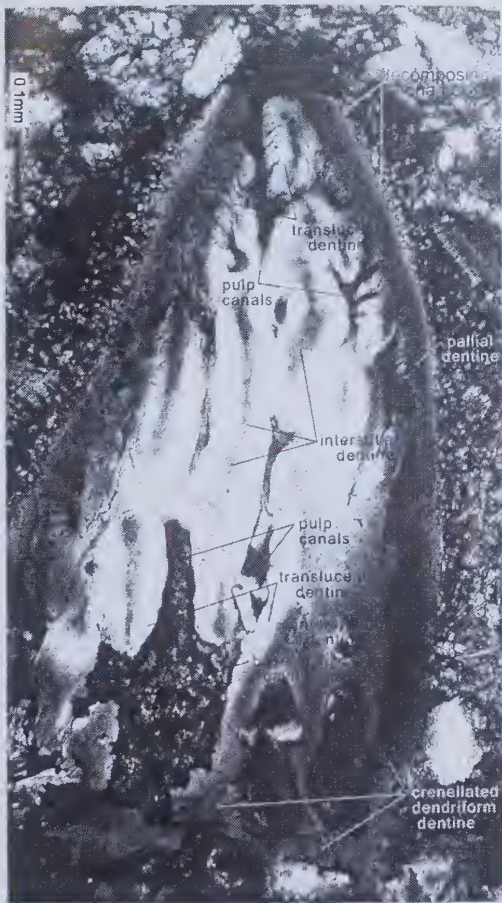


Figure 4 G2004.10.9. Vertical section in single polarized light; specimen was incompletely grown; enamel is largely destroyed; interstitial dentine grey in colour; translucent dentine around pulp canals.

tooth sections we have seen (Figures 4–6; 14E). The largest tooth in the section has a large basal pulp cavity, and the smaller teeth are in process of formation. These show the development of the histological structures.

The largest tooth has lost its apex, but on the same section two other small teeth, one at the lateral edge of the plate (referred to as the **lateral tooth** below) and the other being cut tangentially to the axis of the tooth (referred to as the **tangential tooth** below, Figures 6; 14E). The enamel is present around the margin of the lateral tooth, but it is partly destroyed by decomposition on all sides of the larger tooth. The core dentine consists of two different types of structure, clear translucent columns, and interstitial dentine columns (Figure 14E).

As Figure 4 shows, the **pallial dentine** is thickest towards the apex but fades away somewhat

towards the base. The edges contain some branched tubules which arise directly from the pulp canals, and these are either simple or branched. At higher magnifications, the tubules subdivide extensively towards their outer edges (Figure 5A) making a meshwork-like pattern. In the lower half of the tooth the pallial dentine shows very fine tubules, but at the base of the tooth, the pallial dentine turns inwards (Figure 5B) and has crenellated dendriform pattern. This is best known as **pedestal dentine**. Pallial dentine is well shown on the lateral tooth and the tangential tooth (Figure 6). It forms a dark layer which is also penetrated by tubules. In places the boundary between the pallial dentine and the core dentine is sharp, but in other areas the boundary is gradational.

On G2004.10.9, **interstitial dentine** is clearly exposed (Figures 4, 6). Dark columns of interstitial dentine extend into the basal pulp cavity where their outlines are clear. In the basal pulp cavity at high magnification the interstitial dentine shows an open-work structure, which is seen on all three teeth (Figures 5B; 6B; 14E). The implication is that the growing edge of the material in the basal pulp cavity is made of crenellated dendriform material, which has the same appearance as the pedestal dentine, and laterally this material joins the pallial dentine (Figure 5B). In the central part of Figure 4, and the distal parts of Figures 6A,C, the interstitial dentine becomes vaguely outlined, not because the section is marginal to the dentine layer but the dentine is partly transformed into translucent dentine.

The marginal tooth is very informative with respect to the formation of the interstitial dentine. As shown on Figure 6A, in the core of the tooth the interstitial dentine becomes rough in its outline towards the basal pulp cavity. On the left ventrolateral margin the interstitial dentine grades into the pallial dentine and ventrally into the pedestal dentine as shown on Figure 6B. The tangential tooth (Figure 6C) also shows the interstitial dentine extending to the basal pulp cavity.

The **translucent columns** are the most striking part of the core, and show up in plain light as a clear translucent structure. Near the crest of the large tooth the structure is clear (Figure 5A) and the translucent layer carries many tubules which are derived from the pulp canals, and in places these run through the layer into the pallial dentine. This is in an early stage of the tooth formation. In the central part of the tooth, the fine structure of the translucent layers is not clear, but it does contain small openings and vague lines. The mode of formation of this tissue is clearly demonstrated by this section (Figures 4; 5B; 14E). It was deposited against the interstitial dentine by cells in the pulp canals. The base of the large tooth shows a layer of

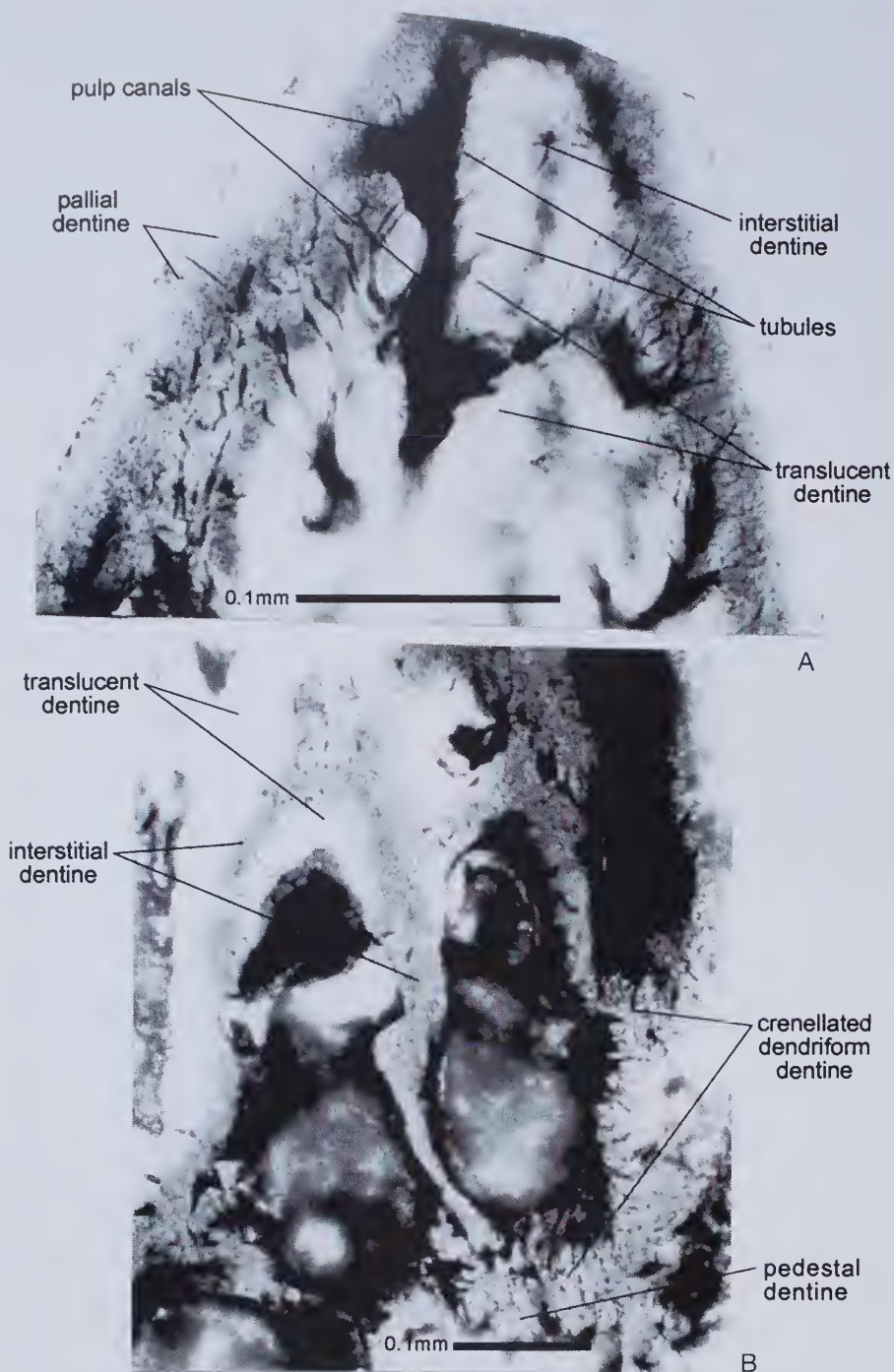


Figure 5 A, apex of Figure 4; tubules penetrating the translucent dentine and connecting with the pallial dentine; translucent dentine has replaced most of the interstitial dentine. B, enlargement of the bottom right of Figure 4; interstitial dentine around the pulp canals and translucent dentine deposited from the pulp canals on the interstitial dentine; crenellated edge of the pallial dentine joined by a column of vertical interstitial dentine, and basally joining the pedestal dentine.

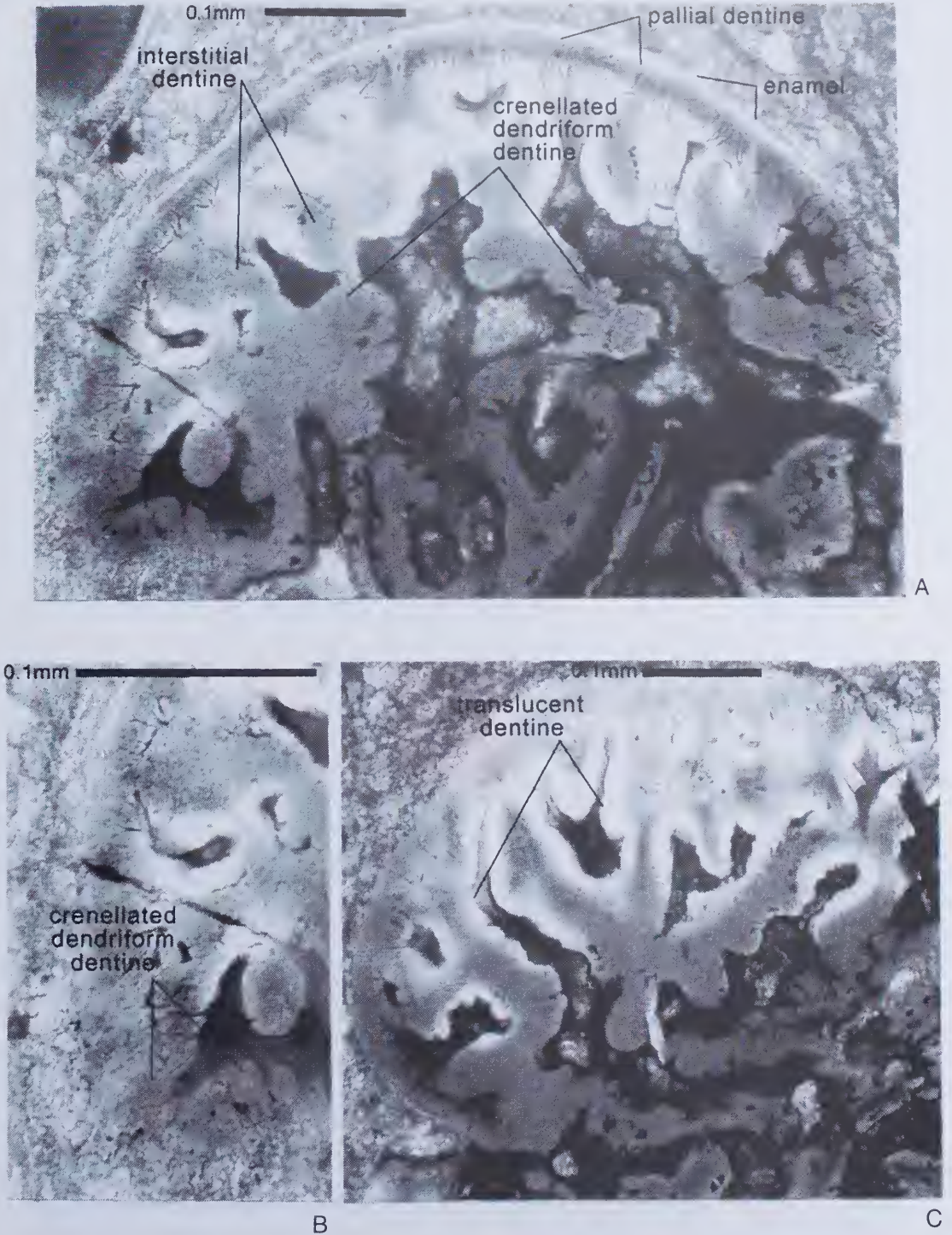


Figure 6 G2004.10.9 as on Figure 14E. A, the lateral tooth rotated; interstitial dentine runs from pulp to pallial dentine; pallial dentine with tubules; translucent dentine around pulp canals. B, bottom left of Figure 6A with pallial dentine joining with the pedestal dentine. C, the tangential tooth, Figure 14E; contact between interstitial and translucent dentine intergrading; translucent dentine often bulbous.

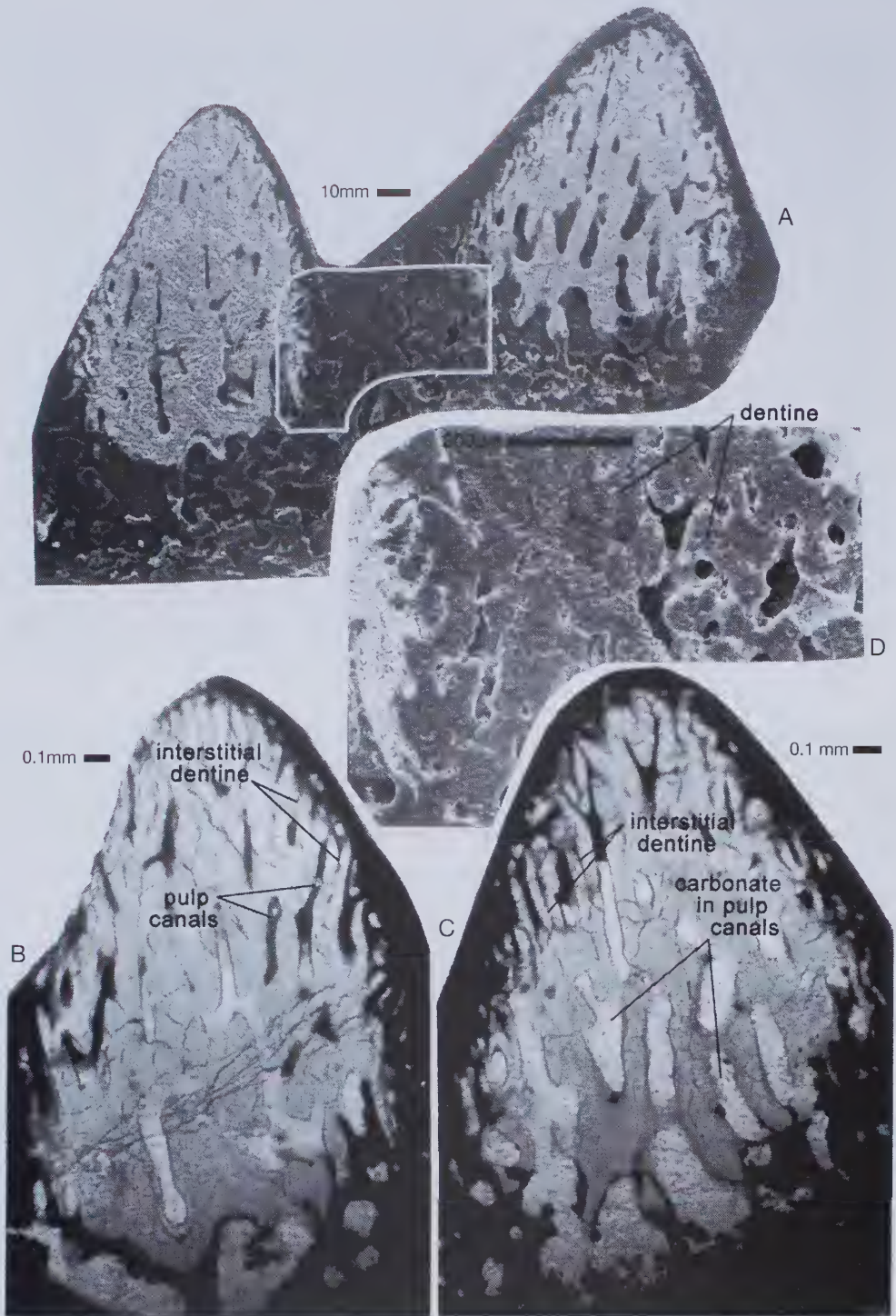


Figure 7 A, G2004.10.5C, slightly etched in acetic acid; core of each tooth extends into the basal bone. B and C, optical sections cut from the opposite face of Figure 7A; base of pulp canals with CaCO_3 ; interstitial dentine near margins but replaced medially by translucent dentine. D, enlargement of the area outlined in A; pallial dentine on left joined with pedestal dentine of right tooth.

translucent material deposited on both sides of the interstitial dentine, which grew down into the basal pulp cavity.

The tangential tooth shows new translucent layers deposited on pulp canals on the left side and open pulp canals with new translucent material on the right. The inner face of the translucent layers form slightly bulbous surfaces against the pulp canals (Figure 6C). The bone below the tooth is clearly distinguishable from the other layers because of the osteocyte spaces. Under high magnification, the pedestal dentine is not solid, but consists of a dendriform mass of material with numerous openings (Figure 6C), and this passes towards the tooth tip as interstitial dentine. The tangential tooth also shows the formation of the translucent layers. It is clearly laid down on the interstitial layers, has a bulbous surface in the pulp canals, and fades away into the basal pulp canal.

Other vertical sections

Two **fully developed teeth** on G2004.10.5 are joined together (Figure 7A). The translucent columns extending to the basal pulp cavity lying on the pterygoid bone. The pallial and pedestal dentine occupy a large part of the space between the adjacent teeth (Figure 7A,D). The enlarged illustration of this space shows the base of the left tooth and the broad base of the right tooth with the pallial, plus pedestal dentine also, preserved. The perforate nature of the translucent dentine as seen in single polarised light, and this is apparent over the whole length of the tooth. Only translucent dentine is visible in most of this section, as the interstitial dentine has been converted to translucent dentine. This change can be seen in both Figures 7B and C. The interstitial dentine is more obvious marginally, and this is what the illustrations on Figure 8 also show. The pallial dentine and the interstitial dentine merge at their junction on the sides of the tooth, and above the basal pulp cavity the two tissues also join. SEM examination shows that this material is composed of clumps of material which are roughly joined together.

This specimen also shows how new material is added to the margins of the tooth during growth. Figure 7B,C, shows the central part of the tooth formed from pulp canals that extend vertically from the basal pulp canal. Laterally some of these pulp canals branch and open to the margins of the tooth. In addition, as the width of the basal pulp cavity expands laterally during growth, new vertical pulp canals are developed and these also produce canals that open to the pallial dentine on the lower surface of the tooth.

On the lateral margins of Figures 7B,C, interstitial dentine is visible. These open to the pallial dentine marginally, but deeper into the tooth they

disappear and are transformed into the translucent dentine. Interpretation of these structures is best understood from the transverse sections of the teeth.

Transverse Sections of Teeth

Sections through G2004.10.5

A palatal plate, showing a number of teeth, has been cut transversely (Figure 8A), and this is one of the most illuminating sections we have seen. In the second row from the left, the second tooth from the front has the greatest number of pulp cavities, and we regard this as the most fully developed tooth in the section (Figure 8B). It shows the large central pulp cavities and new marginally added pulp cavities introduced to increase the diameter of the tooth. The second tooth in the third row from the left has fewer pulp canals and we use this as a tooth which has been cut closer towards its tip (Figure 10A,B).

Each tooth section shows that the margins have the most recently added dentine as shown on the vertical sections described above. Internally to this tissue is the dentine added earlier on in the tooth growth. By examining the sections from the margins to the central part of the core, the sequence of changes that took place can be observed.

The core dentine meets the pallial dentine in a clear edge. Some of the arcs of the crystalline material open outwards to the pallial dentine and are partly filled with pallial dentine (Figure 9C). Others are closed, and the spaces between the arcs are filled with a shiny substance which must be interstitial dentine (Figures 8E,F). This should be compared with Figures 7B,D. We also note that the columns of crystalline material are asymmetrical in that the pulp canals are displaced towards the lateral margins. And finally towards the pallial dentine, the crystalline arcs were open (Figures 8C-F).

What is the nature of these crystalline rings? Under crossed polars transverse sections through the teeth in the central part of the tooth, show that they have a band of dark coloured material around the pulp canals (translucent dentine) and lateral to that is a ring of the light coloured appearance (interstitial dentine). Towards the margin of the tooth, the central ring (translucent dentine) decreases in size and its lateral face is the most reduced; finally only an arc-shaped, incomplete crystalline ring remains. Surrounding these rings, both complete and incomplete, is dark coloured material which we infer from the vertical sections is interstitial dentine. The structure is illustrated in Figures 9A-C; 10C; 13E.

Tracing these dark layers towards the centre of the tooth, they join with shiny layers which separate the crystalline layers, and even further internally

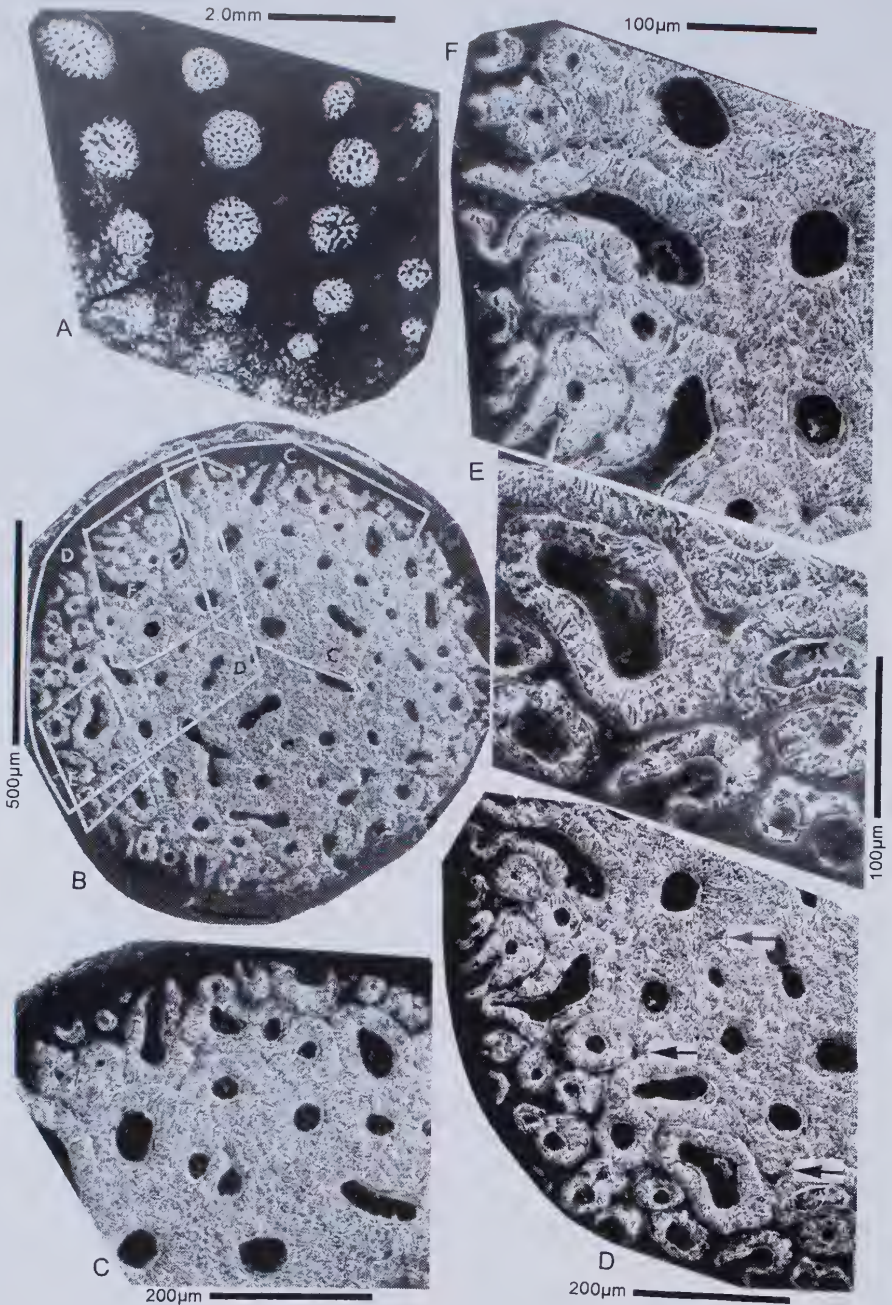


Figure 8 G2004.10.5D. A, SEM of polished surface of a palatal tooth plate; right row with branching. B, clockwise rotation of tooth second from the front in second row in A: large pulp canals central, smaller canals marginally; small marginal units surrounded by dark interstitial dentine; outlines of Figures C-F marked in white lines. C and D, several crystalline layers open to the pallial dentine; outer crystalline layers separated by dark material (interstitial dentine); dark layers become thinner medially, gradually replaced by transformation of the interstitial dentine to modified translucent dentine; circles mark the junction between crystalline layers around adjacent pulp canals; arrows mark the transition of the interstitial dentine incomplete; E and F, dark layers between the crystalline material with a shiny surface; white circles mark junction between adjacent crystalline areas.

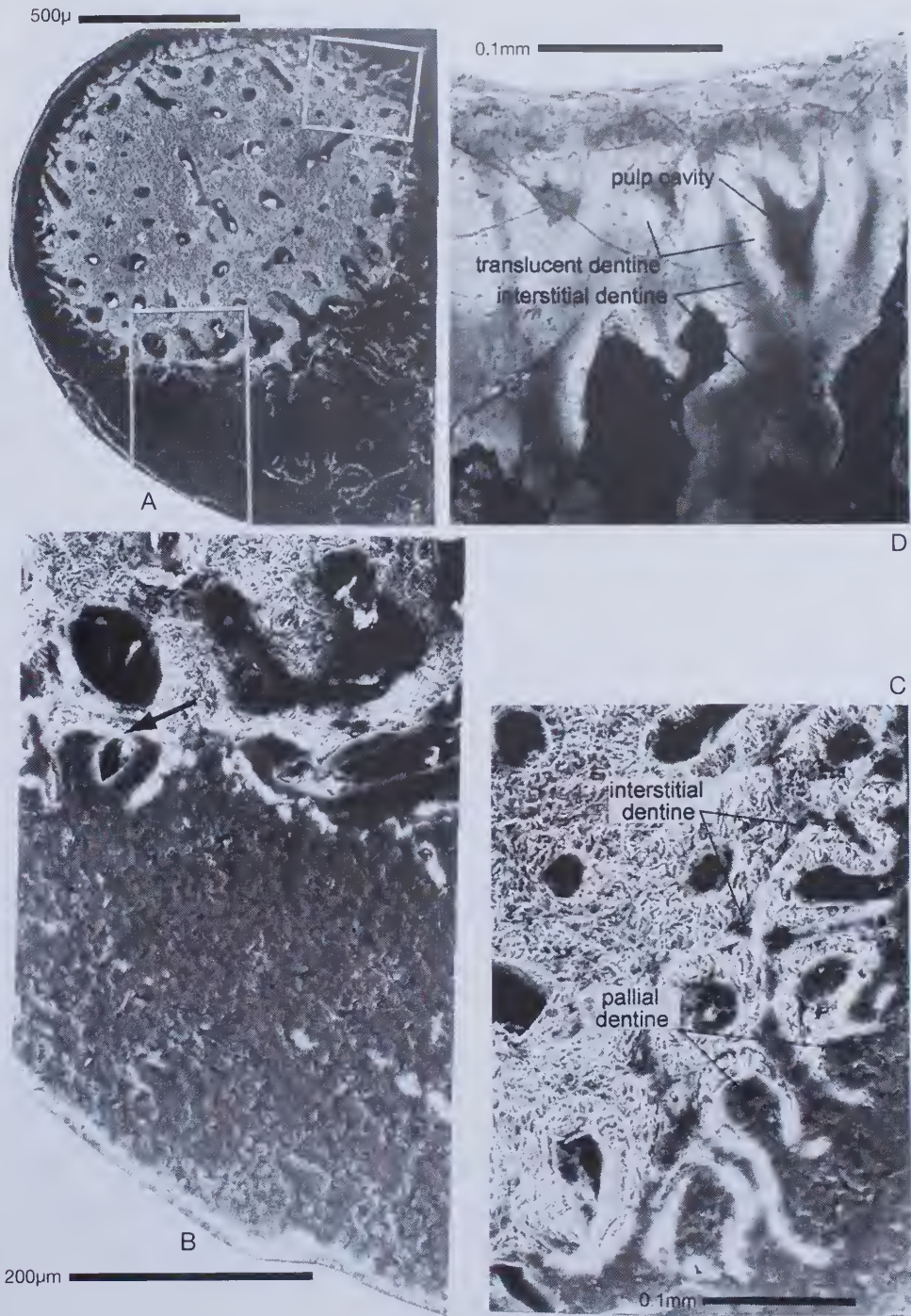


Figure 9 A, rotated oblique cross section of the anterior tooth in top left row in Figure 8A. B, enlargement of the lower area marked on Figure 9A; black arrow marks a pulp canal opening into the space in the open translucent dentine. C, enlargement and rotated area marked on the top right of Figure 9A. Crystalline material passing into pallial dentine; pallial dentine and interstitial dentine occupying spaces in translucent material. D, part of the flat dentine occupying the marginal edge of the tooth plate in G2004.10.10.

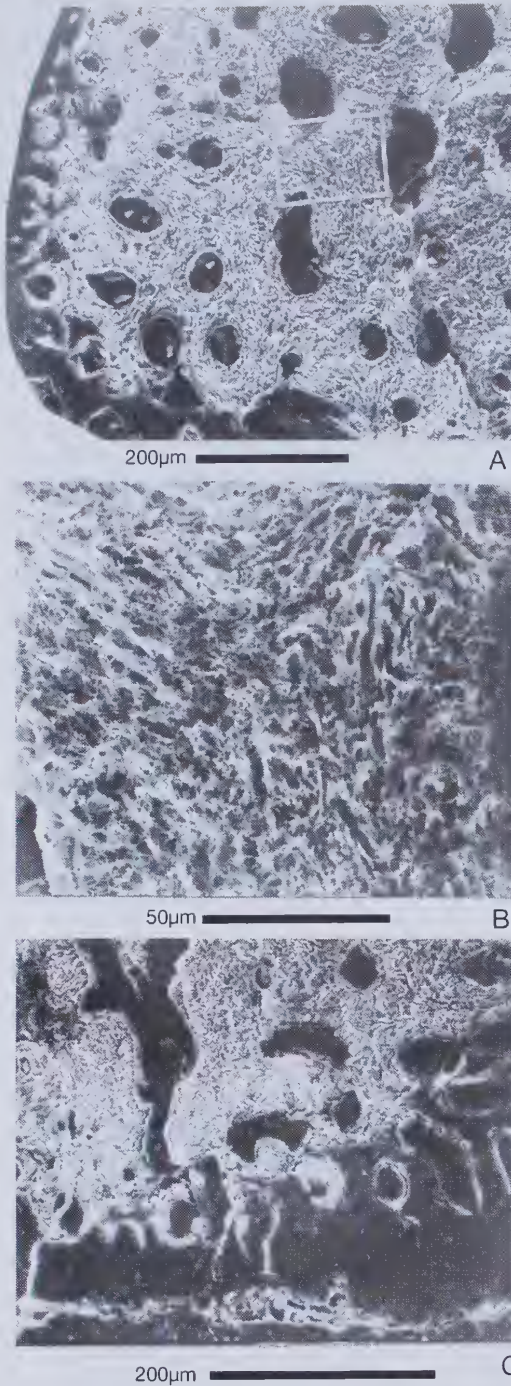


Figure 10 A, tooth second from the end in the third row of Figure 8A. B, enlargement of the area marked in A, with fine divisions in dentine. C, left side of the third tooth in the third row from left in Figure 8A; double edged crystalline layers, beginning to form around the new pulp canals.

these shiny layers become narrower and finally disappear. This is well shown on Figures 8D–F. In Figure 8F the junction between the three crystalline layers around the pulp canals is clear, and are occupied by very narrow bands of shiny material.

From these data we infer that the interstitial dentine is transformed to have a crystalline structure. To do this, histogenetic fluids must pass through the translucent dentine, and produce crystalline dentine from layers which have no internal structure when it is first deposited. The core of the tooth is therefore a composite structure, and shows different features at different levels of growth. This is what we saw in the vertical sections. The whole core structure of the tooth is a dynamically evolving tissue, composite in structure, and containing abundant pores. It does not have most of the features used for defining petrodentine.

These sections also show features of importance with regard to the pallial dentine. In several places the pallial dentine appears as a mass of clusters within which no detail can be seen. The best illustration comes from the margin of the first tooth on the left side, where the pallial dentine is obliquely cut (Figure 9A–C). Clusters of small patches of tissue make up the pallial dentine. Small gaps separate each patch and in places these are joined together to make a narrow canal. Compare this section with the vertical section on Figure 7D.

Isolated teeth from G2004.10.5

Slightly oblique sections show the internal structures admirably (Figures 13A,D,E). The presence of newly added marginal pulp canals in these sections together with the small number of total pulp canals, indicate that the teeth were either juveniles or cut half way along their adult length. The core material is crammed with perforations.

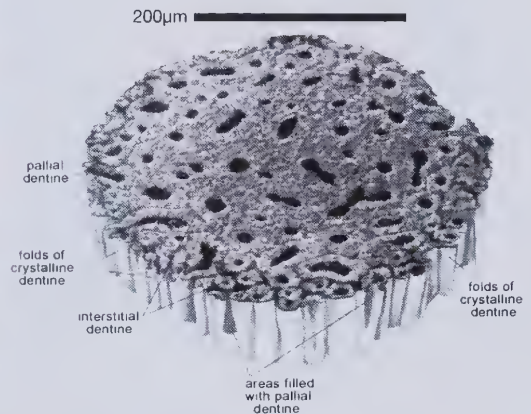


Figure 11 Reconstruction of a tooth drawn from Figure 8B rotated anticlockwise about 90°. Features marked. Scale applies to horizontal axis only.

Presumably the interstitial dentine was converted to translucent material, because the perforations were connected by microscopic canals along which histogenic substances were transmitted. Under crossed polars there is a band of dark-coloured material, and around that is a band of lighter coloured interstitial material. The size of the translucent material is not as large as one would expect from the other figured specimens.

The cross sections examined optically all have very similar structure. This is very important because it is necessary to interpret the section given by Smith (1984, figure 51).

Figures 13B,C,F from G2004.10.12 show a larger tooth which has been cut from near its base. The central part of Figure 13B shows the pattern where around each pulp canal is light coloured material (translucent dentine). Marginal to that the dark brown material (interstitial dentine) shows up well near the margins of the white material, but becomes more obvious marginally where the white material becomes narrower. The central part of the tooth is the oldest section and newer elements were added to the margins. Figures 13C and 13D show up well the different arrangement of the crystals in the translucent and interstitial dentines. In these figures the pallial dentine is very narrow, and gives a better impression of the fully grown tooth.

Compare Figures 13B,C, F with those of 13A,D,E, which is a smaller specimen that has lost its outer edges.

CRYSTALLINE ARRANGEMENT OF THE DENTINE

In this section we examine the crystallographic features of the tissue described above (see Figures 13–14). The dark coloured zone around the pulp canals in the central part of the core as shown up under crossed polars, could be interpreted in two ways. It may consist of fluorapatite crystals with the Z-axis approximately vertical; or alternately a random array of fluorapatite crystals, appreciably smaller than the thickness of the section, so that their net interference colour is close to zero. SEM images of the structure show an array of crystals and perforations which suggest that the second interpretation is correct.

Under crossed polars, there is another ring of light coloured material around this central ring. This seems to be made of crystals more or less parallel with the surface of the section, and fibrous bundles have weak rough ends on the light bands. This band represents the interstitial dentine. Examination under crossed polars and a gypsum plate, but with two quarter wave plates set at right angles forming a Benford Plate (Craig 1961), has been used, because this plate eliminates the quadrate effect produced by the extinction position.

The results of this are best shown on Figures 13E,F and 14D where the circularity of the interstitial dentine is more obvious than on the sections under crossed polars with a gypsum plate. In the corners between the separate pulp canal units there is often a small gap between the circular interstitial dentine. This would have been expected from the cross sections on Figure 8D where the arrows show gaps where the interstitial dentine has not been transformed. In the areas where the interstitial dentine has been altered, these small patches show up with a slightly different pattern.

In the marginal areas of the tooth each pulp canal has its own discrete, sometimes incomplete ring, which have been described above, and which is not in contact with the adjacent rings. The rings are separated by a dark coloured layer which is connected with the interstitial layer deeper in the tooth. Under crossed polars, with the gypsum plate and with the Benford plate inserted, the interference colours on the edge of these rings shows that the tissue represents the translucent dentine. This observation should be compared with the diagram of Smith (1984, figure 51).

COMPARISON WITH THE INTERPRETATION GIVEN BY SMITH (1984)

Smith (1984, figure 51) commented that her cross section of a tooth showed "birefringent bands of opposite sign in tissue between the dentine adjacent to the pulp canals". The central core of the tooth shows the dark array of crystallites formed from the translucent columns around the pulp canals. Note that this dark band of crystallites becomes narrower in the pulp canals closer to the tooth margin, and then opens out into the marginal pallial dentine. This is as we have described above for our material. The light bands in the figure are the interstitial dentine which has been transformed in the central part of the tooth, but marginally it has the appearance of isolated interstitial dentine. As we have shown from our specimens (Figures 8D–F; 13A,D,E) this marginal tissue is crystalline and is surrounded by dark layers which we interpret as interstitial dentine. Figure 51 of Smith's paper matches our interpretation exactly.

The statement by Smith (1984, figure 51) on the figure is not very meaningful, and the comment on page 394 that the presence of petrodentine is indicated by "bands of birefringence of opposite signs produce a woven appearance in polarized light (figure 50)" requires clarification. The inner layer around the pulp canals is translucent dentine and the outer layer is interstitial dentine which has an independent origin from the translucent dentine. The composite nature of the core dentine, made up of interstitial and translucent dentine, make it difficult to interpret her statements.

The other two of her figures of *D. valenciennesi* (figures 49–50) are also difficult to interpret. The plane polarized illustration (figure 49) has many pores and the core shows little differentiation into columns. Smith's figure 50, photographed under crossed polars, has patterns difficult to interpret compared with our Figure 4. Despite this, there is no doubt that it is the same tissue.

COMMENTS ON PETRODENTINE

The reader should examine the definition of petrodentine, a term first used by Lison (1941). In his original paper Lison makes the following points – petrodentine is light in colour; looks roughly homogeneous except near the pulp cavity where it contains cellular prolongations that are petroblasts; does not take up biological stains; much less birefringent than osteodentine in polarized light; calcified bands similar to the collagen bands; and contains little organic matter. Subsequent work by authors working on *Protopterus* and *Lepidosiren* which were used by Lison (Smith 1985; Kemp 2001) shows that petrodentine continues to grow from the from the core dentine in the earliest formed teeth; and petrodentine contains no denteons. Smith (1984) listed in a Table the criteria for the recognition of petrodentine, and this has been a valuable guide.

In the light of our current observations, we note the following characteristics of the core dentine in *Dipterus valenciennesi*.

(a) It was deposited at several levels in the tooth core, and was not deposited only in the early growth stages of the tooth. (b) Translucent dentine was first deposited from the pulp canals, in some instances well away from the basal pulp cavity. (c) Pulp canals are present even to the apical core of the tooth. (d) Tubules appear in the translucent dentine near the apex of the tooth, and extend into the pallial dentine. (e) Thin sections under crossed polars show that the growing translucent material was deposited in layers around the pulp canals. (f) Interstitial dentine occurs between the translucent dentine, and was first formed in the basal pulp cavity and also in the margins of newly formed additions to the tooth as it increases its width. (g) As the tooth grew, the interstitial dentine gradually converted to what appears to be translucent dentine. Additions to the tooth margin during growth also shows similar modifications to the interstitial dentine. (h) Both translucent and modified interstitial dentine contain large numbers of canals throughout their structure.

The next question arises – is there any evidence that the translucent material was deposited from a special layer of cells known as petroblasts? Alternatively could it have been deposited from some other kinds of cells spread more widely

through the pulp canals? Naturally one cannot observe petroblasts in fossils and so one has to observe features which indicate the presence of special cells from the position and distribution of certain hard tissues.

Firstly, the cells depositing the translucent dentine must have been very widely distributed and they were active during much of the life of the tooth. Secondly, the translucent material was not deposited to make a hard surface on which the wear of the teeth could be curtailed. It is even deposited in the core of the basal pulp cavity well away from the wear surface. Thirdly, the translucent material in the most exposed core of the tooth contains large numbers of tubules which would not have strengthened the tooth against wear. These points indicate that the cells used to deposit the translucent material were not petroblasts. The layering of the translucent material and its distribution show that the cells forming the material must have formed on the surface of the pulp canals throughout history of the tooth.

HISTOLOGY OF 'COSMINE' ON THE MEDIAN PALATE

Depositional Sequence of the 'Cosmine'

As we have indicated above, the distribution and histology of the materials forming the 'cosmine' is a matter of concern. The presence of an enamel (see below) layer on the surface indicates that an epithelial layer must have been present. As the tooth plates grew anteriorly and medially, the new sequences of 'cosmine' were added. Each 'cosmine' unit has a down-turned edge, or an edge against which the new layer of dentine was formed. This means that the sequence was not the result of resorption and redeposition, but rather a sequence of successive depositional layers. The same conclusion was reached by Denison (1974: 41).

The pattern of deposition figured by Denison (1974) is different from what we observe in our specimens, and from specimens figured by White (1965, plate 2, figures 2–4). The surface of specimen G2004.10.1 shows the central parts of the palate (Figure 2B). The right palatal plate has five layers of shiny smooth substance laid down in sequence. The oldest layer, labeled 4, lies up against the first formed teeth in the median tooth row. On the left plate the sequence is not so clear, but the pattern is the same. Some of the increments show fine perforations, but the others do not. Some show perforations along the line of increments, and some of these are up to 0.5mm in diameter. In addition the innermost layer covers up the posterior part of this tooth row, and on the left plate it extends posterior to the tooth plate. Presumably this means that soft tissue covered the posterior part of the

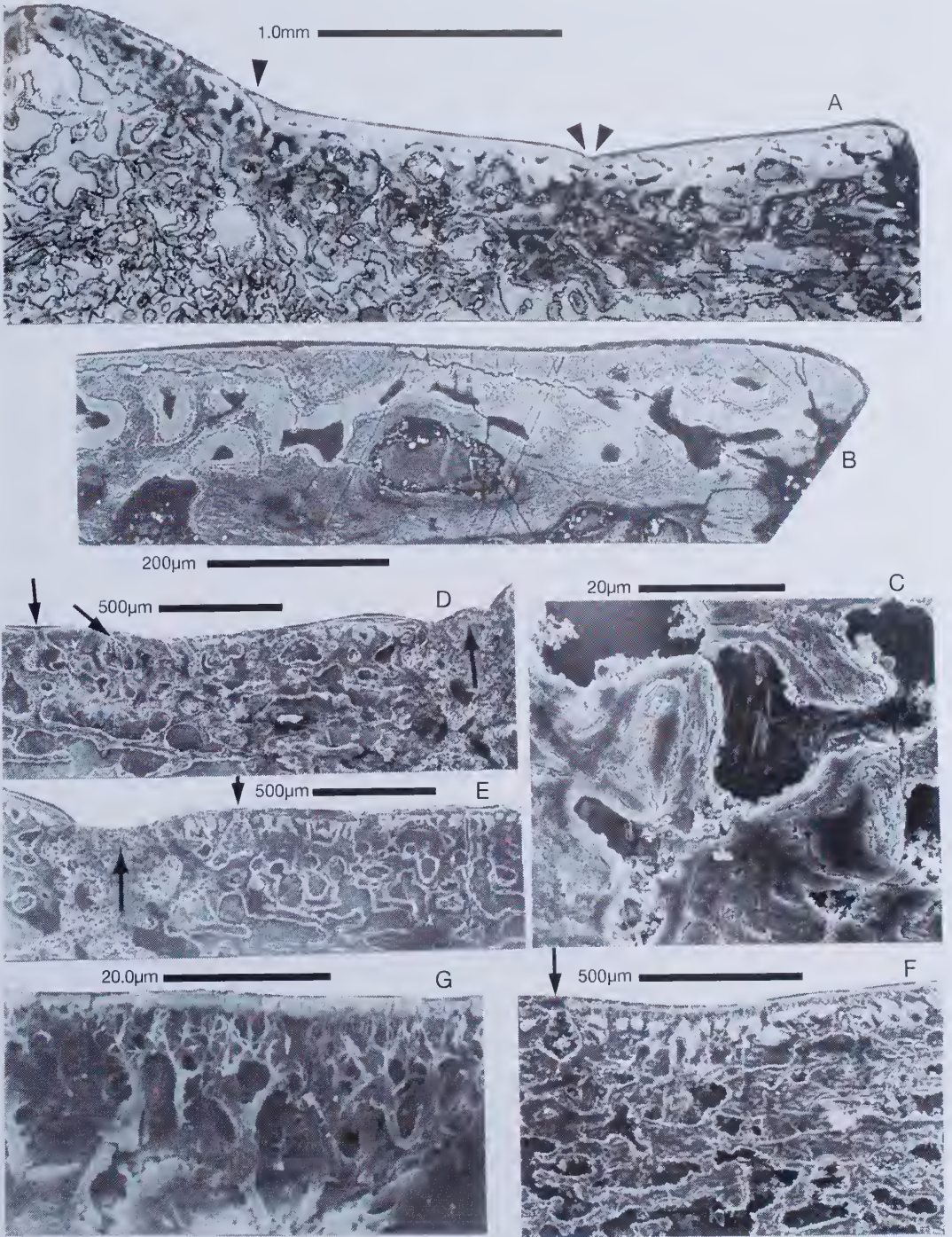


Figure 12 SEM cross sections of the cosmine on the palate. A–C, G2004.10.12; tooth on the left; single arrow marks overlap of completed unit; double arrow another unit completed on left side. B, right side of Figure 12A; white layer around pulp canals; bone at base. C, laminar character of the bone. D and E, G2004.10.2, large arrows indicate the mid-line; small arrows are pores in surface. F, G2004.10.2, cross section of cosmine, bone with osteocytes deeper. G, enlargement of the surface fine pores in the enamel; dentine tubules clear.

plate in the later periods of growth, and this would have been possible because this part of the palatal plate was not in contact with the mandibular plates in the later stage of growth. From the study of this specimen and the illustrations given by White (1965), we conclude that the distribution of the layers and the arrangement of the pores is highly variable, not only between the specimens but also on the two sides of the one specimen.

This still leaves unsolved the significance of the pores in the 'cosmine'. It is unlikely that they contained sensory tissue, but they must have allowed contacts between the soft tissue over the surface, and soft tissue in the canals. Enamel was deposited from an epithelium and this would have been served by nutrients carried through the pores from the canals. This would also account for the lack of symmetry in the distribution of the pores, and also for the concentration of pores along the junction between successive layers in some specimens, where the growing edge would have needed a supply of nutrients. But there are further tests that can be carried out before we reach a conclusion about the use of the term 'cosmine'.

Internal Structure of the 'Cosmine'

One test of the 'cosmine' hypothesis would be the presence of pore-canal beneath the pores in the surface. We note that the specimen figured by White (1965, plate 2 figure 1) does have a surface with many pores, and pores are found in places on some of our specimens. The shiny surface of the 'cosmine' is formed of radially arranged crystals as is normal for enamel. The enamel layer is perforated by abundant pores in Figure 12G. The pores open into the underlying layer with triangular pores (Figure 12D,E), but they have no indication of any internal structure. No section we have examined shows any sign of pore-canal systems, and in this respect it shows no similarity to most dermal cosmine. The large pores penetrate beneath the dentine pores into the underlying bone, but they have no lined connections to the surrounding tissues. The pores are just the means by which the nutrients were transferred to the epithelium which covered the palatal surface of the 'cosmine' during development.

Under the layer of tissue containing the dentine tubules is a layer with pulp canals surrounded by a light coloured material (Figure 12A,B), and around these are layers of banded material. The banded material therefore extends deeply into the light layer (Figure 12B). Beneath that is a layer with complex folding but without cytoplasmic spaces (Figure 12C). This layer of tissue lies directly on bone (Figure 12A).

Most of the above description is derived from G2004.10.12, but similar features can be seen on G2004.10.2.

COMPARISON WITH OTHER PRIMITIVE DIPNOANS

The structure of the dentine in the cores of the teeth of the tooth plates of *Dipterus valenciennesi* has structures different from other Early and Middle Devonian tooth plates whose details now have to be investigated. The following types of plates have been described – *Dipnorhynchus* and *Speonesydrion* from the Emsian of New South Wales (Campbell and Barwick 1984, 2000); *Tarachomyx* from the Early Devonian of Severnaya Zemlya (Barwick *et al.* 1997); *Ichnomyx* from the Taimir Peninsula (Reisz *et al.* 2004); and *Westollrhynchus*, from the Hunsrück Mountains in Germany (Schultze 2001). We do not include the Canadian Early Devonian genus *Melanognathus* here, despite Schultze's (2001) comments. It is a denticulated form with marginal teeth. *Westollrhynchus* is based on a single specimen from which no histology has been obtained. One can only consider this genus as having dubious validity.

Tarachomyx is the only genus which has plates comparable with those of *Dipterus*. Histologically, the translucent layers are separated from one another by layers of material described as interstitial dentine. No internal structure of the interstitial dentine was observed. These layers extend into the basal pulp cavity (Barwick *et al.* 1997, figure 9: 1–4; figure 10: 1–2; figure 13). Deposition of the translucent material took place from cells in the pulp canals. As shown by Barwick *et al.* (1997, figure 11:2), the translucent dentine is porous as is the translucent material in *Dipterus*. Because of the unusual features of this dentine, the authors could not refer to it as petrodentine, and we used the term 'compact dentine'. This view was queried by two of the reviewers of the paper who complained that there was no need for a new term. Barwick *et al.* persisted with the new name, but they did not suggest that it should have a formal status. They did indicate that this dentine did not have the characters of normal petrodentine.

This brings us to a position where we have to discuss why there are so many types of dental structures appearing in the Early Devonian (Campbell and Barwick 1990). Palatal biting first appeared in the Early Devonian, and this is a major change from marginal biting. In *Dipnorhynchus* the margins are added to by small enamel-covered excrescences and the plate thickens by deposition of dentine at the bone dentine boundary. In *Speonesydrion* the conical teeth are added marginally to the tooth plate, and thickening takes place by the deposition of new dentine at various points at the bone-dentine boundary. *Uranolophus* has marginal enamel covered ridges around the plate margins and small denticles covering the main mass of the plates (Campbell and Barwick 1988).

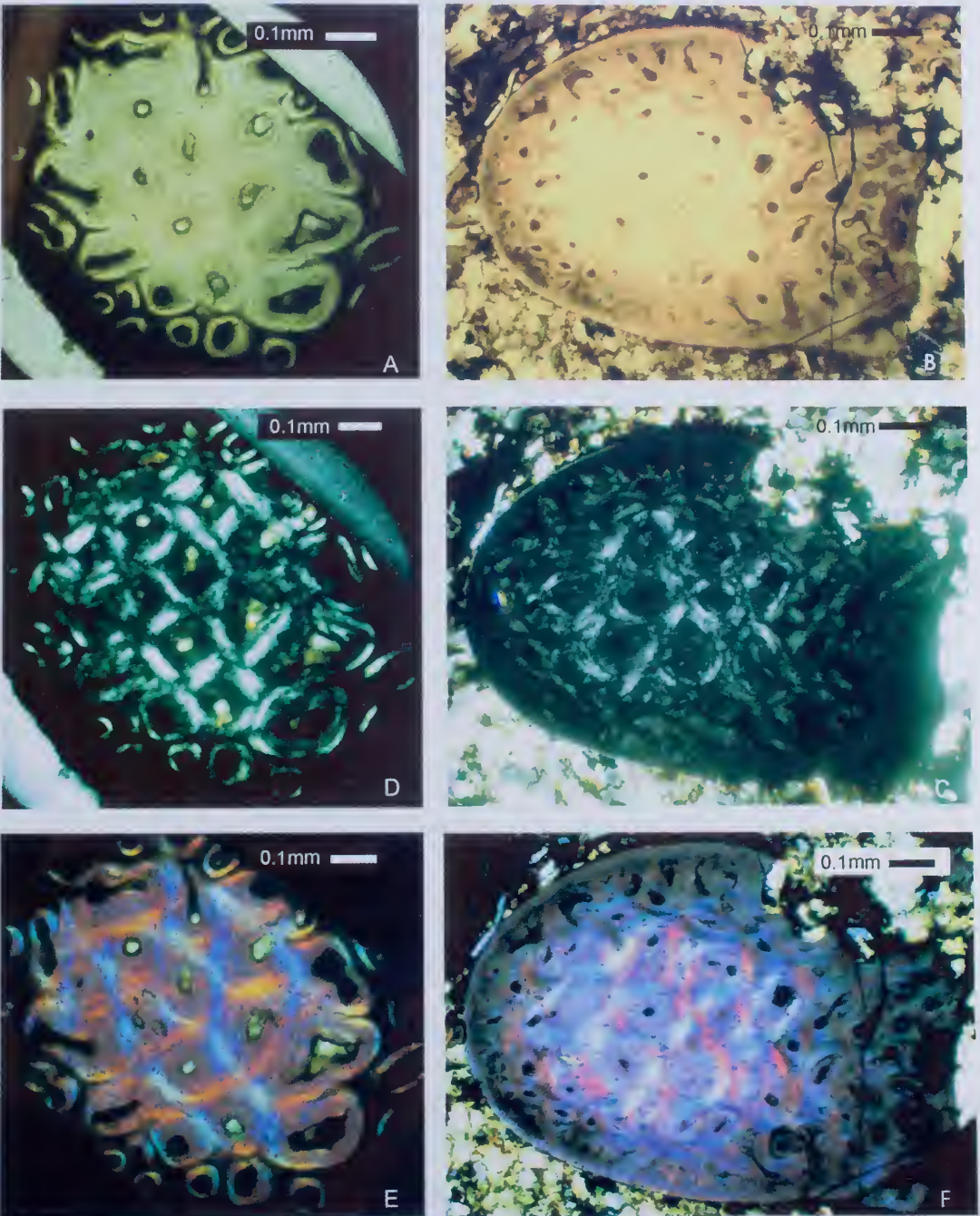


Figure 13 G2004.10.5B. A, in single polarized light; D, under crossed polars; and E with a gypsum plate and a Benford Plate. A, core dentine is finely perforate. D, pulp canals surrounded by dark layers of translucent dentine; bands around the translucent dentine are modified interstitial dentine, grey in colour and forming quadrate bands. E, zones around the pulp canals wider, and the interstitial dentine narrower than in D; circular arrangement of the interstitial dentine bands clearer; from middle of tooth to base, translucent dentine becomes narrower; in E rings of coloured bands formed of altered transitional dentine surrounded by dark interstitial dentine. B,C,F, G2004.10.12. Three similar photos of a single tooth; significance of the different colours explained in the text; F, emphasizes the small new dentines on the lower side, and the larger more open pulp canals at the top where new translucent dentine was being added.

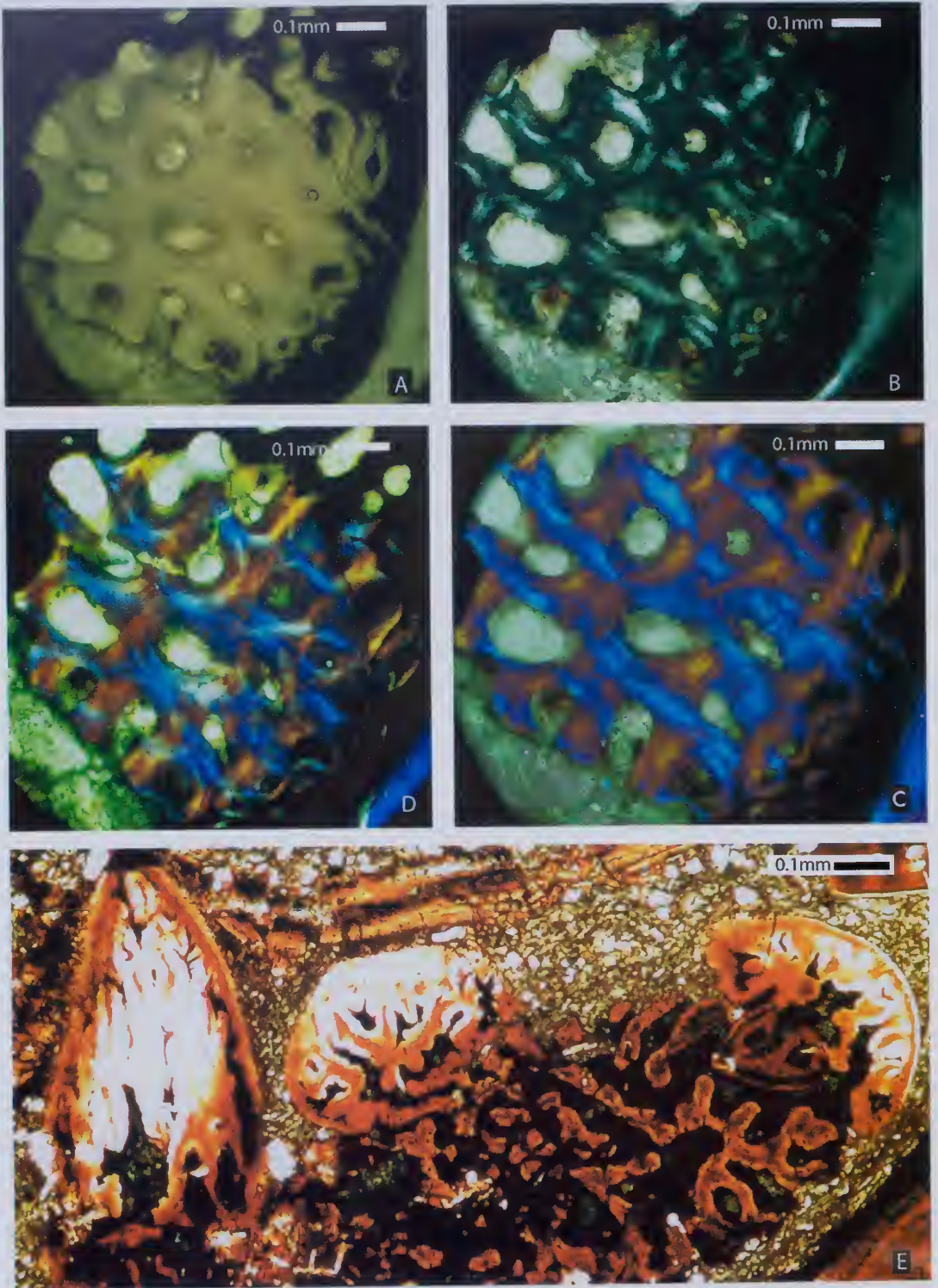


Figure 14 G2004.10.5A. Single tooth. A, in single polarized light; B, under crossed polars; C, under gypsum plate; D, gypsum plate and a Benford Plate. D, slightly rotated, and interstitial dentine shows a more circular pattern. E, G2004.10.9. Three teeth on a single slide; also illustrated on Figures 4-6.

And *Tarachomyx* has teeth as described above. That is, there are four types of plate formation introduced in the Early Devonian. Only teeth of the *Tarachomyx* type are successful in the later history of the Dipnoi. It has been shown that teeth are added marginally in later dipnoans and have a 360 Myr history (Krupina 1995, Reisz and Smith (2001) and Smith and Krupina (2001)).

All of these types are discrete; they cannot be transformed from one type to the other. This then raises the question of the origin of new structures at a time when a major new development takes place in evolution – in this case palatal rather than marginal biting. This matter has been discussed in works by Raff (1996), Shubin and Marshall (2000) and Minelli (2003). It is becoming apparent that the introduction of new major features in the phenotype is probably the result of production by gene regulation. As Shubin and Marshall (2000, p. 331) report... 'major evolutionary changes may not be due to changes in the number or structure of genes *per se*, but may be due to changes in their regulation (Carroll, 1995, 2000). Indeed the changes in the spatial pattern and timing of the gene activity play an important role in generating variation at both small and large phylogenetic scales.' This article was reviewed by Russell (2001). The new designs have a genetic basis, and there is no way these designs can be changed from one type to another.

If gene regulation is the controlling factor in producing new designs in organisms with palatal biting, as the above quotation indicates, similar regulation factors may have operated on each of the basic designs later in their history. Consequently each of the tooth patterns found in the Early Devonian could have developed new structures, and these would be the basis for outlining changes in the Middle and Upper Devonian. So the use of cladistic methods to recognize relationships in these later forms will involve comparison between genera which have already separated into groups which have separated by gene regulation. Hence comparison of so-called synapomorphies will involve comparisons which are convergences carried over from the primitive forms which gave rise to the original dispersion. For this reason the cladistic analysis of the kind given by Schultze (2001), which uses the statistical methods to develop character-state optimization, will be valueless. Attention must be paid to such a possibility in outlining the evolutionary pattern in late Palaeozoic dipnoans. A more complete discussion is given in work on *Speonesydrion* (Campbell and Barwick in press).

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Guide to Authors

Subject Matter:

Reviews, observations and results of research into all branches of natural science and human studies will be considered for publication. However, emphasis is placed on studies pertaining to Western Australia. Longer papers will be considered for publication as a Supplement to the *Records of the Western Australian Museum*. Short communications should not normally exceed three typed pages and this category of paper is intended to accommodate observations, results or new records of *significance*, that otherwise might not get into the literature, or for which there is a particular urgency for publication. All material must be original and not have been published elsewhere.

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The International System of units should be used.

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The original and two copies of manuscripts and figures should be submitted to the Editor, c/- Publications Department, Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986. They must be in double-spaced typescript on A4 sheets. All margins should be at least 30 mm wide. Tables plus heading and legends to illustrations should be typed on separate pages. The desired position for insertion of tables and illustrations in the text should be indicated in pencil. Tables should be numbered consecutively, have headings which make them understandable without reference to the text, and be referred to in the text.

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