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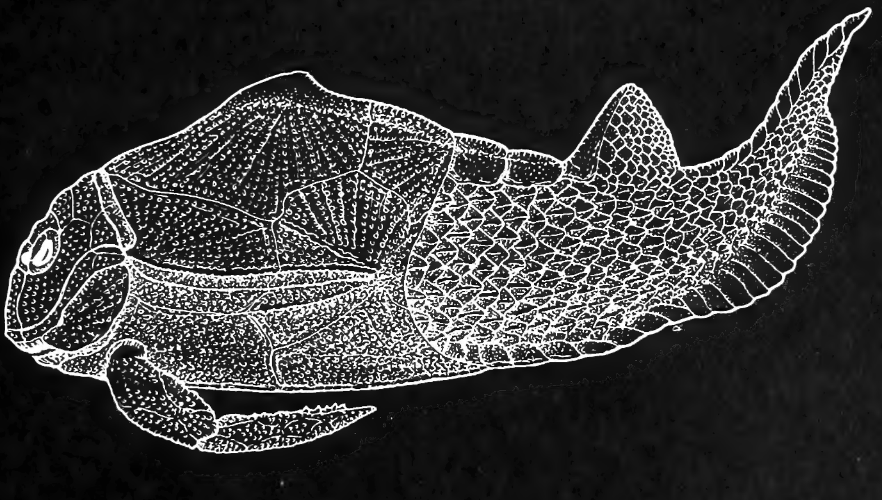

NATURAL HISTORY IN ALL ITS BRANCHES

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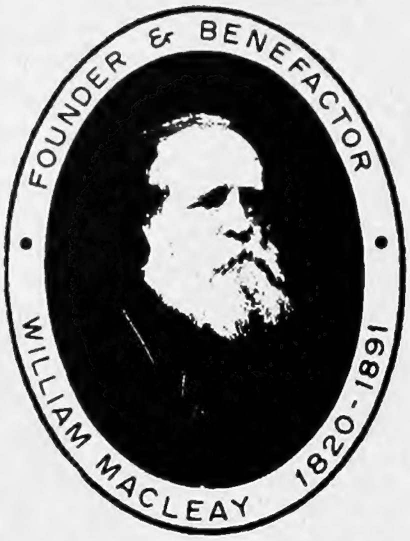

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Cover motif: Reconstruction of the placoderm fish *Sherbonaspis hillsi* Young and Gorter (1981), from Hunt and Young, this volume, page 76.

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Volume 132 will be the last issue of the *Proceedings of the Linnean Society of New South Wales* to be published in hardcopy, paper format. Starting with Volume 133, the *Proceedings* will be published electronically.

Subscriptions and membership fees paid for 2010 will cover both Volumes 131 and 132.

At the end of each year, beginning December 2011, papers published on the net during the year will be compiled as the next sequential volume and put onto a CD disc. That disc will be provided free of charge to all subscribers and members who were financial at the end of 2010.

During the year, as manuscripts are received and processed, they will be put onto the net immediately when accepted.

This is clearly the most dramatic change since the first volume was printed in 1875. However, as can clearly be seen from the small size of this volume, authors are moving away from the slow, traditional means of publication to the more rapid and more widely distributed services offered by electronic journals.

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Full details will be published in Volume 132 and on the Society's web page.

Michael L. Augee
Editor

The Middle Triassic Megafossil Flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 8. The Genera *Nilssonia*, *Taeniopteris*, *Linguifolium*, *Gontriglossa* and *Scoresbya*

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Holmes, W.B. K., Anderson H.M. and Webb, J.A. (2010). The Middle Triassic Megafossil Flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 8. The Genera *Nilssonia*, *Taeniopteris*, *Linguifolium*, *Gontriglossa* and *Scoresbya*. *Proceedings of the Linnean Society of New South Wales* **131**, 1-26.

Ten taxa of simple leaves in the genera *Nilssonia*, *Taeniopteris*, *Linguifolium* and *Gontriglossa* and a lobed leaf in the genus *Scoresbya* are described from two quarries in the Middle Triassic Nymboida Coal Measures of the Nymboida sub-Basin in north-eastern New South Wales. The new species *Nilssonia dissita* and *Taeniopteris adunca* are based on previously unpublished material from Queensland together with conspecific material from Nymboida. An additional four new species from Nymboida are described; *Taeniopteris nymboidensis*, *Linguifolium parvum*, *Gontriglossa ligulata* and *Scoresbya carsburgii*.

Manuscript received 1 March 2010, accepted for publication 29 May 2010.

KEYWORDS: Middle Triassic flora, Nymboida Coal Measures, palaeobotany, simple fossil leaves.

INTRODUCTION

This is the eighth paper of a series describing the early-middle Triassic Nymboida flora. Part 1 of this series (Holmes 2000) described the Bryophyta and Sphenophyta, Part 2 (Holmes 2001) the filicophyta, Part 3 (Holmes 2003) fern-like foliage, Part 4 (Holmes and Anderson 2005a) the genus *Dicroidium* and its fertile organs *Umkomasia* and *Pteruchus*, Part 5 (Holmes and Anderson 2005b) the genera *Lepidopteris, Kurtziana, Rochipteris* and *Walkomiopteris*, Part 6 (Holmes and Anderson 2007) the Ginkgophyta and Part 7 (Holmes and Anderson 2008) the Cycadophyta. In this paper the simple leaves in the genera *Nillsonia, Taeniopteris, Linguifolium* and *Gontriglossa* together with the enigmatic lobed leaf *Scoresbya carsburgii* are described.

A description of the Coal Mine and Reserve Quarries, the source localities of our described material together with a summary of the geology of the Basin Creek Formation, the Nymboida Coal Measures and the Nymboida Sub-Basin were provided in Holmes (2000).

METHODS

The material described in this paper is based mainly on collections made by the senior author and his family from two then-active Nymboida quarries (Coal Mine Quarry and Reserve Quarry) over a period of forty years. The specimens noted in Flint and Gould (1975), Retallack (1977), Retallack et al (1977) and Webb 1980 were examined in the collections of the Australian Museum, Sydney, the Department of Geology and Geophysics of the University of New England, Armidale and the Queensland Museum, Brisbane..

The University of Queensland PhD thesis on "Aspects of Palaeontology of Triassic Continental Sediments in South-East Queensland" by J.A.Webb (1980) included the descriptive taxonomy of fossils of simple leaves, similar to those that form the subject of this paper. In addition to his own extensive field collections Webb also examined all available and relevant material in State and private collections. Descriptive taxonomy in the past has so often been based on very limited and often fragmentary material. From Webb's extensive range of material it was possible to gain a better understanding of species boundaries through the natural range of variation occurring within the fossil populations. On the basis of floral similarities, the Esk Formation (Toogoolawah Group) of south-east Queensland and the Nymboida Coal Measures of north-east New South Wales were deposited contemporaneously in the Anisian-Ladinian (Flint and Gould 1977, Rigby 1977). Regrettably most of Webb's research was never published. Because of its relevance to this paper, two new species presented below are based on his original descriptions and types with Webb acknowledged as the author. Taxonomically comparable Nymboida specimens are illustrated and listed as "Additional Material".

Since the completion of the research by Webb (1980) new studies have been published on similar taxonomic groups from other Gondwana Triassic floras that are relevant to this paper. Retallack (1980) reviewed the Middle Triassic Tank Gully flora of New Zealand and proposed a new combination for *Linguifolium tennison-woodsii*; Artabe (1985) described six *Taeniopteris* species from Los Menucos Formation of Argentina; Anderson and Anderson (1989), in their taxonomic revision of the South African Molteno gymnosperms described and extensively illustrated nine species of *Taeniopteris,* five species of *Linguifolium* and three species of *Gontriglossa*; Gnaedinger and Herbst (1998) described three species of *Taeniopteris* and three species of *Linguifolium* from El Tranquilo Group of Argentina; Gnaedinger and Herbst (2004a) described ten species of *Taeniopteris* from northern Chile, using a statistical analysis of venation characters; Gnaedinger and Herbst (2004b) described one *Linguifolium* sp also from northern Chile and Herbst et al (2005) listed one *Taeniopteris* sp. and two *Linguifolium* spp from the Lake District of Chile.

The Nymboida specimens are preserved in mudstones, siltstones and sandstones as carbonaceous compressions or impressions in which the gross morphology is usually well-preserved. However spores and cuticles have been destroyed by a tectonic heating event during the Cretaceous Period (Russel 1994). Therefore our identification of taxa is based only on characters of gross morphology.

The exact stratigraphic horizon or detailed source of much of our Nymboida specimens is uncertain as most were collected from fallen blocks during quarry excavations. The Coal Mine Quarry has not been active for some twenty years but the high working face, although now rather weathered, provides an excellent exposure of beds that demonstrate the palaeo-environmental conditions at the time of deposition and was described by Retallack (1977). In 2006 the Reserve Quarry was bulldozed into a featureless bowl – "for restoration and safety purposes" and the fossiliferous horizons are now hidden.

The Nymboida material described in this paper has been allocated AMF numbers and is housed in the palaeontology collections of the Australian Museum, Sydney.

DESCRIPTIVE TAXONOMY

Without supporting cuticular evidence and lack of affiliation with any fertile structures for a definite systematic placement, the leaves described below are regarded as form genera in Gymnospermae – sedis incertae. On the basis of preserved cuticle *Nilssonia* leaves with haplocheilic stomata have been placed in the Cycadales and leaves of taeniopterid morphology may belong in several groups from ferns to cycads. Anderson and Anderson (2003) placed their Molteno *Taeniopteris* species in the Pentoxylales based on affiliation evidence and similarly they placed *Gontriglossa* in the Gnetopsida. The affinities of *Linguifolium* remain uncertain although Retallack (1980) suggested an affiliation with the seeds *Carpolithus mackayi*. *Scoresbya* has been speculated as being a fern, a seed fern, a member of the Caytoniales (Taylor and Taylor 2009) or even a pro-angiosperm (Weber 1995).

Gymnospermae incertae sedis
Genus *Nilssonia* Brongniart 1825

Type species

Nilssonia brevis Brongniart 1825

Nilssonia is a form genus that includes simple linear to oblanceolate leaves to irregularly pinnate leaves. It has a worldwide distribution and ranges from the Triassic to the Cretaceous. The main gross distinguishing character of the leaves is the dorsal attachment of the lamina which completely covers the mid vein. The appearance of this character is often an artefact of preservation, eg the fossil may be an impression of the upper or lower leaf surface or an internal or external cast or mould that often masks the form and place of attachment of the lateral veins to the midrib.

The venation pattern of leaves from Gondwana localities differs somewhat from that of species described from the northern hemisphere in the more common bifurcation of the lateral veins and their straight and parallel course to the margin. Similar simple leaves in which the lamina does not completely cover the mid vein and without preserved cuticle are placed in the form genus *Taeniopteris*. Where cuticle information is available, the haplocheilic stomata and trichomes indicate cycadalean affinities. No cuticle is preserved on the Nymboida material. Some specimens in our Nymboida collections can be placed in a previously unpublished species as described by Webb (1980). Note this species is attributed to Webb.

Nilssonia dissita J.A.Webb sp. nov.

Figures 1A–C; 2A, B; 7A

Selected synonymy

1917 *Taeniopteris crassinervis* (Feistmantel) Walkom, p.38, Pl. 1, fig. 2.

1975 *Nilssonia* cf. *princeps* (Oldham and Morris) Seward; Flint and Gould, p.71.

1980 *Nilssonia dissita* Webb, p. 87, Pl.11, figs 3, 6, 8, Text figs 18 c, d (Unpubl.)

Diagnosis

Large simple leaf 65-150 mm wide; midrib 2.5–4 mm in width; lamina covers whole of mid-vein; secondary veins arise from the dorsal surface of a moderately wide central rib at fairly acute angle, then curve broadly to run at 80°–90° to margin; individual veins frequently bifurcate once, usually as they leave the central rib, occasionally fork a second time; density of venation 9–16 / 10 mm.

Description (revised to include new Nymboida material)

Leaves are simple, oblanceolate with undulate to entire margins and wavy to smooth surface, tapering to obtuse apex. Length from c. 200 to >300 mm, the leaf base is not known; width at mid lamina ranges from 60 –150 mm. Lamina is dorsally attached and completely covering the mid vein. Lateral veins diverging from a mid point above the mid vein at an angle of 50°–70°, arching to run at a high angle (70° – 90°) straight and parallel to the margin. Many veins bifurcate once, usually as they leave the central rib; a few subsequently fork a second time but never anastomose; veins coarse with a density 9–16 / 10 mm. Mid vein when exposed ranges in width from 1–4 mm.

Holotype

GSQ F12897

Type Locality

Geological Survey of Queensland Locality 1552, Esk Formation, Toogoolawah Group

Additional material

GSQ12898, Esk Fm. UNEF13443, AMF120989, AMF130180, AMF130181, AMF130182, AMF130183, all from Coal Mine Quarry, Nymboida CM. Also the material listed by Webb (1980), mostly from the Esk Formation of Queensland.

Name derivation

dissitus – Latin – *distant, apart,* referring to the widely spaced venation.

Discussion

Previous material from Nymboida (Flint and Gould, 1975) was recognised by Webb (1980) as questionably belonging to this species. From our new collections specimen AMF130180 is a block showing two leaves (Fig. 2B), one almost complete, preserved in almost three dimensions in white sandstone. The lamina of the more complete leaf, in places, completely covers the mid vein as can be seen by the lateral veins appearing to adjoin in mid lamina. The incomplete specimens AMF130182 (Fig. 2A) and AMF130183 both show sections of a leaf with adjoining lateral vein bases over the mid vein. In other parts of these leaves and similarly in the full length of AMF130181 (Fig.1C) the mid vein is exposed as an artefact of preservation. These leaves are included in this species based on the form, course and density of their veins and there being no evidence that the veins were laterally attached to the margin of the mid vein.

Nilssonia moretonii Walkom 1928

Figure 8A

Synonymy

1928 *Nilssonia moretonii* Walkom, p. 466, Pl. 25, figs 2, 3, 7.

1980 *Nilssonia moretonii* Walkom; Webb, Pl 10, figs 1, 4, 6, 7.

1989 *Taeniopteris moretonii* (Walkom) Anderson and Anderson, comb. nov. p. 376, fig. 3; p.547, figs 5, 6.

Description

A simple strap-shaped leaf with entire or slightly lobed margins; complete leaf unknown, from 30 – 110 mm wide; lamina covering whole of mid vein; lateral veins departing from a central line above the mid vein at an acute angle immediately arching then proceeding straight and parallel to the margin. Veins frequently fork on leaving the central rib and again soon after; density 20 – 35 / 10 mm.

Nymboida Material

Known only from a single specimen, AMF130184 from Coal Mine Quarry, base and apex missing, vein density in lower portion of lamina 30 / 10 mm becoming denser distally, to 40 / 10 mm, straight and parallel at a high angle across lamina and curving slightly upwards to the margin.

Discussion

This leaf fragment is placed in *N. moretonii* on the basis of the very dense venation and its mid dorsal attachment to the mid vein.

Anderson and Anderson (1989) transferred *Nilssonia moretonii* to the genus *Taeniopteris* without additional comment. Under "Intergeneric comparisons" those authors noted that entire specimens of *Nilssonia* can hardly be effectively distinguished from *Taeniopteris* and did not use the genus *Nilssonia*. Many of the leaves placed in *Taeniopteris* (see below) show evidence of lateral attachment of the lamina but towards the dorsal edge of the mid vein. The degree of the lamina overtopping of the mid vein makes for a subjective differentiation between *Nilssonia* and *Taeniopteris* in the absence of preserved cuticle.

Genus *Taeniopteris* Brogniart 1832

Type species

Taeniopteris vittata Brongniart 1832

Taeniopteris is a form genus for simple strap-shaped leaves with entire lamina and occasionally forking lateral parallel venation running at a high angle to a prominent midrib and with unknown cuticle (Meyen 1987, Taylor and Taylor 1993, Anderson and Anderson 2003). Numerous species have been described world-wide from the Upper Carboniferous to Recent. While this leaf form is diverse and widespread it rarely occurs in abundance. Many species have been erected for Gondwana Triassic material, often based on limited or dubious specimens that do little to demonstrate the natural variation within a species. Recent papers on Triassic South American *Taeniopteris* have been useful but some species appear to be based on very few specimens (eg for Argentina, Artabe 1985, Gnaedinger and Herbst 1998. For material from Chile, Gnaedinger and Herbst (2004a) have used a statistical analysis of venation sequence for ten species of *Taeniopteris*. Triassic material from South Africa was described by DuToit (1927) and very comprehensive collections from the Molteno Formation by Anderson and Anderson (1989, 2003) who described ten species from 29 assemblages (localities) and used the "palaeodeme approach" and illustrated the range of variation in a species. From Australia there are numerous species in the literature but most have been based on fragmentary material, inadequate descriptions and have often been poorly illustrated. Rarely has the natural range of variation that may exist in a species been recognised. In our Nymboida collections taeniopterid leaves comprise c. 3% of numbered specimens. Few leaves, especially the larger forms, are found complete. Occasional bedding planes (possible sub–authocthonous assemblages) show numerous individual leaves resembling a natural autumnal-like leaf fall. In many specimens the leaf lamina appears to be dorsally attached to the midrib but without totally covering it as in *Nilssonia*.

In our Nymboida collections the majority of taeniopterid leaves fall within the range of variation as recognised by Webb (1980) from his examination of over 170 specimens, mostly from the Esk Formation for his unpublished species *Taeniopteris adunca* which is here validated using his type specimen and slightly emended diagnosis. Other rare Nymboida leaves with clearly distinguishing characters are described as the new species *T. nymboidensis*.

Sterile leaves of the enigmatic fern *Ogmos adinus* (Webb 1983, Holmes 2001) may be placed as a form species of *Taeniopteris* but are not included here.

***Taeniopteris adunca* J.A.Webb sp. nov.**

Figures 3A–H; 4A–C; 5A–C

Selected synonymy

1892 *Taeniopteris* sp. indet. Etheridge, p. 374, Pl. 16, fig. 4.

1924 *Taeniopteris* (? *Danaeopsis*) *crassinervis* (Feistmantel) Walkom; Walkom, p. 84, Pl. 18, fig. 3.

1925 *Taeniopteris carruthersii*, Tenison-Woods; Walkom, p. 85, text fig. 3.

1965 *Taeniopteris* aff. *lentriculiforme* (Etheridge) Walkom; Hill et al., PL. T8, Fig. 4.
1975 *Taeniopteris* aff. *lentriculiforme* (Etheridge) Walkom; Flint and Gould, Pl. 3, figs 8, 9.
1980 *Taeniopteris adunca* sp. nov. Webb (unpubl.), Pl. 23, figs 1–11; text figs 51 a–i.

Diagnosis

Strap-shaped leaves, very variable in width; leaf surface rarely undulate; secondary veins always leave midrib at moderately acute angle, then quickly arch away and travel straight and parallel to the margin at 70º–90º; individual veins frequently bifurcate twice but anastomose very rarely; vein density ranging from 15 to 25 per 10 mm near the margin.

Description

Leaves elongate, strap-shaped; tapering gradually and fairly uniformly to a stout petiolate base and distally to an obtuse to acute rounded apex; very variable in size, from 9–60 mm in width and from 110 mm to >250 mm in length; lamina rarely undulate, margins entire. Midrib sometimes striate, appearing as a prominent groove or ridge, 1-2 mm wide in mid leaf and expanding basally to c. 3 mm. Leaf lamina attached to the dorsal edge of the mid vein without overlapping the dorsal surface. Lateral veins always leave the mid vein at a moderately acute angle (usually less than 45°) and arch rapidly within 1 to 2 mm then proceed straight and parallel to the margin at an angle of c. 75° – 85° and more acutely towards the apex. Veins fork close to the mid vein and then once or rarely twice across the lamina. Conjoining of the veins is rare. Density of the veins varies between populations and leaf sizes and averages c. 15–25 /10 mm near the margin.

Holotype

UQF 18836

Type locality

G. R. 380 551 Blackbutt 1: 63 360 Sheet, Esk Formation, Toogoolawah Group, Anisian–Ladinian

Illustrated specimens from Queensland

UQF18836, UQF72601, UQF18830, UQF2103, UQF72814, UQF72813, UQF72811, UQF21494, see Fig. 3.

Additional material

AMF130185, AMF130186, AMF130187, AMF-130188, AMF130189, AMF130190, AMF130191, AMF130193, AMF130194, AMF130215. All from Coal Mine Quarry, Nymboida CM.

Name derivation

aduncus, Latin, *bent inward, hooked,* referring to the abrupt curvature of the lateral veins as they leave the midrib.

Discussion

Based on the detailed study of extensive collections of fossil plant material mainly from Queensland, J.A.Webb (1980, unpublished) differentiated two commonly occurring strap-like *Taeniopteris* leaf forms mainly on the basis of the form of attachment of the lateral veins to the mid vein. *Taeniopteris carruthersii,* widespread in the Upper Triassic assemblages, has lateral veins arising straight from the midrib at a high angle, sometimes forking and running at almost right angles to the leaf margin. In *T. adunca* the leaf lamina is attached dorsally to the midrib with the lateral veins diverging from the mid vein at an acute angle, usually forking close to the base then arching and running straight to the margin at a high angle. This arching of the veins close to the mid vein is often obscured through the form of preservation during fossilization but can be revealed from close examination. While there are wide variations within the two species and some overlapping characters, Webb recognised the two species as distinct and with stratigraphic implications. *T. carruthersii* occurs in the Late Triassic Ipswich Coal Measures whereas *T. adunca* is found in the Esk Formation of Queensland and the Basin Creek Formation of the Nymboida Coal Measures, both Middle Triassic units.

T. adunca is the most commonly occurring form of *Taeniopteris* at Nymboida. On some bedding planes (see blocks AMF130190, AMF130216, AMF130193 and AMF130194) the leaves form an almost mono-specific assemblage, probably a seasonal leaf-fall. Both within and between these assemblages there is a wide variation in leaf size and shape. *T. adunca* is regarded as a species complex.

Taeniopteris parvilocus Anderson and Anderson from South Africa (Anderson and Anderson 1989) and from Chile (Herbst et al. 2005) is similar to *T. adunca* in outline and size but differs by the less dense venation (13/10 mm) that runs almost straight from the midrib and then arches upwards towards the margin. See below for comparisons with *T. nymboidensis*.

***Taeniopteris nymboidensis* Holmes and Anderson sp. nov.**

Figures 6 A, B

Diagnosis

Leaf oblanceolate, to 150 mm long, 30 mm wide; apex obtuse; lateral veins dorsally attached at acute angle to strong mid vein, widely spaced at point of attachment, c. 6/10 mm, arching through half the width of the lamina and then running straight to margin at c. 65°–70°, bifurcating in an irregular pattern, once near the base and again across the lamina; vein density in mid lamina c. 14–18/10 mm.

Description

Leaves simple, entire, oblanceolate to 150 mm long and from 25–30 mm wide, apex obtuse; strong mid vein 2 mm wide at mid lamina and tapering distally; base petiolate to >15 mm long. Lateral veins attached on dorsal edge of the mid vein, decurrent, widely spaced at point of attachment, c. 6/10 mm, arching then running straight and parallel to the margin at c. 65°–70° in mid lamina but more acute towards the base and apex. Most veins bifurcate while arching from the base and usually once again at irregular distances from the margin. The pattern of bifurcation is very irregular. Vein density in the mid lamina c. 14–18/10 mm.

Holotype

AMF130197

Type locality

Coal Mine Quarry, Nymboida, Basin Creek Formation, Nymboida Coal Measures.

Other material

AMF130198, Coal Mine Quarry.

Name derivation

nymboidensis- with reference to the type locality

Discussion

Only two slabs in the collections display this new species. The holotype is on a block on which are the remains of seven leaves, four appearing to arise from a common point but the point of attachment is not preserved (Fig. 6A). *T. nymboidensis* differs from *T adunca* by its oblanceolate shape, by the arching of the lateral veins which continues half way across the lamina and by the irregular bifurcation of the lateral veins. In shape and venation pattern *T. nymboidensis* is similar to *T. troncosoi* Gnaedinger and Herbst (2004a) but differs by the less dense venation. *T. fissiformis* Anderson and Anderson (1989) is similar to *T. nymboidensis* in vein density (15/10 mm) but is a much smaller leaf; *T. anavolans* Anderson and Anderson (1989) is similar in shape and size but has coarser venation of c. 12/10 mm.

Taeniopteris* sp *A

Figure 7B

Description

Mid portion of a very large leaf >100 mm wide; mid-vein to 5 mm wide, longitudinally striate; lateral veins attached to the dorsal edge of the mid vein at 60°–70° and quickly arch and run at c. 80° straight and parallel to each other across the lamina and curve slightly upwards towards the margin. Some of the lateral veins bifurcate close to the mid-vein and others occasionally fork at varying distances towards the margin. The vein density is ca 10–12/10 mm.

Material

AMF130199 Coal Mine Quarry.

Discussion

This fragment differs from *T. adunca* and *T. nymboidensis* by the larger size and broader mid vein and from *N. dissita* by the lateral veins not overtopping the mid vein. *Taeniopteris* sp. *A* of Anderson and Anderson (1989) from the Triassic Molteno Formation of South Africa is a very much larger leaf with a finer mid rib and lateral veins almost overtopping the mid vein. Another large leaf from the Molteno Formation, *Taeniopteris homerifolius* Anderson and Anderson (1989) has a venation pattern with veins upcurving towards the margin similar to *T.* sp. *A* but differs by the lateral attachment of the lamina to the mid-vein. Webb (1980 p. 218) described a *Taeniopteris* sp. (unpublished) with much larger leaves – to 240 mm wide and lateral veins occasionally anastomosing which he compared with a leaf from South Africa described by DuToit (1927) as *Taeniopteris lata.*

Genus *Linguifolium* Arber 1913 emend. Retallack 1980

Type species

Linguifolium lilleanum Arber 1913

Linguifolium was erected for simple entire leaves, linear, spathulate, lanceolate or obovate; apices sub-acute to rounded; with mid vein persistent to apex; lateral veins arising at very acute angle to the mid rib then arching to meet the margin at an acute angle, forking once and occasionally twice in the nearer third of their length. The status of the genus *Linguifolium* was well-discussed by Retallack (1980). *Linguifolium* leaves are extremely rare in the Nymboida collections.

Linguifolium tennison-woodsii (Jack and Etheridge 1892) Retallack 1980
Figures 8B, C

Selected synonymy

1892 *Angiopteridium tennison-woodsii*, Jack and Etheridge, p. 365
1898 *Taeniopteris tennison-woodsii*, Shirley, comb. nov. p. 23, Pl. 9, fig. 2.
1947 *Doratophyllum tennison-woodsii*, Jones and deJersey, p.37, Pl. 6, fig. 1.
1980 *Linguifolium tennison-woodsii*, Retallack, comb nov. fig. 7 F–H.
1980 *Linguifolium tennison-woodsii*, Webb, p.172, Pl. 20, figs 1–4, Pl.21, figs 1–15, text fig. 41, a–p, (unpubl.).
1989 *Linguifolium tennison-woodsii*, Anderson and Anderson, p.522, figs 1–3.
1998 *Linguifolium tennison-woodsii*, Gnaedinger and Herbst, Pl.1, fig. d.

Description

A portion of a small linear leaf with the base missing, tapering slightly distally to an incomplete apex. Length preserved 80 mm, width 6 mm. Mid vein not well defined, lateral veins decurrent on mid vein, arching across lamina to meet entire margin at c. 75°, forking once close to mid vein. Vein density in mid lamina c.12/10 mm.

Material

AMF130200, Coal Mine Quarry, Basin Creek Formation, Nymboida Coal Measures.

Discussion

Linguifolium tennison-woodsii differs from most *Linguifolium* spp. by its narrow linear form and from the extremely narrow *Linguifolium gracile* from the Molteno of South Africa (Anderson and Anderson 1989) by its more arching and denser veins.

Linguifolium parvum sp. nov. Holmes and Anderson 2010
Figures 9A–C

Diagnosis

Small spathulate sessile leaves less than 100 mm long, lateral veins decurrent on striated mid vein, arching across lamina to meet margin at acute angle, number of veins forking near base variable, very occasional veins forking and conjoining. Vein density 8–12/10 mm.

Description

Leaf spathulate; maximum length 100 mm; width from 11–20 mm, apex rounded, lamina tapering to sessile base; midrib with longitudinal striations, width at base 1.5 mm, contracting in width through length of the leaf; lateral veins decurrent, arching from mid-vein across lamina to reach the margin at an angle of 30°–45°; c. half the veins fork once close to the mid vein; occasional veins fork in the mid lamina and conjoin to form a long narrow areole. Density of the veins at mid lamina ranges from 8 to 12/10 mm.

Holotype

AMF130201

Type locality

Coal Mine Quarry, Basin Creek Formation, Nymboida Coal Measures.

Other Material

AMF130202, AMF130203, AMF130204, and AMF130207 from Coal Mine Quarry. AMF130205 and AMF130206 from Reserve Quarry.

Name derivation

parvum – Latin – small, referring to the small size of the leaves of this taxon..

Discussion

Linguifolium parvum is similar in form to *L. lilleanum* Arber (1913), *L. ascium* Webb (1980) and *L. patagonicum* Gnaedinger and Herbst (1998) but differs by the short length and by the density and course of the lateral veins. In the Nymboida collections these *Linguifolium* leaves are very rare. The generic diagnosis of *Linguifolium* states that the lateral veins do not anastomose. However on some specimens of *L. parvum* very occasional lateral veins fork and conjoin to form a long narrow areole, hardly reason to remove it from *Linguifolium*.

? _Linguifolium_ sp. _A_
Figures 8D, E

Description

A small spathulate leaf somewhat resembling in shape *L. parvum,* is 74 mm long and 14 mm wide, with base and apex missing. The lateral veins are sparse, c. 8/10 mm and arch slightly across the lamina at c. 45° to each terminate at a tooth along a unique finely serrate margin; occasional veins forking once between mid vein and mid lamina.

Material

AMF130208 and counterpart AMF130209, Coal Mine Quarry.

Discussion

This form is based on a single specimen and its counterpart. It differs from all described species of *Linguifolium* by the serrate margin. *Jungites polymorpha* from the Molteno Formation (Anderson and Anderson 1989) has a finely serrate margin but differs by the dense parallel venation and the variably entire to pinnate lamina margin.

Genus *Gontriglossa* Anderson and Anderson 1989

Type species

Gontriglossa verticillata (Thomas 1958) Anderson and Anderson 1989

The genus *Gontriglossa* was erected by Anderson and Anderson (1989) for elliptic, petiolate leaves with veins attached at an acute angle, arching and anastomosing towards the margin. Some specimens of *G. verticillata* from the Molteno Formation of South Africa (Anderson and Anderson 1989, 2003) show stems with well-spaced opposite fascicles of three leaves. From Nymboida, Holmes (1992) described some reticulate veined leaves that were identified as Triassic "*Glossopteris*-like leaves". Those leaves are here transferred to the genus *Gontriglossa.* Amongst the Nymboida material is a specimen showing 10 leaves attached in a whorl or a close spiral (10A, 12A). To accommodate this form in *Gontriglossa* requires a slight emendation of the generic diagnosis to include the attachment of leaves as either terminal whorls, close spirals or well-spaced opposite fascicles.

***Gontriglossa grandis* (Walkom) Holmes and Anderson comb. nov.**

Figures 10A; 12A

Synonymy

1928 *Anthrophyopsis grandis* Walkom, p. 464, text fig. 2, Pl. 26, fig. 5.

1992 ?*Glossopteris grandis* Holmes, p. 122, Pl. 2, figs1, 2.

Description

Leaves oblanceolate, to 150 mm long, and to 95 mm wide but usually much smaller, attached as a terminal whorl or a close spiral, apex rounded acute to obtuse, tapering basally to a short petiole; midrib distinct, striate; lateral veins leave the midrib at an acute angle and for about one third of the width of the lamina they bifurcate and anastomose to form a wide elongate mesh with a general inclination of c. 45° to the midrib; for the remainder of the lamina they form a narrower elongate mesh inclined at 65°–70° to the midrib; closer to the midrib the meshes are 1–2 mm wide, wider in the proximal than the distal part, while towards the margin they narrow to form 7–8 meshes per 5 mm of width.

Holotype

UQF1724-5, University of Queensland, Brisbane from Sheep Station Creek in the Esk Beds.

Other material

AMF 78254–78258, Australian Museum, Sydney – from Coal Mine Quarry, Nymboida.

Discussion

The Nymboida leaves placed in this species are much smaller (c. 80 mm long and c. 30 mm wide) than the holotype specimen but are closely similar in gross form and the anastomosing venation pattern. The Nymboida specimens are notable for the whorled or closely spiral arrangement of the leaves. Individual leaves of *G. verticillata* (Thomas) Anderson and Anderson (2003) are similar in size and venation pattern to the Nymboida leaves but differ by the known cuticle and the well-spaced opposite attachment of fascicles of three leaves to an elongated stem.

***Gontriglossa nymboidensis* Holmes and Anderson comb. nov.**

Figures 11A, B

Selected Synonymy .

1975 *Anthrophyopsis grandis* Walkom, Flint and Gould, Pl. 1, fig. 9.

1992 *?Glossopteris nymboidensis* Holmes, P. 122, Pl. 1, figs 3,4; Pl.. 2, fig.1.

Holotype

UNEF13528 and paratype UNEF13639, both from Coal Mine Quarry. Now housed in the Australian Museum as specimens AMF126731 and AMF126730 respectively.

Additional material

AMF130214, Coal Mine Quarry.

Description

A reticulate veined leaf known only from apical and mid lamina fragments. Leaf of unknown length, width 50 mm, tapering distally to an acutely rounded apex; midrib distinct, striated; lateral veins leaving midrib at c. 20°–30° at intervals of ca 0.5 mm and quickly arch over a distance of c. 5 mm where they bifurcate and then run straight to the margin at an angle of 75°. After the initial bifurcation the veins fork again two or three times to join with adjacent veins to form long narrow meshes, each subsequent mesh being narrower than the proceeding one. The density of the veins in the mid lamina is c. 12–14/ 10 mm and at the margin c. 18/10 mm.

Additional material

AMF130214, Coal Mine Quarry.

Discussion

G. nymboidensis differs from all other *Gontriglossa* species by the very fine narrow parallel meshes formed by the lateral veins. *Cetiglossa balaena* Anderson and Anderson (2003) from the Molteno of South Africa is much larger leaf with more elongate reticulate venation that does not arch from the mid vein. The somewhat similar reticulate veined leaf from Patagonia, *Santacruzia hunickenii* Gnaedinger and Herbst (1998) differs by the serrate to incised margins and the lateral veins attached at a high angle and running straight to the margin. (See comparison of *Santacruzia hunickenii* with *Gontriglossa lacerata* below).

Gontriglossa lacerata (Holmes 1992) Holmes and Anderson comb. nov.

Figures 11C, D

Synonymy

1992 ?*Glossopteris lacerata* Holmes, p. 124, Pl. 2,4.

Holotype

AMF78259. Coal Mine Quarry, Basin Creek Formation, Nymboida Coal Measures.

Additional material

AMF130210 and AMF130213 from Reserve Quarry

Description

Known from three incomplete specimens. Leaf broad-elliptic or oblanceolate, >180 mm long, 65 mm wide, petiolate; apex broadly rounded; margin irregularly lacerate, dentate or lobed; venation somewhat similar to *G. nymboidensis*, arching from mid-vein, bifurcating and anastomosing to the margin.

Discussion

This is a bizarre species. It differs from other *Gontriglossa* species by the irregularly lacerate margins which we believe to be natural and not resulting from insect damage.

Gnaedinger and Herbst (1998) described from the Triassic Tranquilo Group of Santa Cruz, Argentina a leaf with reticulate venation and serrate to deeply incised margins and placed it in their new genus and species *Santacruzia hunickenii.* They were perhaps unaware of the paper by Holmes (1992) as they made no comparisons with *?Glossopteris* (now *Gontriglossa) lacerata. S. hunickenii* differs from *Gontriglossa retculata* by the less deeply incised margin and by the much denser venation that passes at 90° from the mid-vein to the margin. Gnaedinger and Herbst did compare *Santacruzia* with the Molteno species *Gontriglossa balaena* that has been transferred to the genus *Cetiglossa* Anderson and Anderson (2003) which lacks the lacerate lamina margin.

Gontriglossa ligulata Holmes and Anderson sp. nov.

Figures 12B–D

Diagnosis

Leaf ligulate, lateral veins decurrent on mid vein, widely spaced, arching and bifurcating once then running straight at a high angle towards the margin; forking again in mid lamina and conjoining to form a longitudinal row of transverse rhomboidal areoles and a row of triangular areoles parallel and adjacent to the margin.

Description

An incomplete strap-shaped leaf 80 mm long but with base and apex missing; lamina 14 mm wide above broken base, tapering gradually over whole length to 8 mm; mid vein 1 mm wide; lateral veins decurrent and widely spaced on mid vein, arching and bifurcating once then passing to margin at c. 75°. Between mid lamina and margin each vein bifurcates twice and anastomoses with adjacent veins to form a longitudinal row of transverse rhomboidal areoles and a row of triangular areoles parallel to the margin; vein density near margin c. 16/10 mm.

Holotype

AMF130211

Type Locality

Reserve Quarry, Nymboida, Basin Creek Formation, Nymboida Coal Measures.

Name derivation

ligulata – Latin, *strap-shaped*, referring to the broad-linear form of the leaf.

Discussion.

This new species is based on a single incomplete specimen. While recognising that some species of *Taeniopteris*, eg *T. fissiformis* and *T. anavolans* (Anderson and Anderson 1989; Gnaedinger and Herbst 2004a) may show rare and irregular anastomoses, we believe that from the regular and distinctive anastomosing venation (see Fig. 12D) this leaf is best placed in *Gontriglossa,* The linear shape of the leaf and the details of the anastomosing venation pattern differentiate *G. ligulata* from the other *Gontriglossa* species described above and from the cordate based leaf, *G. hilaryjanea* (Anderson and Anderson 1989, 2003). The regular form of the marginal areoles diffentiates *G. ligulata* from the *Scoresbya* sp. described below.

Genus *Scoresbya* Harris 1932

Type species

Scoresbya dentata Harris 1932

Scoresbya dentata was described by Harris (1932) for small palmate leaves with reticulate venation and dentate margins from Scoresby Sound in the Jurassic of Greenland. Additional specimens of *Scoresbya dentata* have been described from the Jurassic of Germany (Krausel and Schaarschmidt 1968), from China (Cao 1982), Afghanistan and Iran (Schweitzer and Kirchner 1998) plus an additional species from the Late Triassic of Mexico (Weber 1995). An incomplete specimen showing parts of several segments of a palmate leaf with dentate margin and reticulate venation from the Ipswich Coal Measures of Queensland was described by Shirley (1898) as *Phlebopteris* (?) *dichotoma* and later transferred by Herbst (1974) to the *Scoresbya* genus.

Scoresbya carsburgii Holmes and Anderson sp. nov.

Figures 13A, 14A, B.

Diagnosis

A large leaf bifurcating irregularly into broad linear lobes; margins entire to irregularly serrulate; lateral veins decurrent on striate mid vein, then arching and running to margin, forking near base, occasionally in mid lamina and then forking and sometimes conjoining to form small areoles adjacent to the margin; vein density in mid lamina c. 12 / 10 and c. 18 / 10 mm near margin.

Description

An incomplete palmate leaf; mid vein longitudinally striated, 3 mm wide in proximal section of leaf; lamina bifurcating at 10 mm from the base of leaf as preserved. The minor fork produces a broad linear pinna or lobe 90 mm long and 28 mm wide. After 43 mm the main rachis again bifurcates to form a major elongate lobe (pinna) 120 mm long and 30 mm wide and a minor lobe 60 mm long and 20 mm wide, both tapering slightly distally. The margins of the lobes are entire to irregularly undulate or serrulate. Throughout the leaf the decurrent lateral veins are widely spaced as they arch at an acute angle from the main rachis, soon forking irregularly and then running straight to the margin at c. 30°–45°, again sometimes forking at irregular distances across the lamina; close to the margin some veins again fork and conjoin to form small triangular areoles adjacent and parallel to the margin (Fig. 14B). Density of the lateral veins in mid lamina c 12/10 mm and near the margin c 18/10 mm.

Holotype

AMF130212

Type Locality

Reserve Quarry, Nymboida, Basin Creek Formation, Nymboida Coal Measures.

Name derivation

carsburgii – named for the collector of the specimen, amateur fossil plant and insect enthusiast, Mr Allan Carsburg.

Discussion

Scoresbya carsburgii is based on a single incomplete specimen that overlies another lobe fragment. It differs from the northern hemisphere species *S. dentata* Harris by its larger size, less obvious dentate or pinnatifid margins and by the form of venation. *Scoresbya dichotoma* (Shirley) Herbst (1974) from the Ipswich Coal Measures of Queensland is a smaller leaf and as described by Herbst has veins conjoining to form an intramarginal vein similar to that in the genus *Yabiella.* From the late Triassic of Chile *Mollesia melandeziae* Melchior and Herbst (2000) is described as particularly similar to *Scoresbya* but with a different venation pattern. The affinities of *Scoresbya* are not well understood. Herbst (1992) excluded *Scoresbya* from the Dipteridaceae and Taylor et al (2009) discussed it under the Caytoniales while Weber (1995) inferred a possible link with angiosperms. *S. carsburgii* is an interesting addition to the Nymboida flora and illustrates the many puzzles still to be solved in these ancient floras.

CONCLUSION

This paper deals with leaves of simple form placed in the form genera *Nilssonia, Taeniopteris, Linguifolium* and *Gontriglossa* and a unique lobed leaf referred to the genus *Scoresbya.* Described are two species of *Nilssonia* including a new species *N. dissita;* three species of *Taeniopteris* including the new species *T. adunca* and *T. nymboidensis*; two species of *Linguifolium* including the new species *L. parvum*; four species of *Gontriglossa* including three new combinations and a new species *G. ligulata.* A unique specimen of a lobate leaf is described as *Scoresbya carsburgii* sp. nov.

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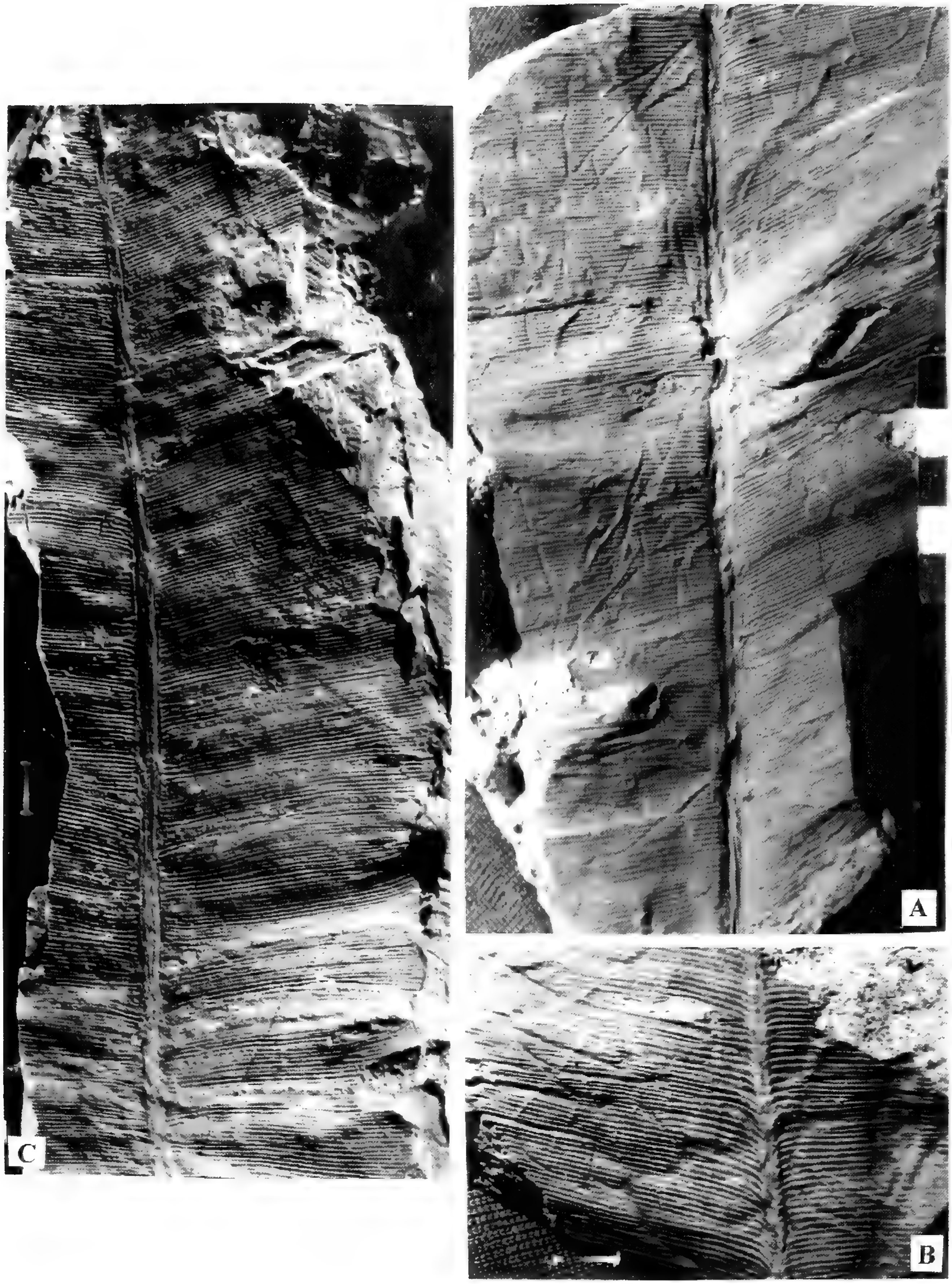

Figure 1. A–C. *Nilssonia dissita* Webb sp. nov. A. GSQF12897, Holotype, GSQ Locality 1552, Esk Fm. B. GSQF12898, GSQ Locality 1552, Esk Fm. C. AMF130181 Coal Mine Quarry, Nymboida CM. Scale bar = 1 cm.

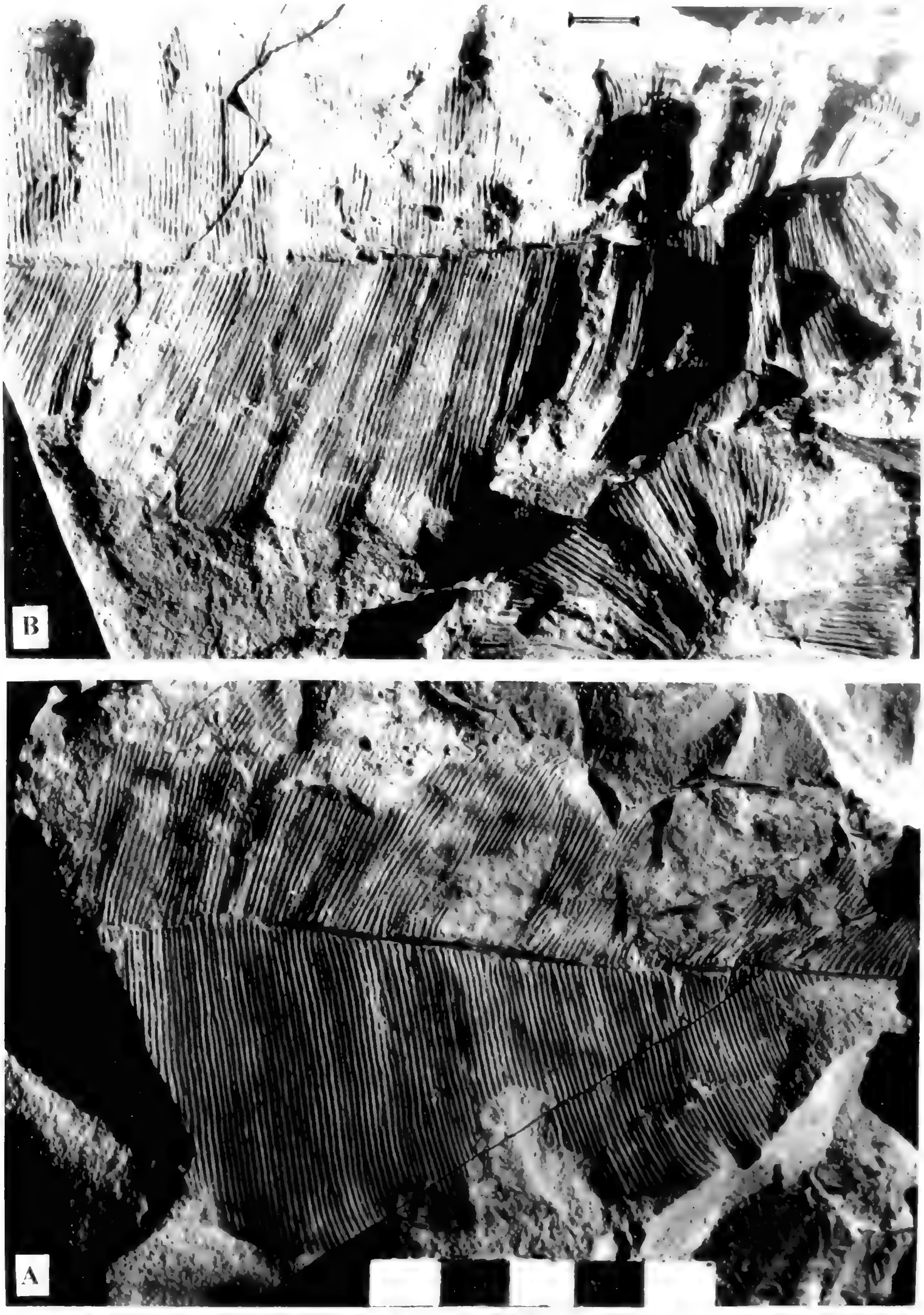

Figure 2. A. B. *Nilssonia dissita* Webb sp. nov. A. AMF130182, Coal Mine Quarry. Scale bar = 5 cm. B. AMF130180, Coal Mine Quarry, Nymboida CM. Scale bar = 1 cm.

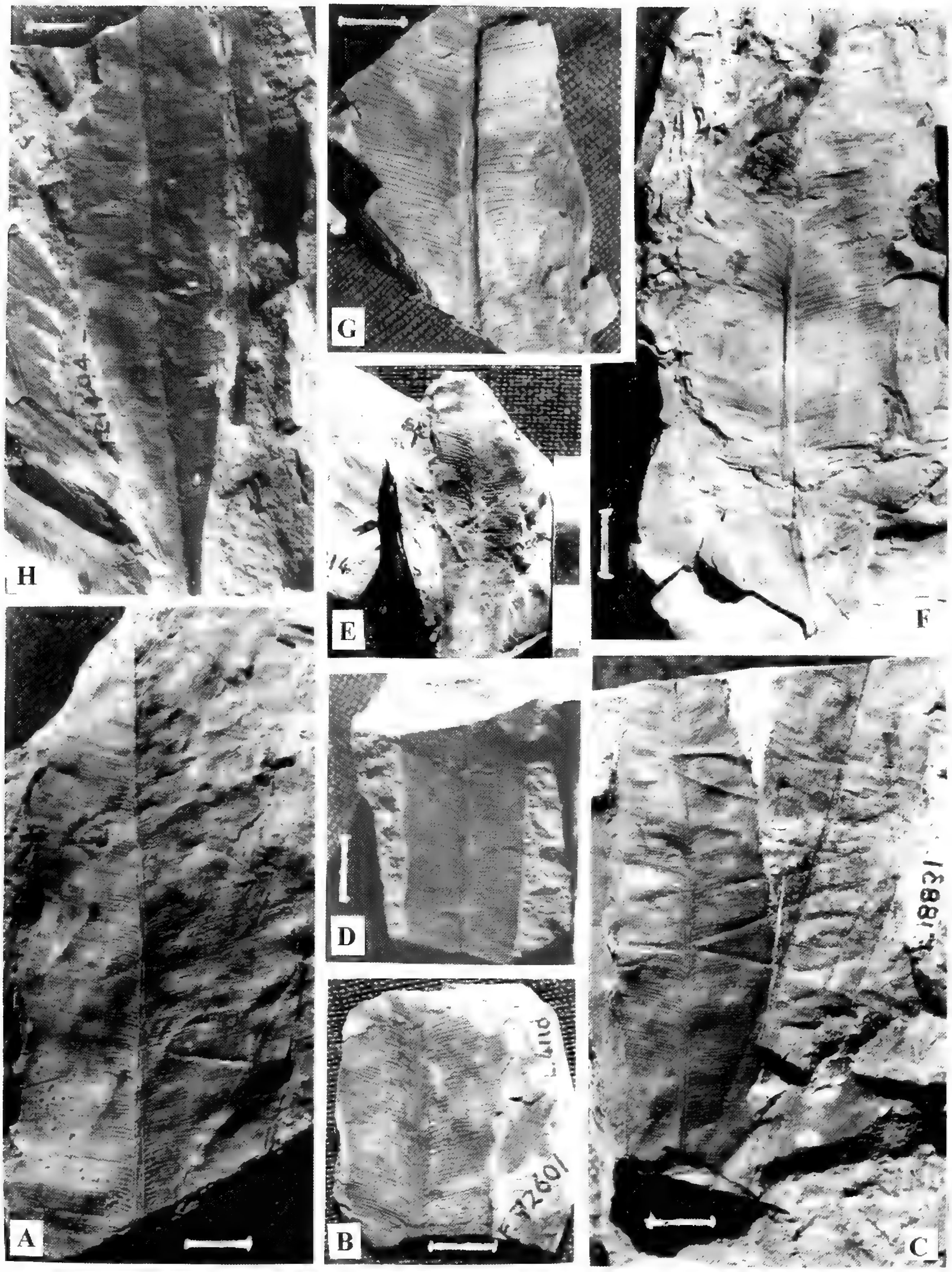

Figure 3. A–H. *Taeniopteris adunca* Webb sp. nov. A. UQF18836, Holotype. 380 551 Blackbutt Sheet. B. UQF72601, UQL4110. C. UQF18830, 445 486 Blackbutt Sheet. D. UQF2103. UQL4238. E. UQF72814, UQL4255. F. UQF72813, UQL4238. G. UQF72811, UQL4110. H. UQF21494, UQL585. All from Esk Fm. Scale bar = 1 cm

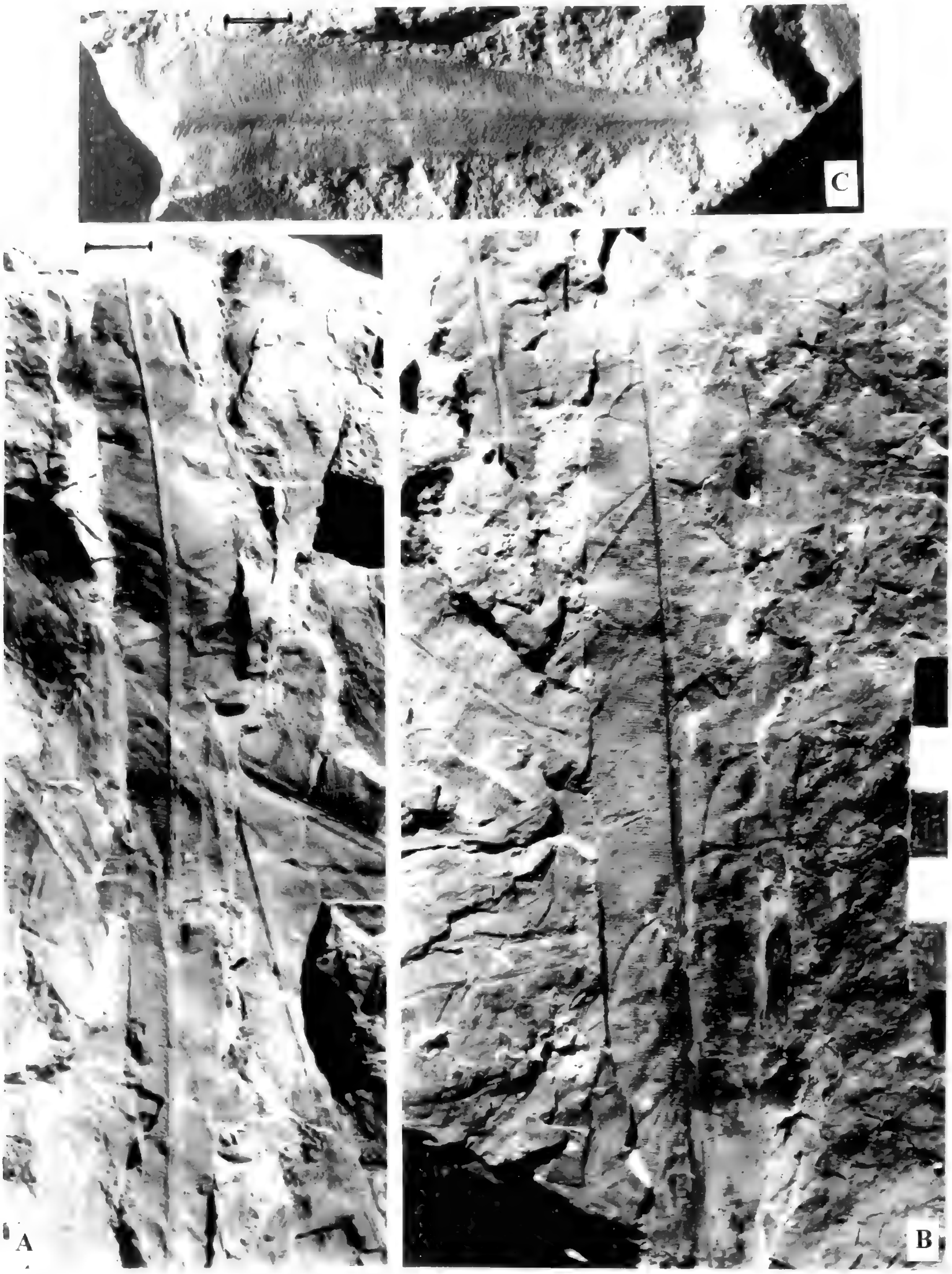

Figure 4. A–C. *Taeniopteris adunca* Webb sp. nov. AMF130194, Reserve Quarry. B. AMF130195, Coal Mine Quarry. C. AMF130186, Coal Mine Quarry. All Nymboida CM. Scale bar A, C = 1 cm, B = 5 cm.

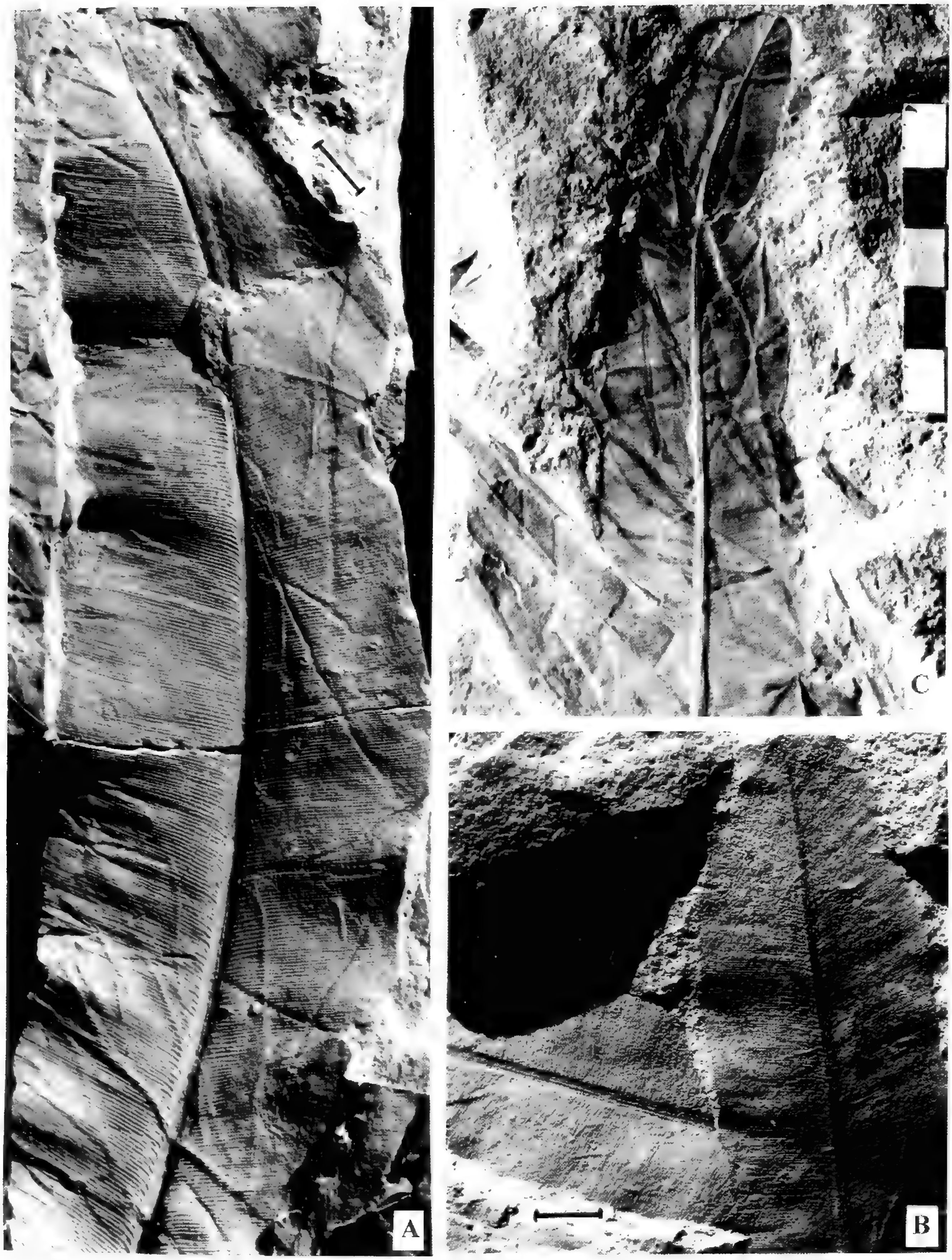

Figure 5. A – C. *Taeniopteris adunca* Webb sp. nov. A. AMF130187. B. AMF130189. C. AMF130196, all from Coal Mine Quarry. Nymboida CM. Scale bar A, B = 1 cm. C = 5 cm.

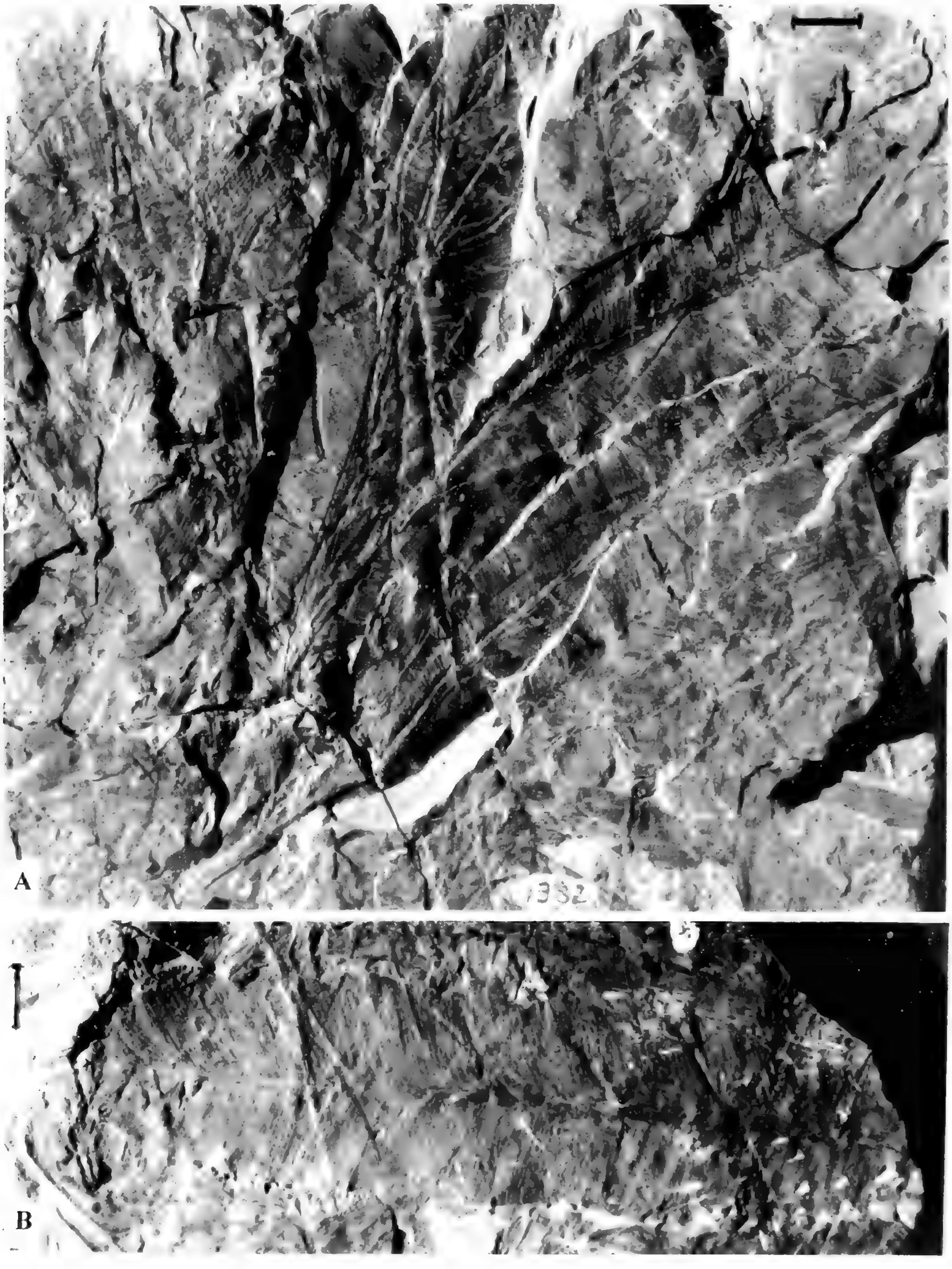

Figure 6. A, B. ***Taeniopteris nymboidensis*** **Holmes and Anderson sp. nov. A. AMF130197. B. AMF130198, both from Coal Mine Quarry. Nymboida CM. Scale bar = 1 cm.**

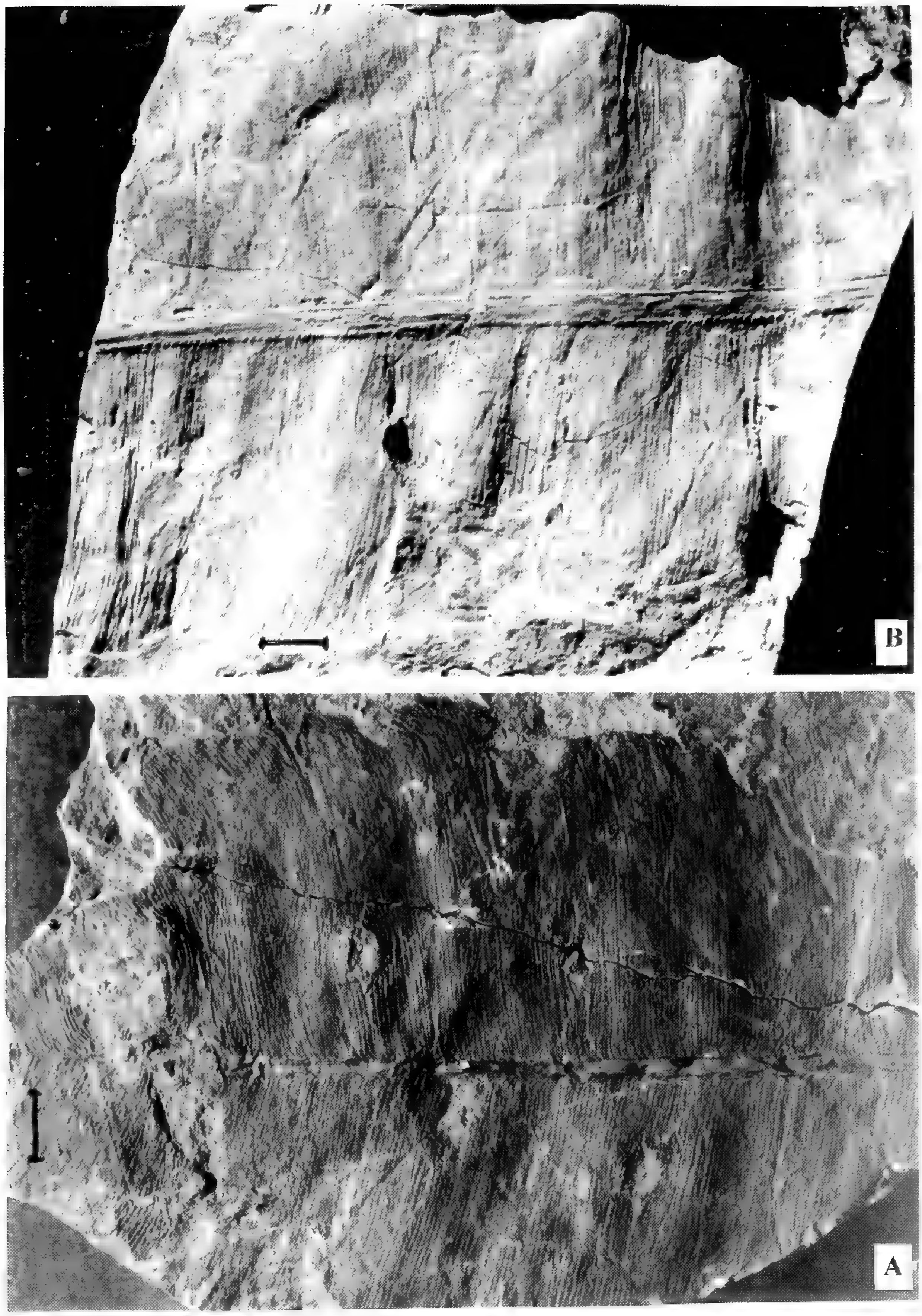

Figure 7. A, B. *Nilssonia dissita* Webb sp. nov. AMF120939. B.Taeniopteris sp A. AMF 130199, both Coal Mine Quarry. Nymboida CM. Scale bar = 1 cm.

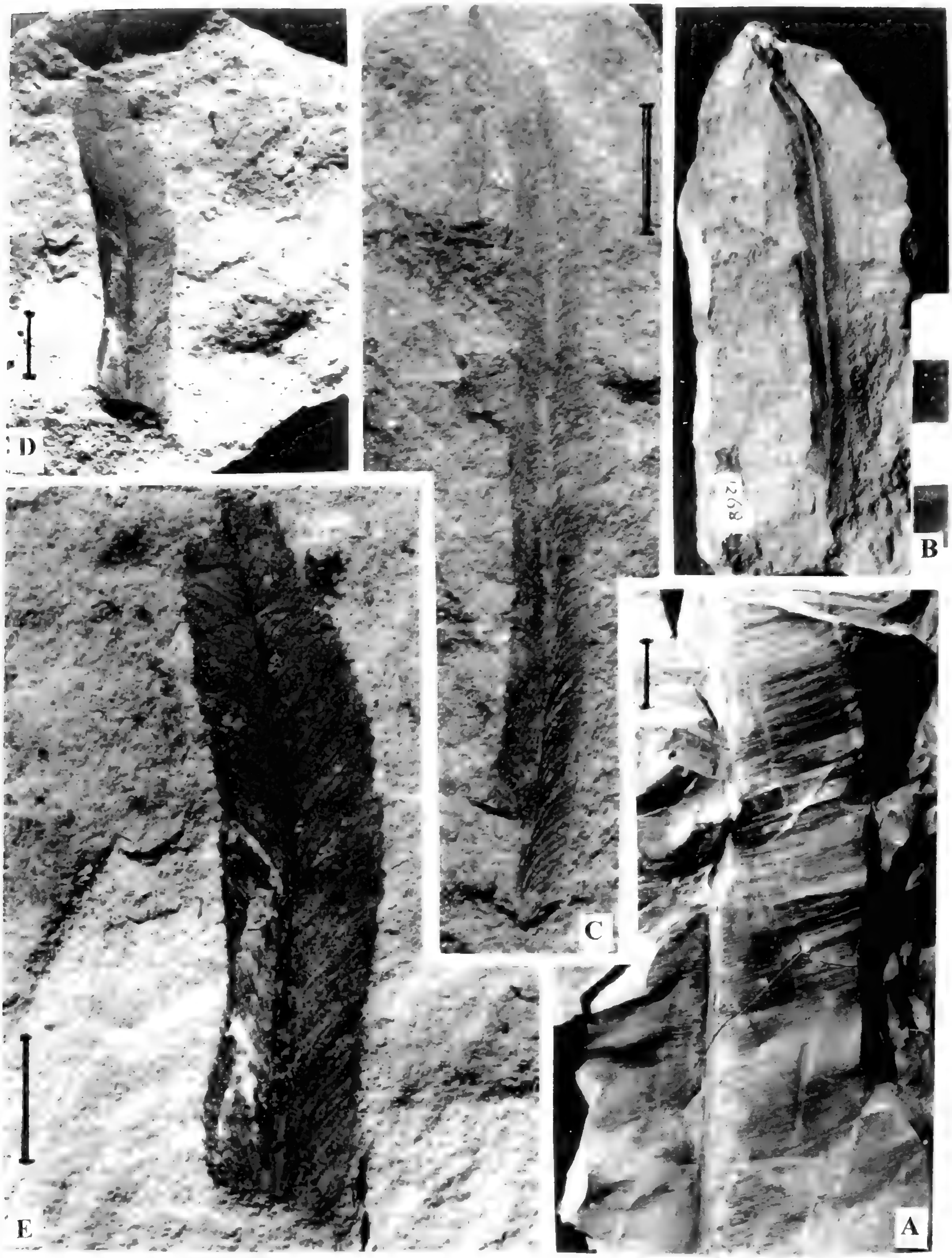

Figure 8. A. ***Nilssonia moretonii*** **AMF130184. B, C. Linguifolium tennison-woodsii AMF130200. D, E. Linguifolium sp A AMF130208. Numboida CM. Scale bar A, C, E = 1 cm, B = 5 cm.**

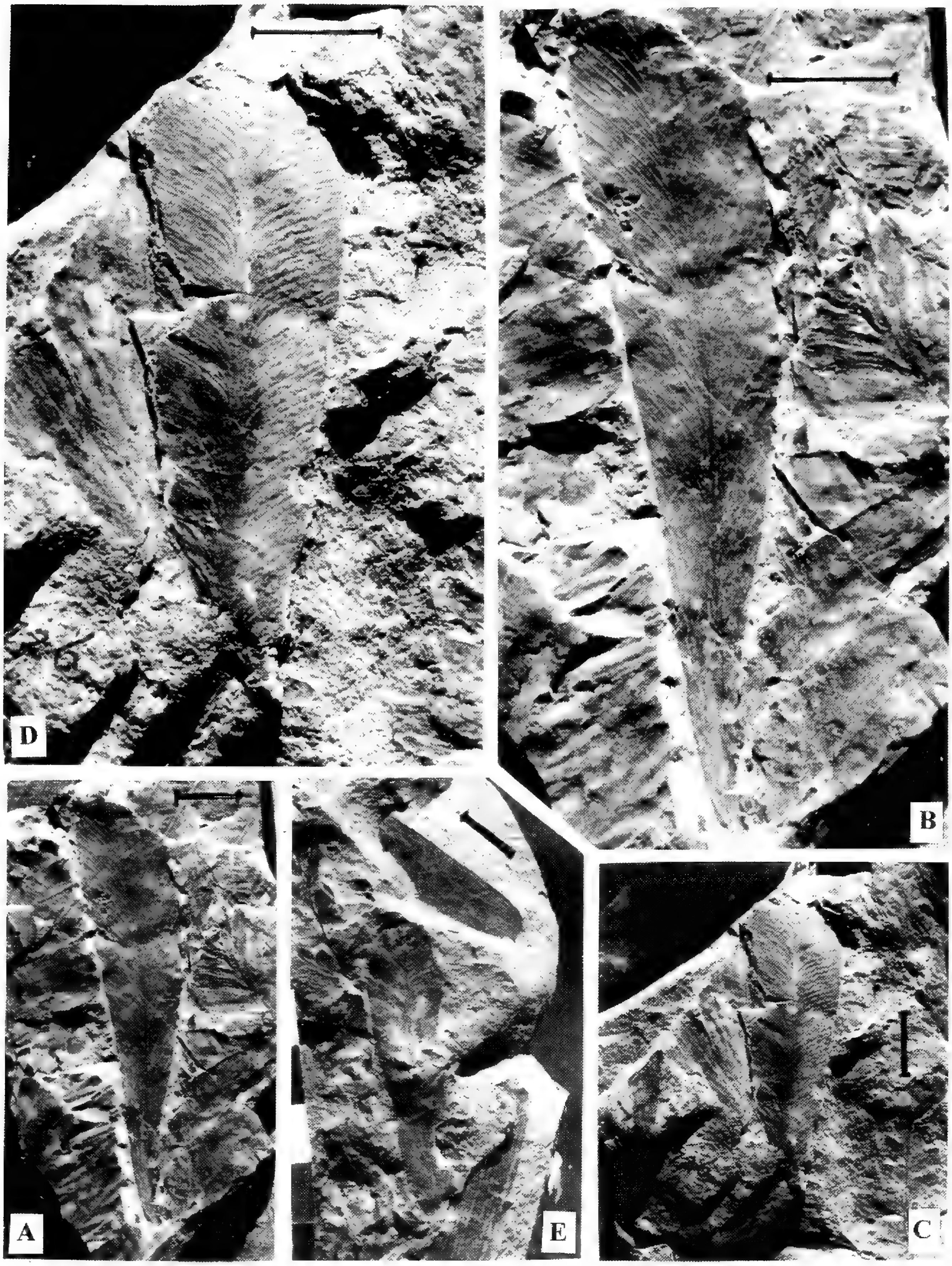

Figure 9. A – E. *Linguifolium parvum* Holmes and Anderson sp. nov. A, B. Holotype AMF130201, Coal Mine Quarry. C, D. AMF130207, Coal Mine Quarry. E,. AMF130206, Reserve Quarry. Nymboida CM. Scale bar = 1 cm.

Figure 10. A. ***Gontriglossa grandis*** **(Walkom) Holmes and Anderson comb. nov. Holotype AMF 78254 Coal Mine Quarry. Nymboida CM. Scale bar = 1 cm.**

Figure 11. A, B. *Gontriglossa nymboidensis* (Holmes) Holmes and Anderson comb. nov. A. Holotype AMF126730. Coal Mine Quarry. B. Paratype AMF126731. Coal Mine Quarry. C, D. *Gontriglossa lacerata* (Holmes) Holmes and Anderson comb. nov. C. Holotype AMF78259 Coal Mine Quarry.. D. AMF130210, Reserve Quarry. Nymboida CM. Scale bar = 1 cm.

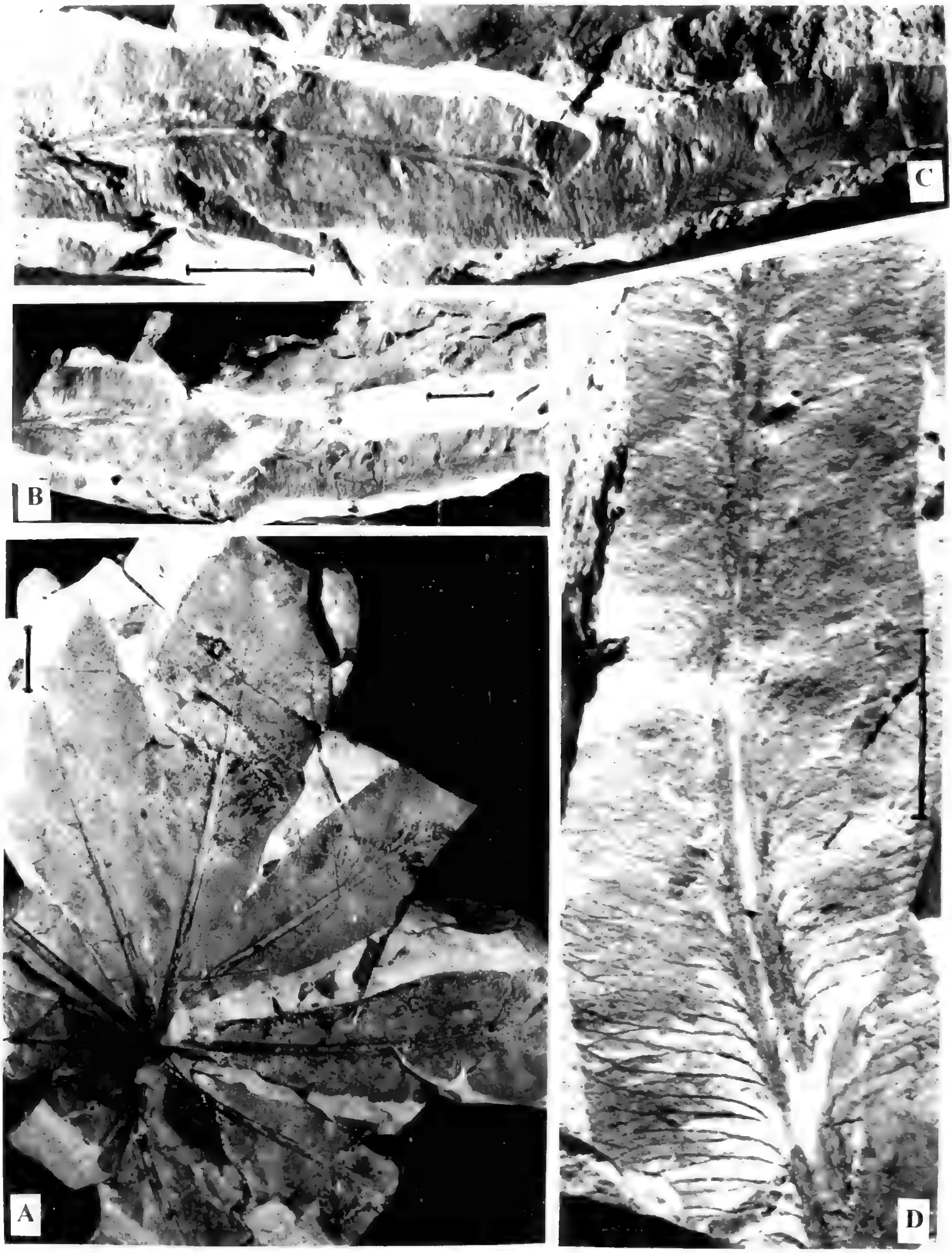

Figure 12. A. ***Gontriglossa grandis*** **(Walkom) Holmes and Anderson comb. nov. AMF78254 Coal Mine Quarry. B –D. Gontriglossa ligulata Holmes and Anderson sp. nov. AMF130211, Reserve Quarry. Nymboida CM. Scale bar = 1 cm.**

Figure 13. A. ***Scoresbya carsburgii*** **Holmes and Anderson sp. nov. Holotype AMF130212, Reserve Quarry. Nymboida CM. Scale bar = 1 cm.**

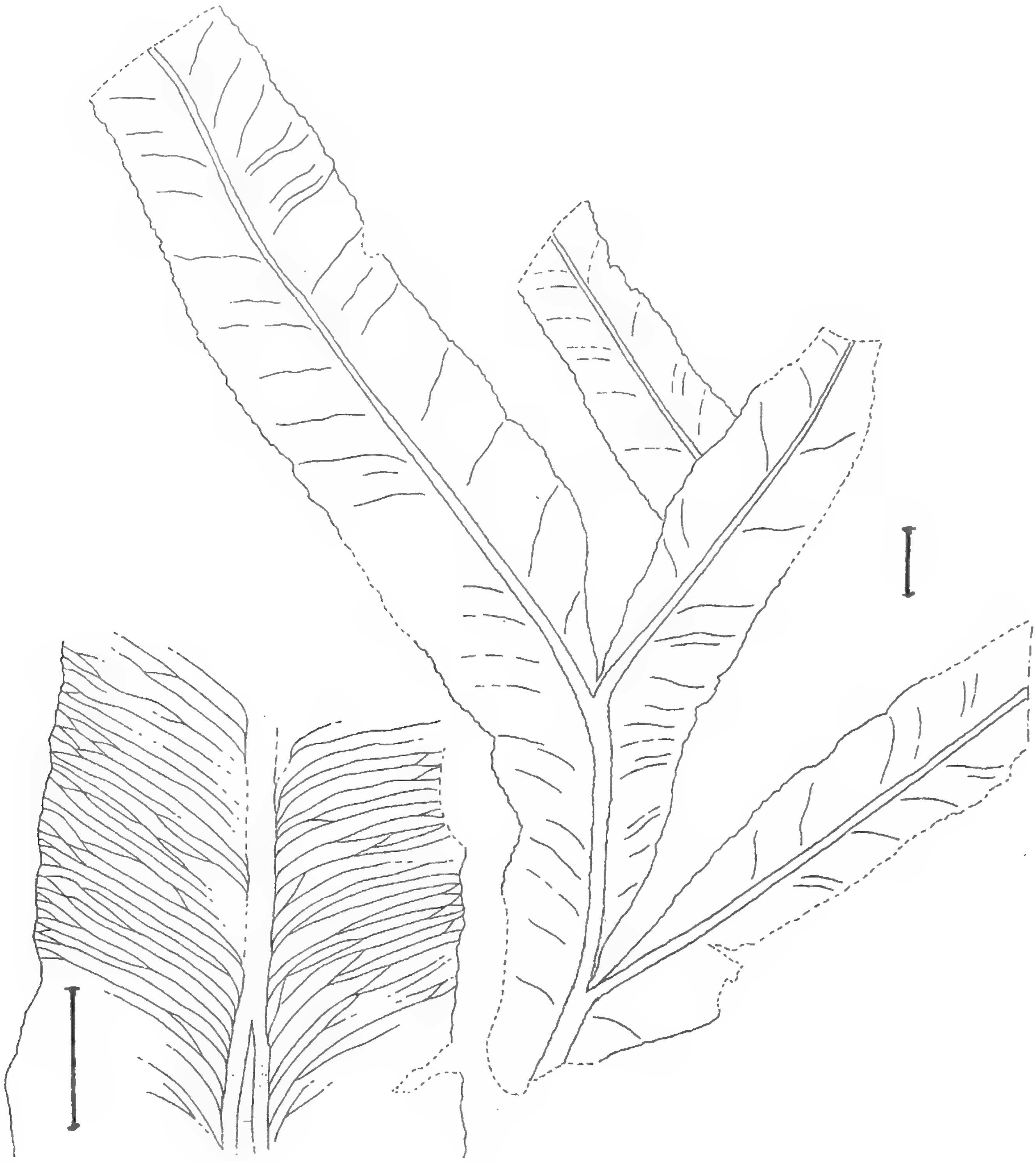

Figure 14. A, B. *Scoresbya carsburgii* Holmes and Anderson sp. nov. A. Line drawing of Holotype. AMF130212. B. Details of venation. Scale bar = 1 cm.

Catalogue of Insects Collected by William Sharp Macleay in Cuba 1825-1836

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All of William Sharp Macleay's labelled Cuban insects are now in a separately labelled Cuban insect cabinet in the Macleay Museum. There are over 7,349 labelled, pinned and partially identified. Other unlabelled specimens are still to be found throughout the collection. The geographical area where Cuba lies is also within the bio-geographical area for the southern United States, the Bahamas, the Caribbean and the northern most areas of South America. The biological scientists of these surrounding countries will find the information and knowledge of the distributions of insects of Cuba found in 1825 to 1836 of tremendous interest in relation to the possible distributions of insect faunas found or no longer found in these areas today.

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KEYWORDS: Catalogue, Coleoptera, Cuba, Cuban insects, Curculionidae, Havana, Hymenoptera, Lepidoptera, Macleay Museum, Slave trade, William Sharp Macleay.

INTRODUCTION

The following is a catalogue of Cuban insects collected by William Sharp Macleay during his appointment as commissioner for the abolishment of the slave trade in Havana from 1825 to 1836. The specimens were taken from Cuba to England at the conclusion of his posting and consequently were moved to Sydney, Australia, with W.S. Macleay when he moved there to live. The collection of over 7000 insects were spread throughout the Macleay Museum's entomology collection but were readily identified using locality labels. This is the first account of the Macleay Cuban collection and although initially the collection may have been larger, it is probable that over 170 years, specimens have had labels removed, been damaged beyond usefulness, or removed from the Macleay Museum altogether. All the remaining labelled Cuban specimens are now reunited in a single collection and are for the most part in good condition.

The collection consists of 7349 insects across at least 11 orders as follows:

Blattodea	33
Coleoptera	2172
Diptera	385
Hemiptera	729
Hymenoptera	3509
Lepidoptera	407
Neuroptera	40
Odonata	24
Orthoptera	1
Phasmatodea	20
Siphonaptera	29

While care was taken to provide the most up to date species names, information was not able to be found on some of the labelled species name, and these have been included as written on the label. Where the year has been omitted it is where we were unable to find the complete documentation of the description and the publication.

William Sharp Macleay left England for Cuba in October 1825, to take up his duties in connection with the Mixed British and Spanish Court of Commission for the Abolition of the Slave Trade established at

Havana. His residence in Cuba lasted from December 1825 to early in the year 1836. The catalogue of insects included in this paper, includes all those insects (over 7000) that are clearly labelled with the locality Cuba. William collected many specimens during those eleven years in Cuba, and then brought them to Australia. All of William Sharp's collection is now housed in the Macleay Museum at the University of Sydney. There may be many more Cuban insects in the Macleay Museum but this catalogue only deals with specimens with the label Cuba.

William Sharp Macleay was born in London, on 21st July 1792, the eldest son of Alexander Macleay (1767 - 1848) who amassed probably the finest insect collection in Europe and which eventually Alexander brought with him to Australia in 1826. William Sharp Macleay arrived in Australia in 1839 with his own insect collection from European collecting trips, his collection from Cuba and a collection of insects from his trip to the United States with Mr Titian Peale (Fletcher 1920).

William was educated at Westminster and Trinity College Cambridge and graduated with a BA in 1814 and MA in 1818. On leaving the University he was appointed as Attache to the British Embassy in France. What awakened and developed his interest in Zoology seems primarily to have been his father's example, influence and fine collection of insects. During his time in Paris he had the opportunity of meeting Cuvier, Latreille and other distinguished naturalists of that time, as well as appreciating the importance of the magnificent establishment of the Jardin des Plantes. He subsequently was appointed Secretary to the Board for liquidating British claims on the French Government, established at the peace of 1815 - 1825. He was then sent as Commissioner of Arbitration of the Slave Trade established at Havana in Cuba. In 1830 he became the Commissary Judge of the same court. In 1836, he was appointed to be the Judge of the mixed British and Spanish Court of Justice, established under the treaty of 1835 – 1836. In 1836 he returned to England. In 1837 he retired from the Public Service. He left England in 1838 for Australia with his cousins William and John and arrived in Sydney in March 1839. Here he continued to collect insects and studied marine life. He was also a trustee of the Australian Museum from 1853 - 1862. He was universally recognised as the leading zoologist in Sydney from 1839 up to the time of his death. William Sharp died in Sydney on the 26th January 1865 and was buried in the family tomb in Camperdown Cemetery (Fletcher 1920).

William Sharp's published work began in 1819 and ended in 1847 (over 30 published papers). There were no publications on any of the insects that he collected in Cuba.

During his voyage to Cuba, in the months of October, November and December of 1825, he made notes on the Ornithology of the Islands of Madeira, Teneriffe and Saint Jago, as well as observations at Barbados, Martinique and off the coast of Saint Domingo. He always seemed to be taking notes of his natural surroundings wherever he went. However there seems to be no detailed notes of his insect collecting in Cuba, or at least none that has been found. However there is one interesting letter he wrote to his trusted friend Kirby, dated 3rd 1827 January, about a year after his arrival. William writes:

> *"The climate has, I thank God, hitherto agreed with me much better than that of England: but there is a languor attendant upon every kind of exertion, which makes reading or study here a very different thing from what it is in England."*
> *"This is a good place for Wading Birds, Lizards, Butterflies and Sphinges, (a term meaning Hawk Moths), but apparently nothing else. I live in the country, where I have a large house and garden: this is my principal amusement, as I take great pleasure in cultivating Orchideae, particularly those which are parasitical on trees. The disagreeable are ants, scorpions, mygales and mosquitoes. The latter were quite a pest on my first arrival within the tropics, but now I mind them as much as I did gnats in England. "*

The place of his residence in Cuba was Guanabacoa, (an Indian name meaning "site of the waters ") which he described as if " living in the country is a picturesquely situated amid woods, on high hills which furnish a fine view, is a town a few kilometres from the capitol of Cuba, Havana."

During his leisure hours, natural history soon began to claim his attention as he sent specimens of lizards, bats and 45 species of birds to England to be exhibited at meetings of the Zoological Club of the Linnean Society in 1828. Later William, sent a foetal specimen of a dolphin (Fletcher 1920).

While no papers dealing especially with Cuban insects were published by W.S. Macleay, among his papers were thirty nine water-colour drawings of lepidopterous larvae, from which he may have reared adults. Besides these there are a number of pencil or pen and ink sketches of Lepidoptera, scorpions, ticks and mites (Fletcher 1920).

The scientific world of today has been given an opportunity to know what was on the Island of Cuba in the years 1825 to 1836 due to the scientific endeavours of William Sharp Macleay in the form of over 7000 dry pinned labelled insects now placed together as the Cuban insect collection are housed in the insect collection in the Macleay Museum at the University of Sydney.

ACKNOWLEDGEMENTS

In July 2009 Dominic Cross was awarded the Macleay Miklouho-Maclay Fellowship at the Macleay Museum. At this time his supervisor of the Fellowship was Ms Elizabeth Jefferys, who was the Curator of natural History at the Macleay Museum at the University of Sydney. We thank the Macleay Museum for giving us the opportunity to complete this catalogue. We appreciate the fact that most of the identifications of the Cuban insects were organized by Dr Woody Horning a Curator at the Macleay Museum from 1982 to 1994. Dr Woody Horning identified much of the insects himself and organized other American taxonomists to identify material as well.

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CATALOGUE

Blattodea

FAMILY	GENUS	SPECIES	NUMBER
Blattidae			5
Nocticolidae			28

Coleoptera

FAMILY	GENUS	SPECIES	NUMBER
Anthribidae	*Exophthalmus*	*sommeri* Rausenhauer 1840	2
Bostrichidae	*Amphicerus*	*cornutus* (Pallas) 1772	2
Bostrichidae	*Apate*	*monachus* Fabricius 1775	12
Bostrichidae	*Dinoderus*	*minutus* (Fabricius) 1775	3
Bostrichidae	*Tetrapriocera*	*tridens* (Fabricius) 1792	4
Bostrichidae	*Xylomeira*	*torquata* (Fabricius) 1801	1
Bostrichidae			1
Brentidae			29
Buprestidae	*Asthechrysa*	*spotoica*	20
Buprestidae	*Polycesta*	*angulosa*	2
Buprestidae	*Psiloptera*	*aulica* Dejean	11
Buprestidae	*Psiloptera*	*torquata* Dalman	2
Buprestidae			14
Carabidae	*Calosoma*		1
Carabidae	*Cicindela*	*sagra*	19
Carabidae	*Galerita*	*ruficollis* Fabricius	2
Carabidae	*Megacephala*	*acutipennis* Dejean 1825	1
Carabidae	*Megacephala*	*affinis* Dejean 1825	4
Carabidae	*Megacephala*	*havanensis*	2
Carabidae	*Scarites*	*subterraneus* Fabricius 1775	32
Carabidae			17
Cerambycidae	*Amphidesmus*		2
Cerambycidae	*Callichroma*		1
Cerambycidae	*Clytus*	*devastator* Laport & Gory	2
Cerambycidae	*Eburia*		2
Cerambycidae	*Eburodacrys*	*havanensis* Chevrolat 1862	1
Cerambycidae	*Eburodacrys*		2
Cerambycidae	*Elaphidion*	*irroratum* Linnaeus 1767	2
Cerambycidae	*Elateropsis*	*erythromera*	4
Cerambycidae	*Elateropsis*	*fuliginosa* Fabricius	2
Cerambycidae	*Elateropsis*	*lineate* Linnaeus	5
Cerambycidae	*Elateropsis*	*venusta* Chevrolat	2
Cerambycidae	*Elateropsis*		15
Cerambycidae	*Eupogonius*	*maculicornis* Chevrolat 1862	2
Cerambycidae	*Eupogonius*		4
Cerambycidae	*Leptostylus*		2
Cerambycidae	*Malladon*	*maxillosus* Drury	2
Cerambycidae	*Odontocera*		2
Cerambycidae	*Orthomegas*	*sericeus* Oliver	2
Cerambycidae	*Ptychodes*	*trilineatus* Linnaeus	6
Cerambycidae	*Solenoptera*	*thomae* Linnaeus 1767	1
Cerambycidae	*Spalacopsis*	*filum* Klug 1829	5

Cerambycidae	*Stenodontes*	*damicornis* Linnaeus 1771	5
Cerambycidae			161
Chrysomelidae	*Cassida*	*dorsopunctata* Boheman	16
Chrysomelidae	*Coptocycla*		2
Chrysomelidae			27
Ciidae			6
Curculionidae	*Attelabus*		4
Curculionidae	*Baridius*	*madrimaculatus* Boheman	2
Curculionidae	*Calandra*	*agaves*	1
Curculionidae	*Calandra*	*sericea* Olivier 1807	1
Curculionidae	*Diaprepes*		14
Curculionidae	*Eurhinus*		5
Curculionidae	*Exophthalmus*	*lactus* Olivier	2
Curculionidae	*Exophthalmus*	*luctuosus* Gyllenhal	2
Curculionidae	*Exophthalmus*	*scalaris* Champion 1911	3
Curculionidae	*Exophthalmus*	*spengleri* Linnaeus	2
Curculionidae	*Exophthalmus*		2
Curculionidae	*Hilipus*	*freyreissi* Boheman 1836	2
Curculionidae	*Hilipus*	*guttatus* Boheman 1843	2
Curculionidae	*Hilipus*	*rusticus* Boheman 1836	1
Curculionidae	*Lachnopus*	*curvipes* Fabricius	2
Curculionidae	*Lachnopus*	*hispidus* Gyllenhal	2
Curculionidae	*Lachnopus*	*vittatus* Gyllenhal	2
Curculionidae	*Lachnopus*		1
Curculionidae	*Pachnëus*	*azurescens* Gyllenhal	10
Curculionidae	*Pachnëus*	*litus* Germar	2
Curculionidae	*Peltophorus*		5
Curculionidae	*Polydacrys*	*modestus* Gyllenhal	2
Curculionidae	*Prepodes*	*spectabilis* Dejean	14
Curculionidae	*Ptilopus*	*vittatus* Dejean	19
Curculionidae	*Rhina*	*scrutator* Olivier	4
Curculionidae	*Scyphophorus*	*atheniunus* Schedl	1
Curculionidae	*Sphenophorus*	*sericeus* Latreille	5
Curculionidae	*Sphenophorus*		1
Curculionidae	*Tetrabothynus*	*spectabilis* Gyllenhal	1
Curculionidae	*Tetrabothynus*		1
Curculionidae	*Tylomus*		2
Curculionidae	*Xyleborus*		25
Curculionidae			454
Dytiscidae	*Rhantus*	*calidus* Fabricius 1792	3
Dytiscidae			9
Elateridae	*Conoderus*	*lobatus* Say	2
Elateridae	*Pyrophorus*	*phosphorescens*	1
Elateridae			7
Gyrinidae			7
Histeridae			225
Lampyridae			6
Lycidae	*Calopteron*	*bicolor* Linnaeus	1
Lycidae			17
Mordellidae			5

Passalidae	*Passalus*	*convexus* Schonsafer	1
Passalidae	*Passalus*	*interstitialis* (Escholtz) 1829	2
Rhipiphoridae			5
Scarabaeidae	*Dyscinetus*		3
Scarabaeidae	*Phileurus*	*valgus* (Olivier) 1789	2
Scarabaeidae	*Planophileurus*	*planicollis* (Chevrolat) 1825	1
Scarabaeidae	*Rutela*	*Formosa* Burmeister 1844	2
Scarabaeidae			52
Tenebrionidae			18
Throscidae	*Drapetus*	*azureus* Dejean	1
Throscidae			2
Trogidae	*Trox*		8
Trogossitidae			80
UNIDENTIFED			652

Diptera

FAMILY	GENUS	SPECIES	NUMBER
Tachinidae			8
Tipulidae			5 (EBH)
UNIDENTIFIED			367
UNIDENTIFIED			5 (EBH)

Hemiptera

FAMILY	GENUS	SPECIES	NUMBER
Belastomatidae			11
Berytidae			1
Cicadidae	*Cicada*	*poeyi* Macleay	1
Cicadidae	*Cicada*	*viridicincta* Macleay	6
Cicadidae			13
Cicadidae			8 (EBH)
Coreidae			18
Eurymelidae			61
Gerridae			35
Membracidae			23
Membracidae			7 (EBH)
Miridae			1
Nepidae			4
Notonectidae	*Anisops*		3
Notonectidae			1
Pentatomidae			20
Pyrrhocoridae			29
Reduviidae	*Phymata*	*crassipes* Fabricius 1775	36
Reduviidae	*Ploiaria*		17
Reduviidae			38
Tingidae	*Galeatus*	*cubensis*	1
UNIDENTIFIED			387
UNIDENTIFIED			6 (EBH)

Hymenoptera

FAMILY	GENUS	SPECIES	NUMBER
Anthophoridae			186
Apidae	*Xylocopa*	*fimbriata* Fabricius 1804	1
Apidae			110
Bethylidae			8
Braconidae			3
Chalcididae	*Brachymeria*	*belfragei* Crawford 1910	1
Chalcididae	*Brachymeria*	*incerta* Cresson 1865	8
Chalcididae	*Brachymeria*	*robusta* Cresson	44
Chalcididae	*Brachymeria*		47
Chalcididae	*Chalcis*	*flebilis* Cresson 1872	8
Chalcididae	*Chalcis*		3
Chalcididae	*Conura*	*debilis* Say 1836	4
Chalcididae	*Haltichella*	*xanticles* (Walker)	8
Chalcididae	*Spilochalcis*	*cubule* (Cresson)	19
Chalcididae	*Spilochalcis*	*femorata* (Fabricius)	8
Chalcididae	*Spilochalcis*	*maniae* (Riley)	2
Chalcididae	*Spilochalcis*	*nintifemoea*	2
Chalcididae	*Spilochalcis*	*transitive* (Walker)	33
Chalcididae	*Spilochalcis*		100
Chalcididae	*Spilochalcis*		11
Chalcididae	*Spilochalcis*		25
Chalcididae			21
Chrysididae	*Caenochrysis*	*doriae* (Gribodo)	1
Chrysididae	*Chrysis*	*insularis* Guérin	5
Chrysididae	*Chrysis*	*insularis* Guérin	5
Chrysididae	*Chrysis*	*purpuriventris*	15
Chrysididae	*Chrysis*	*purpuriventris*	6
Chrysididae	*Chrysis*	*superba* Cresson	5
Chrysididae	*Holopyga*	*ventralis* Say	2
Chrysididae			1
Cynipidae			10
Encyrtidae			1
Euchartidae	*Kapala*	*furcata* Fabricius 1804	2
Euchartidae			24
Eurytomidae			2
Formicidae	*Acromyrmex*		14
Formicidae	*Atta*		17
Formicidae	*Camponotus*		13
Formicidae	*Crematogaster*		1
Formicidae	*Cyphomyrmex*		1
Formicidae	*Odontomachus*	*relictus*	13
Formicidae	*Odontomachus*		6
Formicidae	*Pheidole*		11
Formicidae	*Pseudomyrmex*		6
Formicidae			73
Ichneumonidae			16
Leucospidae			1

Megachilidae			2
Mutillidae			72
Platygastridae			6
Pompilidae	*Pepsis*		1
Pompilidae			265
Scoliidae	*Elis*	*trifasciata* Burmeister	1
Scoliidae	*Elis*	*trifasciata* Burmeister	1
Scoliidae			152
Sphecidae	*Monedula*	*insularis* Dahl	1
Sphecidae	*Nysson*	*albilabris*	1
Sphecidae	*Nysson*	*collaris*	1
Sphecidae	*Nysson*	*hyalius*	1
Sphecidae	*Nysson*	*sericeus*	1
Sphecidae			198
Tiphiidae			97
Vespidae	*Ancistrocerus*	*cingulatus* Cresson	1
Vespidae	*Eumenes*		1
Vespidae	*Euodynerus*		2
Vespidae	*Monobia*		1
Vespidae	*Pachodynerus*		50
Vespidae	*Parancistrocerus*	*enyo* (Lepeletier) 1841	27
Vespidae	*Parancistrocerus*		18
Vespidae	*Zeta*		12
Vespidae	*Zethus*		14
Vespidae			23
UNIDENTIFIED			1657

Lepidoptera

FAMILY	GENUS	SPECIES	NUMBER
Lycaenidae	*Cyclargus*	*ammon* (Lucas) 1857	2
Lycaenidae	*Eumaeus*	*atala* Poey 1832	1
Lycaenidae	*Leptotes*	*theonus* (Lucas) 1857	1
Lycaenidae			13
Lycaenidae			5 (EBH)
Nymphalidae	*Anaea*	*troglodyte* Fabricius 1775	3
Nymphalidae	*Apatura*	*pavonii* Latreille	3
Nymphalidae	*Eunica*		2
Nymphalidae	*Hypanartia*	*paullus* Fabricius 1793	2
Nymphalidae	*Megalura*	*eleucha* Hübner	4
Nymphalidae	*Metamorpha*	*stelenes* Linnaeus 1758	1
Nymphalidae	*Phyciodes*	*clio*	4
Nymphalidae	*Siderone*	*ide* Hübner 1823	5
Nymphalidae	*Siderone*		1
Nymphalidae			8
Nymphalidae			152 (EBH)
Papilionidae	*Papilio*	*andraemon* Boisduval	4
Papilionidae	*Papilio*	*androgeus*	1
Papilionidae	*Papilio*	*caiguanabus*	2
Papilionidae	*Papilio*	*caiguanabus*	2

Papilionidae	*Papilio*	*cresphontes*	1
Papilionidae	*Papilio*	*lamarchei*	1
Papilionidae	*Papilio*	*lycophron* (Hübner)	2
Papilionidae	*Papilio*	*oxynius* (Geyer) 1827	1
Papilionidae	*Papilio*	*victorinus* Doubleday 1844	3
Papilionidae	*Papilio*	*villersi* Boisduval	3
Pieridae			71
Sphingidae			27
UNIDENTIFIED			62
UNIDENTIFIED			20 (EBH)

Neuroptera

FAMILY	GENUS	SPECIES	NUMBER
Myrmeleontidae			4
UNIDENTIFIED			31
UNIDENTIFIED			5 (EBH)

Odonata

FAMILY	GENUS	SPECIES	NUMBER
UNIDENTIFIED			24

Orthoptera

FAMILY	GENUS	SPECIES	NUMBER
UNIDENTIFIED			1

Phasmatodea

FAMILY	GENUS	SPECIES	NUMBER
UNIDENTIFIED			20

Siphonaptera (slide mounted)

FAMILY	GENUS	SPECIES	NUMBER
Pulicidae	*Ctenocephalides*	*felis* (Bouché) 1835	9
Pulicidae	*Ctenocephalides*	*felis* (Bouché) 1836	8
Pulicidae	*Pulex*	*simulans* Baker 1895	5
Pulicidae	*Pulex*	*simulans* Baker 1896	5
Pulicidae	*Pulex*		1
Tungidae	*Tunga*	*penetrans* (Linnaeus) 1758	1

Description of a New Species of *Inola* Davies (Araneae: Pisauridae), the Male of *I. subtilis* Davies and Notes on Their Chromosomes

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Tio, M. and Humphrey, M. (2010). Description of a new species of *Inola* Davies (Araneae: Pisauridae), the male of *I. subtilis* Davies and notes on their chromosomes. *Proceedings of the Linnean Society of New South Wales* **131**, 37-42

A new pisaurid spider, *Inola daviesae* sp.n. is described from northern Queensland together with the first description of the male of *I. subtilis*. The meiotic chromosomes of both species are discussed.

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KEYWORDS: chromosomes, *Inola*, Pisaurid, Queensland, rainforest, spider.

INTRODUCTION

Australian pisaurid spiders are generally not web builders, except for members of *Inola* Davies, 1982 and *Dendolycosa* Koch, 1876. The genus *Inola* includes three species from northeastern Queensland (Davies, 1982). Like Davies' *Inola* species, *Inola daviesae* sp.n. described here is a delicate, medium-sized spider associated with tropical rainforest. As with other members of the genus, this spider runs on the upper surface of its horizontal sheet web. These webs project from the trunks of rainforest trees or embankments. A short silken funnel extends from the sheet web to a retreat in a tree trunk or embankment. The females, like those of other pisaurids, grasp their egg sacs in their chelicerae when disturbed and carry them into their retreat (Davies, 1982).

Abbreviations: CL cephalothorax length; CW cephalothorax width; AL abdomen length; AW abdomen width; MOQ median ocular quadrangle; AM Australian Museum; QM Queensland Museum.

MATERIALS AND METHODS

Morphology

Measurements were made with an ocular micrometer and converted to millimetres. Measurements are for a single specimen with a range of variation if significant. Spines have been recorded as number per surface for each segment, as they were often staggered.

Chromosomes

Live penultimate male spiders were anaesthetized with CO_2. The testes were dissected out and sections were spread, fixed and stained after the method of Rowell (1991). These preparations were viewed and photographed using a light microscope. Counts and other observations were noted from photographs of many (>50), suitable meiotic cells in metaphase and chromosome numbers for species determined by the mode.

SYSTEMATICS

Genus *Inola* Davies, 1982

Inola Davies, 1982: 479
Type species: *Inola amicabilis* Davies, 1982, by original designation (page 480).

***Inola daviesae* n.sp.**
Figs (1-4, 7-11)

Types

Holotype: male, Leo Creek, MacIlwraith Ranges, North Qld. [13°32'S 143°29'E], July, 1995, M. Humphrey, M. Moulds, KS58316 (AM). Paratypes: 1 female, same data as holotype, KS58322 (AM); 1 male, 5 females, Qld. MacIlwraith Ranges, Leo Creek [13°32'S 143°29'E], 20 Jul 1995, M. Humphrey, M. Moulds, F. MacKillop, KS43933 (AM); 1 male, 1 female, data as for holotype, QMS 83903 (QM).

Other material examined

Eleven juveniles, same data as holotype, KS58315 (AM).

Distribution

Rainforest, MacIlwraith Range, north-eastern Queensland at an altitude of approximately 500m.

Diagnosis

Males can be distinguished from other members of the genus by the distinctive spannerhead-shaped distal portion of the median apophysis of the male palp (Fig. 8). The female scape is narrow while that of *I. cracentis* is broad and that of *I. subtilis* is triangular, pointed posteriorly and broad anteriorly.

Description of male

Measurements of holotype: CL 4.3, CW 2.7, AL 5.9, AW 1.7. Eye group: anterior width 1.1; posterior width 1.1; length 0.6; MOQ: anterior width 0.4; posterior width 0.5; length 0.5. Maxilla: length 1.3; width 0.8; Sternum: length 1.9; width 1.9; Colulus: length 0.2; width 0.3. Leg lengths:

	Palp	1	2	3	4
Femur	4.5	11.9	11.4	7.6	11.3
Patella	1.6	1.9	2.0	1.4	1.5
Tibia	1.9	11.1	11.3	8.9	10.3
Metatarsus	—	15.1	14.6	9.8	15.4
Tarsus	4.6	4.9	4.6	3.5	4.9
Total	12.6	44.9	43.9	31.2	43.4

Spine notation: Palp: femur, d3p1; patella, d5p1r1; tibia, d2r2; tarsus, 0. Leg I: femur, d4p5; patella, d1; tibia, d3p3r2v3; metatarsus, p4r4v1, whorl of four small spines distally ; tarsus, 0. Leg II: femur, d2p5r5; patella, d1; tibia, d2p3r4v3; metatarsus, p3r4, whorl of four small spines distally; tarsus, 0. Leg III: femur, d2p4r5; patella, d1; tibia, p2r4v3; metatarsus, p4r4, whorl of four small spines distally; tarsus, 0. Leg IV: femur, d3p4r2; patella,d1; tibia p3r3v2; metatarsus, d4p4; tarsus,0. Note: four distal spines on end of each metatarsus.

Eye diameters roughly equal. Cephalothorax patterned (Fig.1). Abdomen with central pale stripe to almost half the length of abdomen. Pair of pale latero-dorsal stripes, running three quarters of the abdomen. Two or three pairs of prominent pale spots between the central and the latero-dorsal stripes. Legs banded.

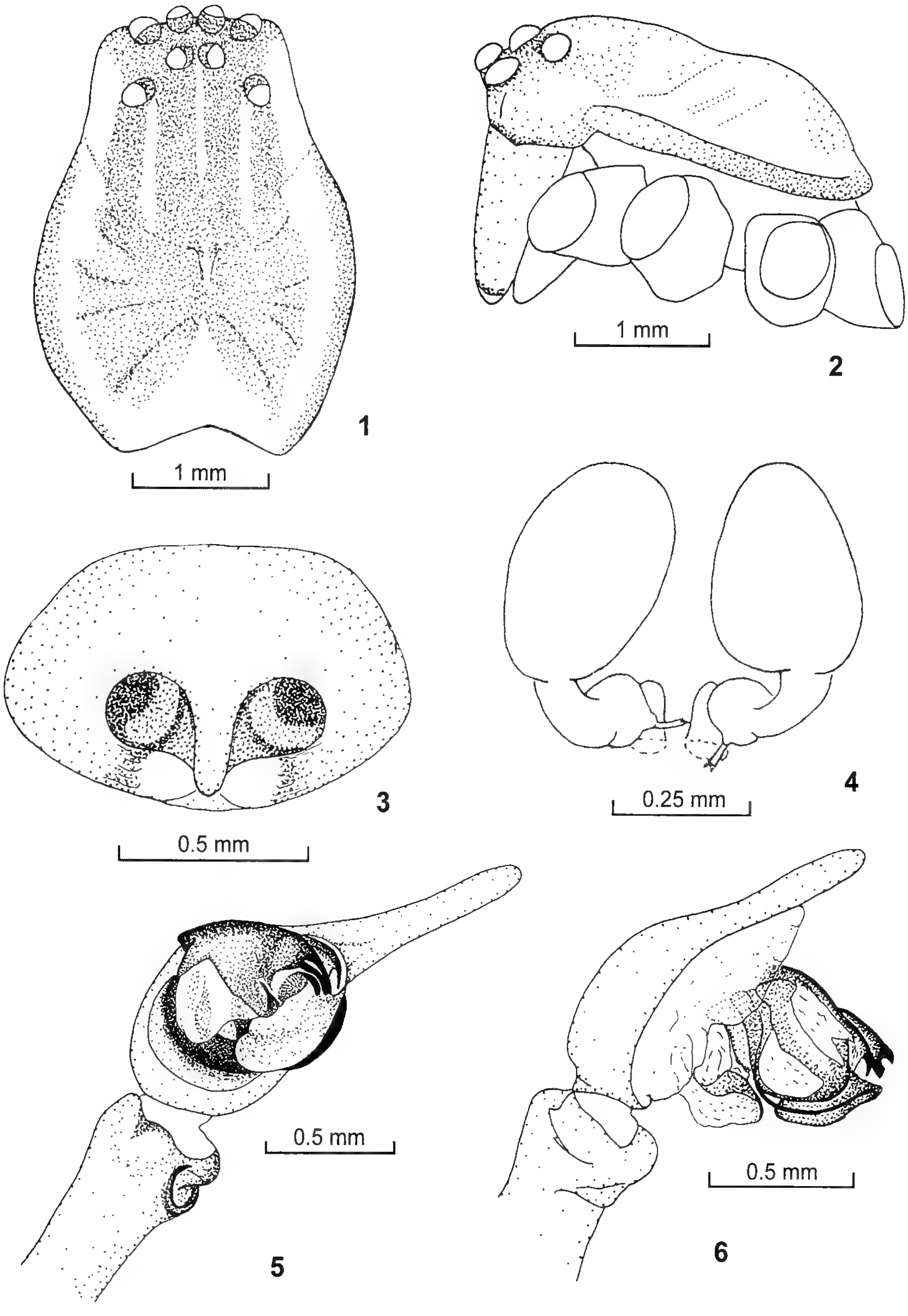
Palp (Figs.7, 8). Digitiform portion half the length of the palpal tarsus. Median apophysis large and partly membraneous, partly sclerotised. Distal sclerotised portion bifid (spanner-like). Embolus slender and curved. Conductor behind median apophysis with a fold distally.

Description of female

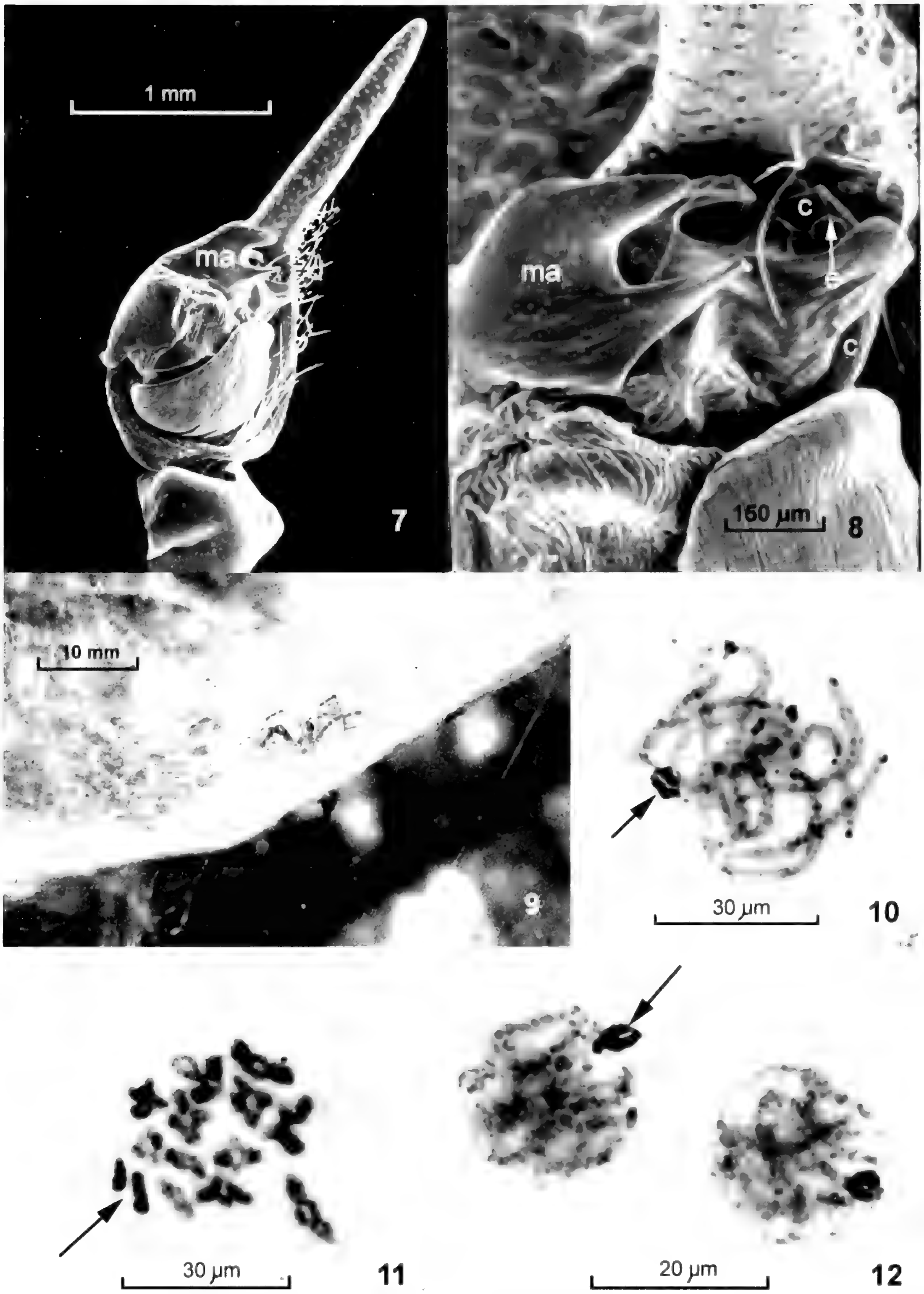
Measurements of KS58322: CL 3.9, CW 3.4, AL 6.9, AW 4.7. Eye group: anterior width 1.5; posterior width 1.6; length 1.0; MOQ: anterior width 0.7; posterior width 0.8; length 0.7. Maxilla: length 1.6; width 1.0. Sternum: length 2.6; width 2.1; Colulus: length 0.2; width 0.3. Leg lengths:

	Palp	1	2	3	4
Femur	2.8	8.6	9.4	7.5	9.4
Patella	1.0	2.2	1.9	1.6	1.6
Tibia	1.4	8.8	9.3	6.1	8.0
Metatarsus	—	10.4	8.6	7.9	12.5
Tarsus	3.1	3.0	3.5	3.1	4.3
Total	8.3	33.0	32.7	26.2	35.8

Spine notation: Palp: femur, d1p1; patella, d1p1; tibia d2p2r1, tarsus, p2. Leg I: femur, d2r2; patella, d1; tibia, d1r2v1; metatarsus, d3r4v2, whorl of four small spines distally, tarsus, 0. Leg II: femur, d2p5r5; patella, d1; tibia, d1p2r2v1; metatarsus, d3p2r4v2, whorl of four small spines distally; tarsus, 0. Leg III: femur, d4p2v1; patella, d1r1; tibia, 0; metatarsus, d1p2r2v2, whorl of four small spines distally; tarsus, 0. Leg IV: femur, d4r5; patella d1r1; tibia, 0; Metatarsus, d2p3r1v2, whorl of four small spines distally; tarsus, 0. Note: four distal spines on end of metatarsus (every leg).



Figures 1-7. 1, *Inola daviesae* sp. n. male carapace, dorsal, (holotype). 2, *Inola daviesae* sp.n. male cephalothorax, lateral, (holotype). 3, *Inola daviesae* sp. n. epigynum, external, (KS58322). 4, *Inola daviesae* sp. n. epigynum, internal, ventral. 5, *Inola subtilis*, male palp, ventral, (KS58321). 6, *Inola subtilis*, expanded male palp, retrolateral, (KS58320).



Figures 7-12. 7, male palp of *Inola daviesae* sp.n. 8, median apophysis (ma), embolus (e) and conductor (c) of *Inola daviesae* sp. n. 9, *Inola daviesae* sp.n. female on sheet web. 10, *Inola daviesae* sp.n., prophase male meiotic chromosomes showing two dense sex chromosomes (arrowed). 11, *Inola daviesae* sp.n., male meiotic cell showing 14 pairs of chromosomes. 12, *Inola subtilis*, male prophase meiosis showing two densely stained sex chromosomes (arrowed).

Epigynum (Figs 3, 4). Scape a narrow bar. Insemination ducts arise near hind edge of the epigastrum and travel forward. Large stalked spermathacae. Insemination duct enters near the base of the posterior spermathacae (fertilisation duct leaves below this junction).

Chromosomes

For males of *I. daviesae* sp. n., 2N = 28 (Fig. 11), including two subequal, darkly staining sex chromosomes. Most of the 13 pairs of autosomes in *Inola daviesae* sp. n. appear to be telocentric. The two sex chromosomes are easily distinguished in prophase of meiosis (Fig. 10). They migrate from the equator of the spindle in metaphase as a pair and earlier than the autosomes. Such sex chromosomes and their behaviour have been observed in other spiders by Rowell (1991). According to a survey of spider chromosome studies, (Rowell, personal comm.), female spiders have double the number of sex chromosomes to those of the male. Presuming this species follows the same sex determination mechanism, males of *Inola daviesae* n. sp. would be XX and females XXXX, giving females 2N = 32.

Etymology.

Named for Valerie Todd Davies who described the genus.

Inola subtilis Davies, 1982
(Figs 5, 6)

Material examined

1 male, Goldsborough S. F., Qld., July, 1995, M. Humphrey, KS58321 (AM); 1 male, data as for KS58321, QMS83902 (QM); 3 males, data as for KS58321, KS58320 (AM); 1 male, Palm Cove, FNQ, J.Olive, 6 Sept 1995, sheet web on fallen log, KS044108 (AM); Goldsborough Valley SF, rainforest strangler fig, 27 Jul 1995, M. Humphrey, KS043900 (AM).

Distribution

Material from Davies' description of the species indicates a distribution on the western edge of suburban Cairns. The material examined above extends this distribution from Palm Cove (north of Cairns) to the Goldsborough Valley in the south.

Diagnosis for male

Unlike the other three members of the genus, the sclerotised distal portion of the male palpal median apophysis forms two, fused, parallel, curved processes (Fig. 5). Proximally is a long, narrow sclerotised spur pointing ventrally, at right angles to the palp. Conductor sclerotised, retrolateral, behind the large median apophysis and bearing a spine distally.

Description of male

Measurements of KS58321: CL 3.5, CW 2.8, AL 4.4, AW 1.44; Eye group: anterior width 0.8; posterior width 1.2; length 0.8; MOQ: anterior width 0.5, posterior width 0.6, length 0.5. Maxilla: length 1.0; width 0.5. Sternum: length 1.8, width 1.7. Colulus: length 0.3, width 0.5. Leg lengths:

	Palp	1	2	3	4
Femur	2.0	10.0	9.3	7.5	9.4
Patella	0.6	1.6	1.6	1.5	1.5
Tibia	0.8	10.3	9.4	6.9	8.9
Metatarsus	—	12.6	12.1	9.1	13.0
Tarsus	1.6	3.9	3.6	2.5	3.3
Total	5.0	38.4	36.0	27.5	36.1

Spine notations: Palp: femur, d2p1; patella, d1p1r1; tibia, d2p2; tarsus, 0. Leg I: femur, d2p8r3; patella, d1; tibia, d3p2r2v4; metatarsus, d3p2r5v2; tarsus, 0. Leg II: femur, p5; patella, d5p6r3; tibia, d2p2r2v3; metatarsus, d1p3r3v1; tarsus, 0. Leg III: femur, d2p5r5; patella, d1; tibia, d2p3r3v3; metatarsus, d2p2r2v2; tarsus, 0. Leg IV: femur, d2p5r2; patella, d2p4r2v3; tibia, d1p1r3v1; metatarsus, d2p2r2; tarsus, 0.

Abdomen long and narrow. Abdominal pattern with pale centre stripe and a pair of pale latero-dorsal stripes. Pairs of prominent pale spots as in *I. daviesae* but spots continue in line and merge to form a pair of additional stripes. Legs banded.

Male palp (see diagnosis): Length of digitiform portion almost half of palpal tarsus. Embolus curved, slender, lying between median apophysis and conductor.

Chromosomes

Because of poor spreading, the number of chromosomes of *I. subtilis* could only be estimated. However, it is between 26 and 32 and most of the chromosomes are telocentric. There are two sex chromosomes (Fig. 12) and like those of *I. daviesae* sp. n., they are darkly staining and migrate from the equator of the spindle earlier than the autosomes.

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A Late Ordovician Conodont Fauna from the Lower Limestone Member of the Benjamin Limestone in Central Tasmania, and Revision of *Tasmanognathus careyi* Burrett, 1979

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Zhen, Y.Y., Burrett, C.F., Percival, I.G. and Lin, B.Y. (2010). A Late Ordovician conodont fauna from the Lower Limestone Member of the Benjamin Limestone in central Tasmania, and revision of *Tasmanognathus careyi* Burrett, 1979. *Proceedings of the Linnean Society of New South Wales* **131**, 43-72.

Ten conodont species, including *Aphelognathus*? sp., *Belodina compressa*, *Chirognathus tricostatus* sp. nov., *Drepanodus* sp., gen. et sp. indet., *Panderodus gracilis*, *Protopanderodus*? *nogamii*, *Phragmodus undatus*, *Tasmanognathus careyi* and *T.* sp. cf. *T. careyi* are documented from the Lower Limestone Member of the Benjamin Limestone, Gordon Group, exposed in the Florentine Valley and Everlasting Hills region of central Tasmania. For the first time since its establishment three decades ago, the type species of *Tasmanognathus, T. careyi,* is revised with recognition of a septimembrate apparatus including makellate M, alate Sa, digyrate Sb, bipennate Sc, tertiopedate Sd, carminate Pa, and Pb (angulate Pb1 and pastinate Pb2) elements. Co-occurrence of *Phragmodus undatus* and *Belodina compressa* in the fauna indicates a latest Sandbian to earliest Katian (*Phragmodus undatus* conodont Zone) age for the Lower Limestone Member of the Benjamin Limestone. All species previously attributed to *Tasmanognathus* are briefly reviewed, and the distribution of the genus is shown to be more widespread than hitherto recognised (in New South Wales, North China, Tarim Basin, South Korea and northeast Russia), with a probable occurrence in North American Midcontinental faunas.

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KEYWORDS: Benjamin Limestone, biogeography, biostratigraphy, conodonts, Late Ordovician, Tasmania, *Tasmanognathus*.

INTRODUCTION

Ordovician conodont faunas of Tasmania are relatively poorly known in comparison to those from the mainland of Eastern Australia. Only three papers – Burrett (1979), Burrett et al. (1983) and Cantrill and Burrett (2004) – have dealt systematically with a small number of species. The present contribution, which describes the comparatively diverse fauna from the lower part of the Benjamin Limestone, is the first part of a revision of all known conodonts from Tasmania. This project aims to provide a firm basis for conodont-based correlations of the carbonate-dominated Gordon Group with limestones along the Delamerian continental margin in New South Wales, with strata in offshore island arc settings in central N.S.W. (Macquarie Arc), and with isolated limestone pods in the New England Orogen in northeastern N.S.W. and central Queensland.

Given the rarity of graptolites in the predominantly shallow-water platformal succession forming the Delamerian margin succession, and the sparsely documented occurrences of conodonts, biostratigraphical zonation in Ordovician rocks of Tasmania is currently largely reliant on shelly macrofossils. Banks and Burrett (1980) established a series of twenty successive faunas (designated OT assemblages 1-20), one of which (OT 12) was defined by the occurrence of several conodont species including *Tasmanognathus careyi*, *Chirognathus monodactyla*, *Erismodus gracilis* and *Plectodina aculeata* in the basal Benjamin Limestone. This fauna (based at the time on unpublished studies by Burrett, with no species illustrated or described in the 1980 paper) is revised here. Our study has not identified the last two named species, and has recognised a new species of *Chirognathus* in place of *C. monodactyla*. Burrett (in Webby et al. 1981, p.12) summarised the occurrences of conodonts in the Tasmanian Ordovician succession. He noted the first appearance of the biostratigraphically important species *Phragmodus undatus* in strata immediately above the Lords Siltstone Member in the middle of the Benjamin Limestone; however, our reassessment of the fauna has identified the presence of this species in the underlying lower part of the Benjamin Limestone. Laurie (1991) defined an alternate series of 20 faunal assemblages based on Tasmanian brachiopods, ranging in age from Early Ordovician (Tremadocian) to earliest Silurian. Where possible, these brachiopod faunas were tied in to conodont occurrences, mainly derived from Burrett's (1978) unpublished thesis studies.

A biogeographically significant component of the Tasmanian conodont fauna is *Tasmanognathus* Burrett, 1979, which was first identified from the Lower Limestone Member of the Benjamin Limestone exposed in the Florentine Valley and Everlasting Hills region of central Tasmania (Fig. 1). This genus has subsequently been widely recognized as occurring in rocks of early Late Ordovician (Sandbian) age in eastern Australia and China. Low yields (averaging two specimens per kg) of conodonts from the Gordon Group carbonates collected and processed by Burrett (1978) resulted in *Tasmanognathus* being imperfectly defined. Thirty years after its initial documentation, revision of the type species, *T. careyi* Burrett, 1979 has become urgently needed in order to better understand its multielement apparatus, phylogenetic relationship and precise stratigraphic range in the type area. The purpose of this paper is to describe the conodont fauna from the middle part of the Gordon Group in the Settlement Road section of the Florentine Valley area, equivalent to the level yielding *Tasmanognathus*, based on five recently collected bulk samples of limestone totalling 49.5 kg that on dissolution in acetic acid have yielded an average of six elements per kg. These additional collections are supplemented by re-examination of Burrett's original material including types and topotypes of *T. careyi*, and for the first time all the accompanying conodont fauna is documented by description and/or illustration, including *Aphelognathus*? sp., *Belodina compressa* (Branson and Mehl, 1933), *Chirognathus tricostatus* sp. nov., *Drepanodus* sp., *Panderodus gracilis* (Branson and Mehl, 1933), *Protopanderodus*? *nogamii* (Lee, 1975), *Phragmodus undatus* Branson and Mehl, 1933, and gen. et sp. indet.

REGIONAL GEOLOGIC AND BIOSTRATIGRAPHIC SETTING

Platform sedimentary rocks of the Early Palaeozoic Wurawina Supergroup, that are widespread in the western half of Tasmania, consist of the Late Cambrian – Early Ordovician Denison Group (mainly siliciclastics), conformably overlain by the Gordon Group (predominantly carbonates of Early to Late Ordovician age), in turn conformably or disconformably overlain by the Hirnantian (latest Ordovician) to mid-Devonian Eldon Group, which consists mainly of siliciclastics (Burrett *et al.* 1984; Laurie 1991). The Gordon Group attains a thickness of 2100m of carbonates and minor siltstones in its redefined type section in the Florentine Valley where it is divided into three limestone formations. The uppermost of these, the Benjamin Limestone, is divided into two limestone members (Upper and Lower) separated by a thin but regionally extensive, macrofossiliferous siltstone member (Lords Siltstone Member). The Benjamin Limestone predominantly consists of interbedded microcrystalline peritidal dolomitic micrite, dolostone and calcarenite with a maximum thickness of about 1200m. Some 400 conodont samples were initially collected over a 5m interval by Burrett (1978) from the various localities of the Gordon Group, but many of these samples were barren or had a very low yield, due to the peritidal to shallow subtidal depositional setting and high rate of sedimentation in the tropical shelf environments. Continuous efforts in the last 30 years by post-graduate students and academic staff of the University of Tasmania have accumulated significant amounts of conodont material for the age determination and biostratigraphic analysis of the Gordon Group (Burrett 1979; Burrett *et al.* 1983, 1984; Cantrill and Burrett 2004).

Carbonates that are coeval with the Lower Limestone Member of the Benjamin Limestone occur in many sections in northern, western and southern

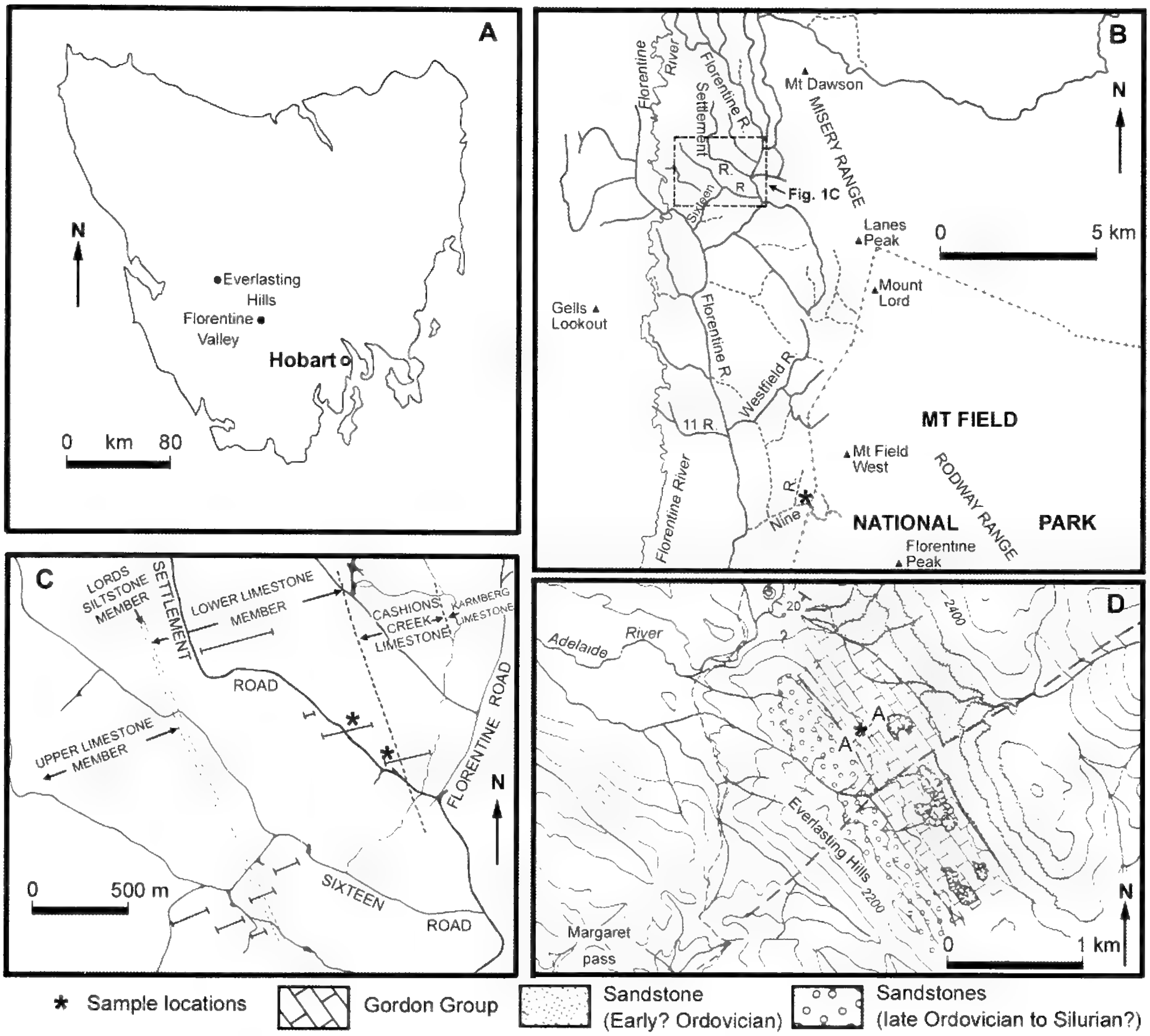

Figure 1. Maps showing the studied areas in central Tasmania and sample locations. A, Map of Tasmania showing the locations of Florentine Valley and Everlasting Hills (from Burrett 1978, 1979); B, Map showing the Florentine Valley area and sample location of the Nine Road Section (modified from Laurie 1991); C, Map showing the Settlement Road Section of the Florentine Valley and sample locations (modified from Laurie 1991); D, Map showing Everlasting Hills area and sample location (from Burrett 1978).

Tasmania, but the *Tasmanognathus careyi* fauna has only been definitely found in the Florentine Valley and in the Everlasting Hills. The Florentine Valley sections (Figs 1 and 2) are found in the eastern side of a mid-Devonian synclinorial structure. This area was first mapped geologically by Corbett and Banks (1974) and because of its completeness, has subsequently been the focus of numerous palaeontological and sedimentological studies. However, active timber logging in this area has meant that some sections are now inaccessible, having been replanted with dense, almost impenetrable, forest.

The Everlasting Hills section (Fig.1D) was discovered in remote and moderately dense to thick vegetation and mapped by Ian McKendrick and Clive Burrett in 1975 (Fig.1D). This doline and cave-rich area has since been included in the South West Tasmania World Heritage wilderness area, and has undergone extensive regrowth so that it is now extremely difficult to access. The palaeotropical limestones in the Everlasting Hills are identical to those in the Lower Limestone Member of the Benjamin Limestone in the Florentine Valley, and consist of 3-6m thick Punctuated Aggradational Cycles (Goodwin and Anderson 1985) of mainly dolomitised, intertidal micrites with tidal channels and top beds containing a lower intertidal to high subtidal macrofauna. Somewhat deeper water, coeval carbonates (the Ugbrook Formation) occur in

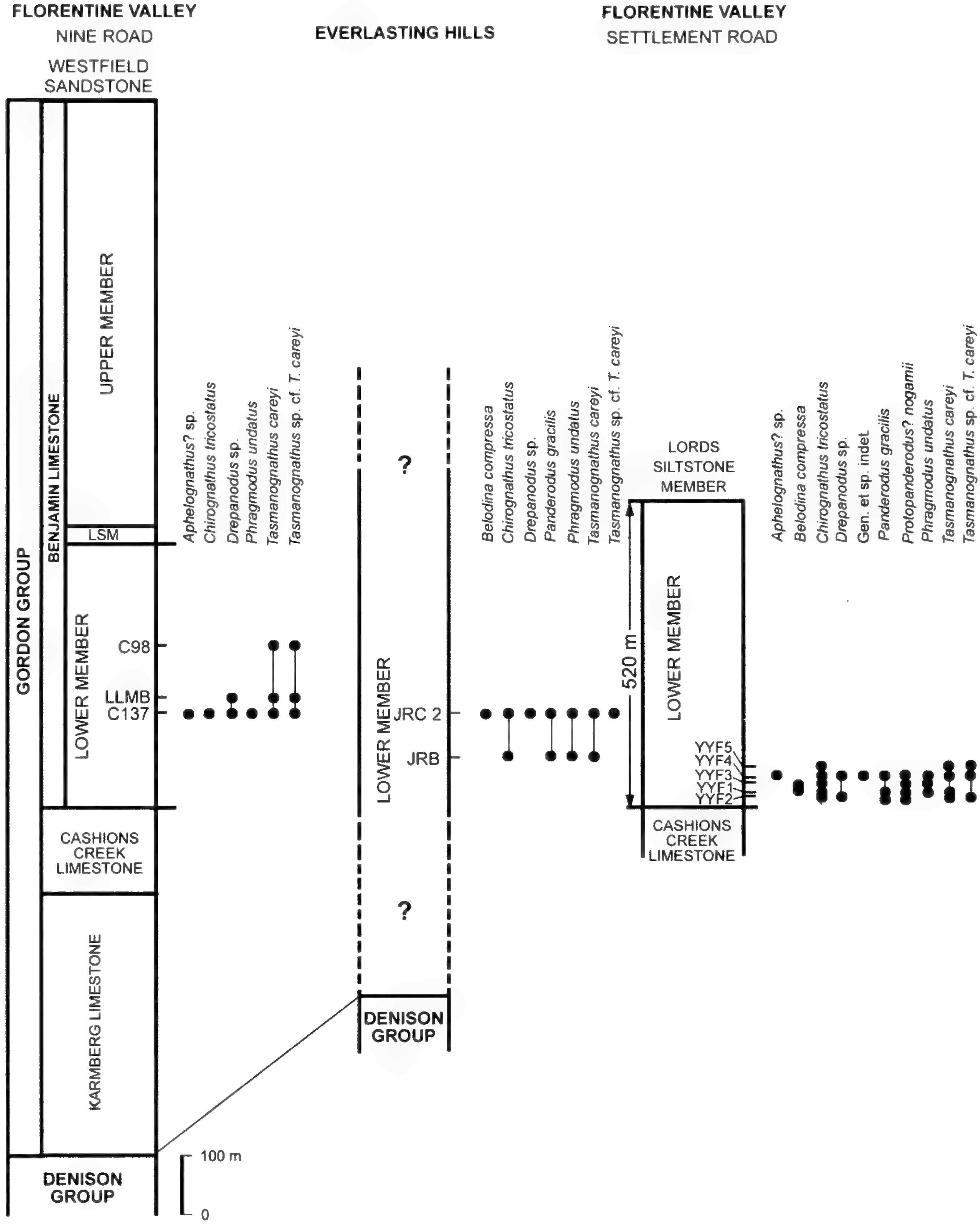

Figure 2. Three stratigraphic sections showing the sample horizons and ranges of the conodont species in the Lower Limestone Member of the Benjamin Limestone, Gordon Group, in central Tasmania.

northern and western Tasmania (Burrett et al. 1989) but these lack *Tasmanognathus*. This suggests that *Tasmanognathus* was mainly restricted to peritidal tropical environments in the Late Ordovician.

The *Tasmanognathus* fauna is associated with a strongly endemic macrofauna in the lower and middle parts of the Lower Limestone Member, Benjamin Limestone, including the brachiopods *Lepidomena* Laurie, 1991, *Tasmanorthis* Laurie, 1991 and the nautiloids *Gorbyoceras settlementense* Stait and Flower, 1985, *Paramadiganella* Stait, 1984 and *Tasmanoceras zeehanense* Teichert and Glenister, 1952 (Laurie 1991; Stait 1988). *Tasmanognathus careyi* is found in two of the twenty Ordovician brachiopod assemblages (or biozones) recognised by Laurie (1991); the *Tasmanorthis calveri* and the younger *Tasmanorthis costata* assemblages.

AGE AND CORRELATION OF THE FAUNA

In the conodont fauna associated with *Tasmanognathus careyi* from the Lower Limestone Member of the Benjamin Limestone in central Tasmania, occurrence of *Phragmodus undatus* and *Belodina compressa* is crucial for age determination and regional correlation, as both species are cosmopolitan and age diagnostic. The former had a relatively long stratigraphic range, extending from the base of the *Ph. undatus* Zone (in the upper Sandbian) to the top of the Katian, and the latter first occurs at the base of the *B. compressa* Zone and extends to the base of the *B. confluens* Zone (Sweet 1988). Co-occurrence of these two species and absence of any diagnostic species of either the *B. confluens* or *P. tenuis* zones indicates a latest Sandbian to earliest Katian age (*Phragmodus undatus* Zone) for this Tasmanian fauna.

Chirognathus is also morphologically distinctive with the two previously-reported species (*Chirognathus duodactylus* Branson and Mehl, 1933 and *Chirognathus cliefdenensis* Zhen and Webby, 1995) restricted to the upper Sandbian-Katian interval (Sweet 1982; Zhen & Webby 1995). The new species from Tasmania described herein is morphologically similar to the type species of the genus, *C. duodactylus* Branson and Mehl, 1933. This species with a well-known multi-element apparatus is widely distributed in Sandbian strata of the North American Mid-continent ranging from the *Pygodus anserinus* Zone to the *Phragmodus undatus* Zone (Sweet in Ziegler 1991). The second species, *Chirognathus cliefdenensis* Zhen and Webby, 1995, occurs in a stratigraphically slightly younger interval in central New South Wales, where it is recorded from the upper Fossil Hill Limestone to the lower Vandon Limestone (early Katian) of the Cliefden Caves Limestone Subgroup (Zhen and Webby 1995), from the Downderry Limestone Member (late Katian) of the Ballingoole Limestone of the Bowan Park Limestone Subgroup (Zhen et al. 1999), and from allochthonous limestones of Katian age emplaced in the Silurian Barnby Hills Shale (Zhen et al. 2003a).

The Lower Limestone Member of the Benjamin Limestone exposed in the Everlasting Hills and Florentine Valley areas in central Tasmania is the type stratum of *Tasmanognathus careyi* Burrett, 1979. Since the initial documentation of this species, at least ten additional species from lower Sandbian to upper Katian strata predominantly of North China and eastern Australia have been accommodated in *Tasmanognathus* (see Systematic section for further discussion). The origin and phylogenetic relationships of *Tasmanognathus* remain uncertain as most of these species were poorly documented and need to be revised. Reassessment of *T. careyi* herein suggests that *Tasmanognathus* may be closely related to so-called "Ordovician ozarkodinides" (Sweet 1988, p. 91-92), an informal group including forms like "*Plectodina*", *Aphelognathus* and *Yaoxianognathus*. Based on similarities of their general morphology and apparatus construction, *Tasmanognathus*, as a sister group, seems closely related to *Yaoxianognathus*. *Tasmanognathus* is potentially the direct ancestor of the latter, which was mainly restricted to eastern Gondwana and peri-Gondwanan terranes during the Late Ordovician (Katian). Strong biogeographic similarities (including *Tasmanognathus*) between the North China Terrane (or block) and eastern Australia were part of the evidence used by Burrett et al. (1990) to suggest that these blocks were contiguous or closely proximal during the Ordovician.

Tasmanognathus was widely reported from the Sandbian in North China with recognition of three biozones based on the inferred lineage of *Tasmanognathus* species (An and Zheng 1990; Lin and Qiu 1990), from the oldest *T. sishuiensis* Zhang in An et al., 1983 from the upper Fengfeng Formation (lower Sandbian), to *T. shichuanheensis* An in An et al., 1985 from the middle-lower part of the Yaoxian Formation (upper Sandbian), and then to the youngest *T. multidentatus* An in An and Zheng, 1990 (the latter is a *nomem nudum*, equivalent to *T. borealis* An in An et al. 1985; see Systematic Section for further discussion) from the upper part of the Yaoxian Formation (upper Sandbian-lower Katian). An and Zheng (1990, p. 95, text-fig. 9) illustrated the morphological changes from *T. sishuiensis* with a robust cusp and small, widely spaced denticles on the processes of the S elements, to *T. multidentatus* with a small, indistinct cusp in the Pa element and closer spaced denticles of variable sizes on the processes of the S elements. Importantly, similar morphological changes have also been observed between the two species of *Tasmanognathus* recognized in the Lower Limestone Member of the Benjamin Limestone in central Tasmania. A species described herein as *T.* sp. cf. *T. careyi* that bears a prominent cusp in the Pa element and small, widely spaced denticles on the processes of the S and Pb elements is more comparable with *T. shichuanheensis* from the middle-lower part of the Yaoxian Formation, whereas *T. careyi* with a small or indistinct cusp in the Pa element and long, closely spaced denticles on the processes of the S elements is closer to *T. multidentatus* from the upper part of the Yaoxian Formation. *T. careyi* was also reported from the middle part of the Yaoxian Formation in association with *T. shichuanheensis* and *Belodina compressa* in Bed 3, about 44 m below the first occurrence of *T. multidentatus* (An and Zheng 1990, p. 86-87), although An's identification cannot be confirmed without re-examination of the original material (An et al. 1985) and further investigations.

Occurrence of *Taoqupognathus blandus* at the top of the Yaoxian Formation in the Taoqupo Section of Yaoxian County (formerly Yaoxian; An and Zheng 1990) suggests that the Yaoxian Formation may well extend to the lower Katian. Therefore, the morphological characters shown by the two species of *Tasmanognathus* from the Lower Limestone Member of the Benjamin Limestone support a correlation between this limestone unit in central Tasmania, and the middle part of the Yaoxian Formation in North China (with the possible occurrence of *T. careyi*), which An and Zheng (1990, p. 92, table 2) correlated with the *C. wilsoni* graptolite Zone (late Sandbian).

An and Zheng (1990, p.115) suggested that the Llandoverian conodonts illustrated by Lee (1982) from the Hoedongri Formation in the Taebaeksan Basin, Kangweon-Do of South Korea were comparable with the *Tasmanognathus sishuiensis* assemblage from the upper Fengfeng Formation of North China. In fact, in their revision of Lee's original identifications (An and Zheng 1990, table 5, pp. 118-119), they believed what Lee (1982) illustrated as *Pterospathodus celloni* (Walliser) should belong to *Tasmanognathus sishuiensis*, and considered that the Hoedongri Formation should be correlated with the Baduo Formation or the upper part of the Fengfeng Formation (Sandbian) of North China.

MATERIAL AND SAMPLING LOCALITIES

The current study is based on 683 identifiable specimens from 10 samples (See Table 1). Of these,

Table 1. Distribution of conodont species in the samples studied.

species	JRC 2	JRB	LLMB	C137	C98	YYF1	YYF2	YYF3	YYF4	YYF5	Total
Aphelognathus? sp.				2					2		4
Belodina compressa	9							1			10
Chirognathus tricostatus sp. nov.	36	6		12		2	1	1	5	8	71
Drepanodus sp.	20		1	2		1	1		2		27
Gen. et sp. indet.									3		3
Panderodus gracilis	41	2	4				3		2		52
Protopanderodus? *nogamii*						4	44	3	18		69
Phragmodus undatus	25	2		6		1		31	51		116
Tasmanognathus careyi	156	5	20	26	26	7	23		23	11	297
Tasmanognathus sp. cf. *T. careyi*	3					8	7		14	2	34
Total	290	15	25	48	26	23	79	36	120	21	683

378 specimens are Burrett's (1979) original material including types of *Tasmanognathus careyi* recovered from five samples collected from the Florentine Valley and Everlasting Hills sections (see Burrett 1979, p. 32, fig. 1 for sample locations and their stratigraphic horizons within the Lower Member of the Benjamin Limestone). Samples LLMB, C137 and C98 were collected from the Lower Limestone Member of the Benjamin Limestone exposed along the Nine Road (Fig. 1B). The Lower Limestone Member of the Benjamin Limestone is exposed as a 50m thick section (at Grid Ref. DP202157; 42°16.4'S, 146°2.65'E) to the north side of the Everlasting Hills (Fig. 1D). Two samples (JRC 2 and JRB) from this location produced relatively abundant conodonts (Table 1). The remaining 305 specimens were recovered from five large spot samples – YYF1 (13 kg), YYF2 (8 kg), YYF3 (10 kg), YYF4 (7.5 kg), and YYF5 (11 kg) – collected from the lower part of the Lower Limestone Member of the Benjamin Limestone in the Settlement Road section of the Florentine Valley area (Figs 1C, 2).

SYSTEMATIC PALAEONTOLOGY

All photographic illustrations shown in Figures 3 to 17 are SEM photomicrographs of conodonts captured digitally (numbers with the prefix IY are the file names of the digital images). Figured specimens bearing the prefix AM F. are deposited in the type collections of the Palaeontology Section at the Australian Museum in Sydney. All the syntypes except one (UTG96863 not located; figured by Burrett 1979, pl. 1, figs 17-18) and most of the other specimens of *Tasmanognathus careyi* illustrated by Burrett (1979) were relocated and made available for the current study. They have been now transferred to the Australian Museum collection, and a new AM F. registration number has been allocated to each of the specimens illustrated in this contribution.

The following species are documented herein only by illustration as they are either rare in the collection or have been adequately described elsewhere in the literature: *Aphelognathus*? sp. (Fig. 3J-K), *Drepanodus* sp. (Fig. 3C-F), gen. et sp. indet. (Fig. 3G-I), and *Panderodus gracilis* (Branson and Mehl, 1933) (Fig. 6A-I). Authorship of the new species *Chirognathus tricostatus* is attributable solely to Zhen. Taxa documented herein are alphabetically listed according to their generic assignment, with family level and higher classification omitted.

Phylum Chordata Balfour, 1880
Class Conodonta Pander, 1856

Genus BELODINA Ethington, 1959

Type species
Belodus compressus Branson and Mehl, 1933.

Belodina compressa (Branson and Mehl, 1933)
Fig. 3A-B

Synonymy
Belodus compressus Branson and Mehl, 1933, p. 114, pl. 9, figs 15, 16.
Belodus grandis Stauffer, 1935, p. 603-604, pl. 72, figs 46, 47, 49, 53, 54, 57.
Belodus wykoffensis Stauffer, 1935, p. 604, pl. 72, figs 51, 52, 55, 58, 59.
Oistodus fornicalus Stauffer, 1935, p. 610, pl. 75, figs 3-6.
Belodina dispansa (Glenister); Schopf, 1966, p. 43, pl. 1, fig. 7.
Belodina compressa (Branson and Mehl); Bergström and Sweet, 1966, p. 321-315, pl. 31, figs 12-19; Sweet in Ziegler, 1981, p. 65-69, *Belodina* - plate 2, figs 1-4; Leslie, 1997, p. 921-926, figs 2.1-2.20, 3.1-3.4 (*cum syn.*); Zhen et al., 2004, p. 148, fig. 5A-I (*cum syn.*); Percival et al., 2006, fig. 3A-D.
Belodina confluens Sweet; Percival et al., 1999, p. 13, Fig. 8.21.

Material
Ten specimens from two samples (see Table 1).

Discussion
Only compressiform (Fig. 3A) and grandiform (Fig. 3B) elements were recovered from the Tasmanian samples. These elements are identical with those recorded from the upper part of the Wahringa Limestone Member of the Fairbridge Volcanics (assemblage C, see Zhen et al. 2004), and others from drillcore samples in the Marsden district (Percival et al. 2006) of central New South Wales. Morphological distinction between *B. compressa* and closely related species, particularly *B. confluens*, was discussed by Zhen et al. (2004).

Genus CHIROGNATHUS Branson and Mehl, 1933

Type species
Chirognathus duodactylus Branson and Mehl, 1933.

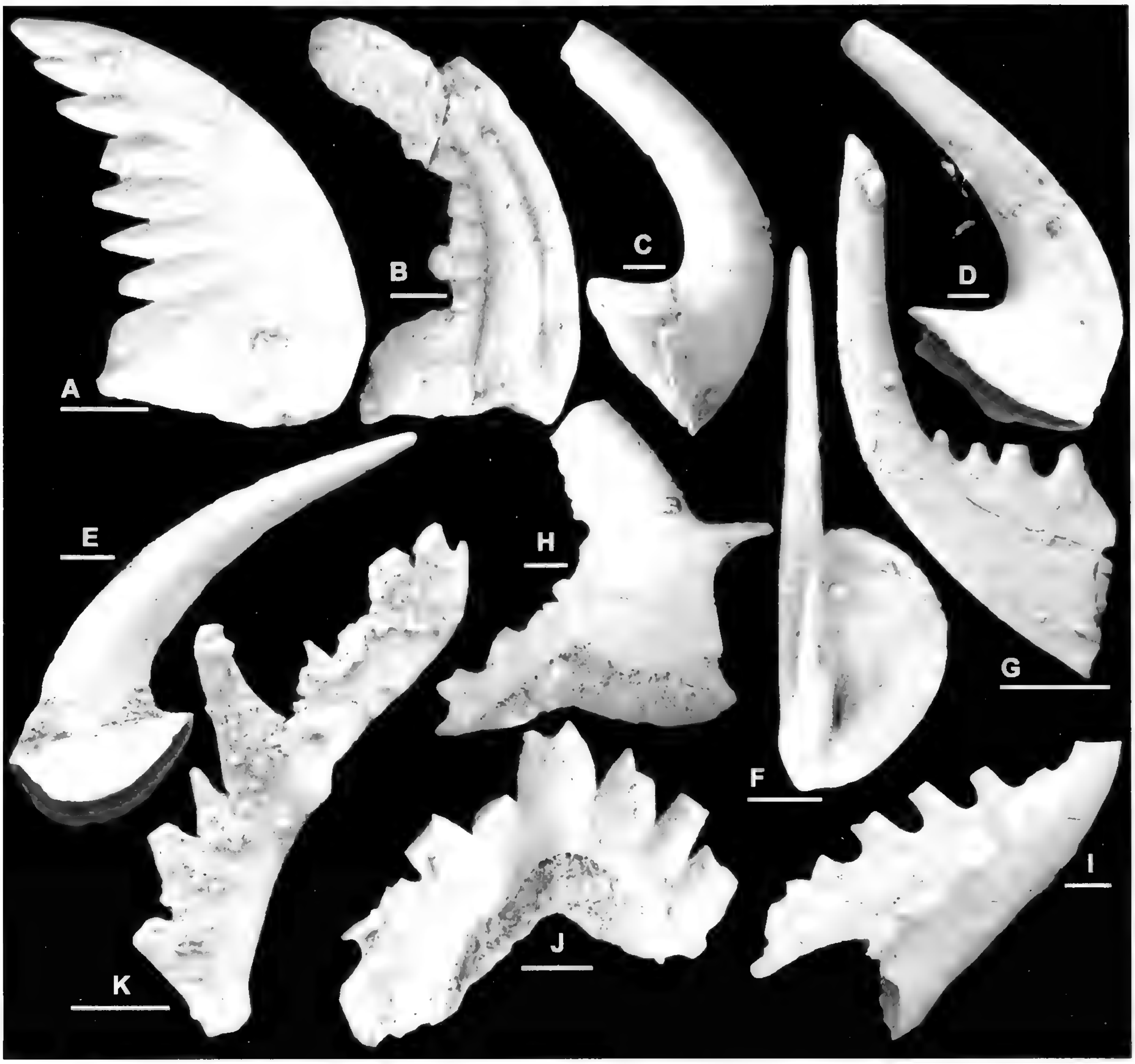

Figure 3. A-B, *Belodina compressa* (Branson and Mehl, 1933). A, compressiform element, AM F.136480, JRC 2, inner-lateral view (IY139-001); B, grandiform element, AM F.136481, JRC 2, outer-lateral view (IY139-003). C-F, *Drepanodus* sp. C, Sb element, AM F.136482, JRC 2, outer-lateral view (IY139-005). D, Sb element, AM F.136483, JRC 2, inner-lateral view (IY139-006). E, F, M element, AM F.136484, JRC 2, E, inner-lateral view (IY139-004); F, basal view (IY139-014). G-I, Gen. et sp. indet., all from YYF4, G, Sc element, AM F.136485, inner-lateral view (IY136-022); H, ?P element, AM F.136486, outer-lateral view (IY136-021); I, Sb element, AM F.136487, outer-lateral view (IY136-019). J-K, *Aphelognathus*? sp. from YYF4, J, Pb element, AM F.136488, inner-lateral view (IY135-025). K, Pa element, AM F.136489, inner-lateral view (IY136-024). Scale bars 100 µm.

Discussion

Chirognathus was established on 23 form species recognized by Branson and Mehl (1933, pp. 28-34, pl. 2) from the Harding Sandstone in Canyon City, Colorado with *Chirognathus duodactylus* as the type species. Later Stauffer (1935) erected 15 form species of *Chirognathus* from the upper Glenwood Beds in the upper Mississippi Valley. Sweet (1982) revised the type species as having a seximembrate or septimembrate apparatus, and concluded that the 29 out of the 42 species recognized by Branson and Mehl (1933), Stauffer (1935), and others since the establishment of the genus could be confidently assigned to the genus, and in fact might belong to a single species apparatus of his revised *C. duodactylus*. He regarded 15 of Branson and Mehl's (1933) and 13 of Stauffer's (1935) form species as junior synonyms of *C. duodactylus*, with the M element represented by form species *C. duodactylus* (= *C. gradatus* Branson and Mehl, 1933, = *C. planus* Branson and Mehl, 1933), Sa by form species *C. multidens* Branson and Mehl, 1933, Sb by form species *C. panneus* Branson and Mehl, 1933 (= *C. isodactylus* Branson and Mehl, 1933), Sc by form species *C. eucharis* Stauffer, 1935, Pa by form species *C. varians* Branson and Mehl, 1933 (= *C. alternatus* Branson and Mehl, 1933), and Pb by form species *C. monodactylus* Branson and Mehl, 1933 (= *C. reversus* Branson and Mehl, 1933). As defined by Sweet (1982, p. 1039), *C. duodactylus* has a ramiform-ramiform species apparatus including a bipennate M element with a short and laterally deflected anterior process and a long posterior process, an alate Sa element with a straight, laterally extended lateral process on each side, a digyrate Sb element varying from subsymmetrical (with two processes subequal in length) to markedly asymmetrical (with one lateral process longer than the other), a bipennate Sc element with a shorter anterior process, a bipennate Pa element resembling the Sc but with the unit inwardly bowed with a more prominently arched basal margin, and a digyrate Pb element with two lateral processes directed in opposite directions distally.

Chirognathus cliefdenensis Zhen and Webby, 1995, from the Cliefden Caves Limestone Subgroup of central New South Wales, differs from *C. duodactylus* in having distinctive blade-like P elements with high processes bearing closely spaced, basally confluent denticles (Zhen and Webby 1995, pl. 2, figs 13-16).

Chirognathus tricostatus sp. nov.
Figs 4-5

Synonymy

Chirognathus monodactyla Branson and Mehl; Burrett, 1979, pp. 31-32.

Tasmanognathus careyi Burrett, 1979, p. 33-35, *partim*, only pl. 1, fig. 12.

Derivation of name

Latin *tri-* (three) and *costatus* (ribbed) referring to the distinctive character, the tricostate cusp of the Sb, Sc and Sd elements, of this Tasmanian species.

Material

71 specimens from eight samples (see Table 1). Holotype: AMF.136496, YYF5, Sd element (Fig. 5A-C); paratypes: AM F.136490, C137c, Sa element (Fig. 4A-C); AM F.136491, JRC 2, Sa element (Fig. 4D); AM F.136492, YYF5, Sb element (Fig. 4E); AM F.136493, C137c, Sb element (Fig. 4F); AM F.136494 (=UTG96872: Burrett 1979, pl. 1, fig. 12; originally designated as one of the syntypes of *T. careyi*), Sb element (Fig. 4G-H); AM F.136495, YYF5, Sc element (Fig. 4I-J); AM F.136497, C137c, Sd element (Fig. 5D-E); AM F.136498, C137c, Sd element (Fig. 5F-G); AM F.136499, JRC 2, Pa? element (Fig. 5H); AM F.136500 (=UTG96866), JRC 2, Pa element (Fig. 5I); AM F.136501, JRC 2, Pa element (Fig. 5J-K); AM F.136502, YYF1, Pb element (Fig. 5L-N); AM F.136503, YYF4, Pb element (Fig. 5O).

Diagnosis

A species of *Chirognathus* with a seximembrate (possibly septimembrate) ramiform-ramiform apparatus including alate Sa, modified digyrate Sb and Sd, modified bipennate Sc, bipennate Pa and digyrate Pb elements; all elements with long, peg-like denticles, and a shallow, open basal cavity, typically preserved without attachment of a basal funnel.

Description

Sa element symmetrical or nearly symmetrical, with a prominent cusp and a denticulate lateral process on each side (Fig. 4A-D); cusp large, straight, antero-posteriorly compressed, with broadly convex anterior and posterior faces and sharply costate lateral margins; lateral processes extending laterally and bearing three or more denticles of variable sizes, which are also antero-posteriorly compressed; basal cavity flared anteriorly and posteriorly with basal margin nearly straight or slightly arched in posterior or anterior view (Fig. 4A, D).

Sb element (Fig. 4E-H) like Sa, but asymmetrical with outer lateral process slightly curved posteriorly and with a short, but prominent costa developed on the basal part of the anterior face (Fig. 4E, H); outer lateral process slightly curved posteriorly and also with basal margin twisted posteriorly and upper margin anteriorly (Fig. 4G); basal cavity shallow, flared anteriorly and posteriorly and extending distally as a narrow and shallow groove underneath each process (Fig. 4F).

Sc element modified bipennate, strongly asymmetrical with denticulate anterior and posterior processes and a strong costa on the outer lateral face (Fig. 4I-J); both processes extending straight or slightly curved inward; anterior process bearing three or more denticles with the distal denticle (away from the cusp) larger than the other denticles; posterior process bearing two or more denticles with the distal one (away from the cusp) larger than the other denticle; larger denticle on the posterior or anterior

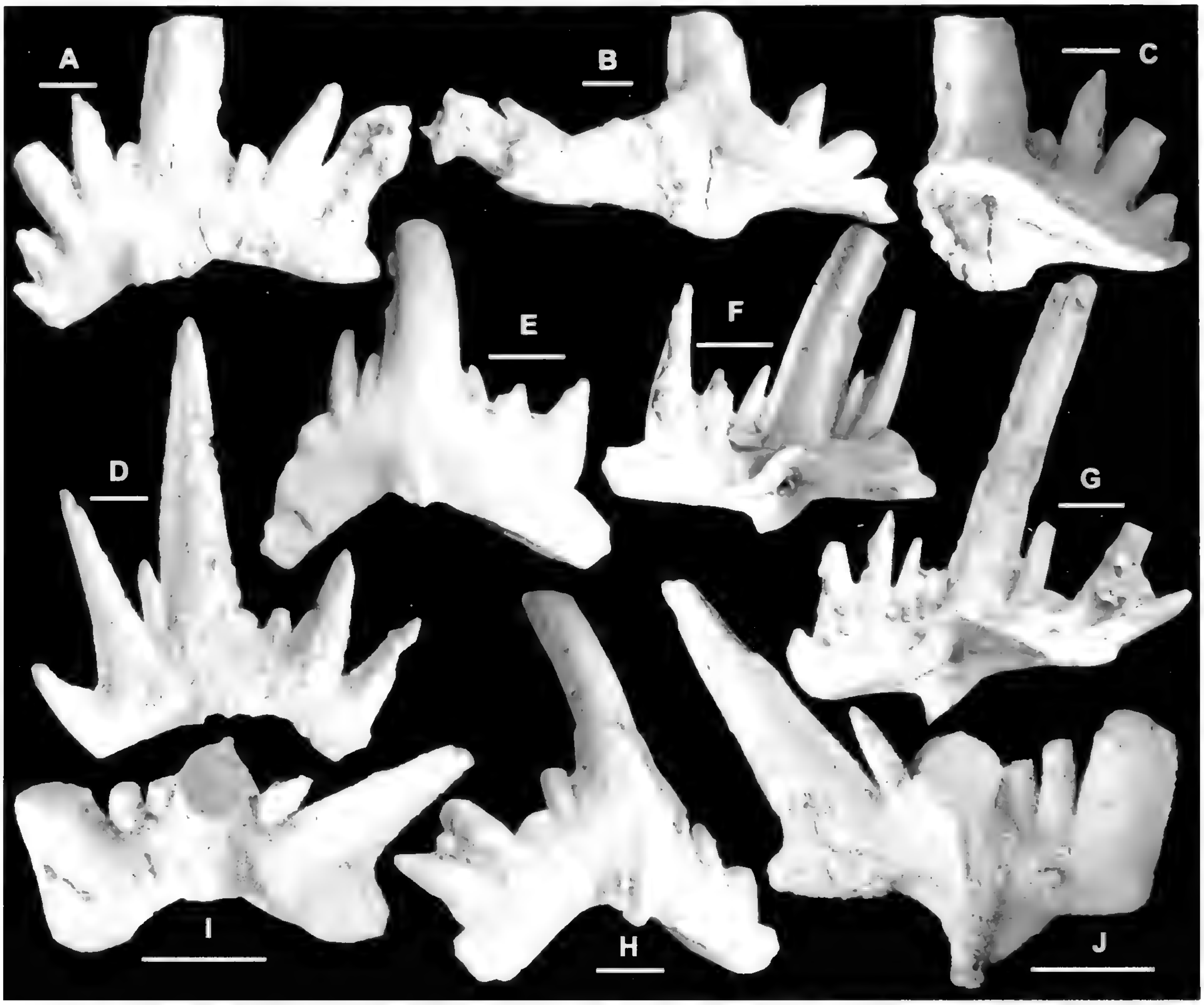

Figure 4. ***Chirognathus tricostatus*** **sp. nov. A-D, Sa element; A-C, AM F.136490, paratype, C137c, A, anterior view (IY138-020), B, basal view (IY138-021), C, posterior view (IY142-023); D, AM F.136491, paratype, JRC 2, anterior view (IY142-002). E-H, Sb element; E, AM F.136492, paratype, YYF5, anterior view (IY135-039); F, AM F.136493, paratype, C137c, posterior view (IY138-022); G-H, AM F.136494=UTG96872 (Burrett 1979, pl. 1, fig. 12; originally designated as one of the syntypes of T. careyi), paratype, JRC 2, G, posterior view (IY141-018), H, anterior view (IY141-019). I-J, Sc element, AM F.136495, paratype, YYF5, I, upper-inner lateral view (IY135-035), J, upper-outer lateral view (IY135-036). Scale bars 100 µm.**

process being as wide as the cusp in the lateral view, but more strongly compressed laterally than the cusp; outer lateral costa prominent, forming a ridge-like process near the base (Fig. 4J).

Sd element modified digyrate, strongly asymmetrical with a robust cusp, a denticulate lateral process on each side and a blade-like costa on the anterior face (Fig. 5A-G); cusp tricostate with a sharp costa along the lateral margins and on the broadly convex anterior face, and a less convex posterior face; anterior costa more strongly developed than that in the Sb element, and extending to near the tip of the cusp, and basally often developed into a short, blade-like process (Fig. 5C-D, G); lateral processes distally curved posteriorly bearing three or more denticles of variable sizes; basal cavity more open and strongly flared posteriorly than that of the Sb element, forming a strongly arched basal margin in posterior view (Fig. 5F).

Pa element bipennate with a prominent cusp and denticulate anterior and posterior processes (Fig. 5H-K); cusp suberect, laterally compressed with sharply costate anterior and posterior margins and broadly convex lateral faces (Fig. 5H-J); both anterior and posterior processes bearing three or more denticles of variable sizes, which are also laterally compressed;

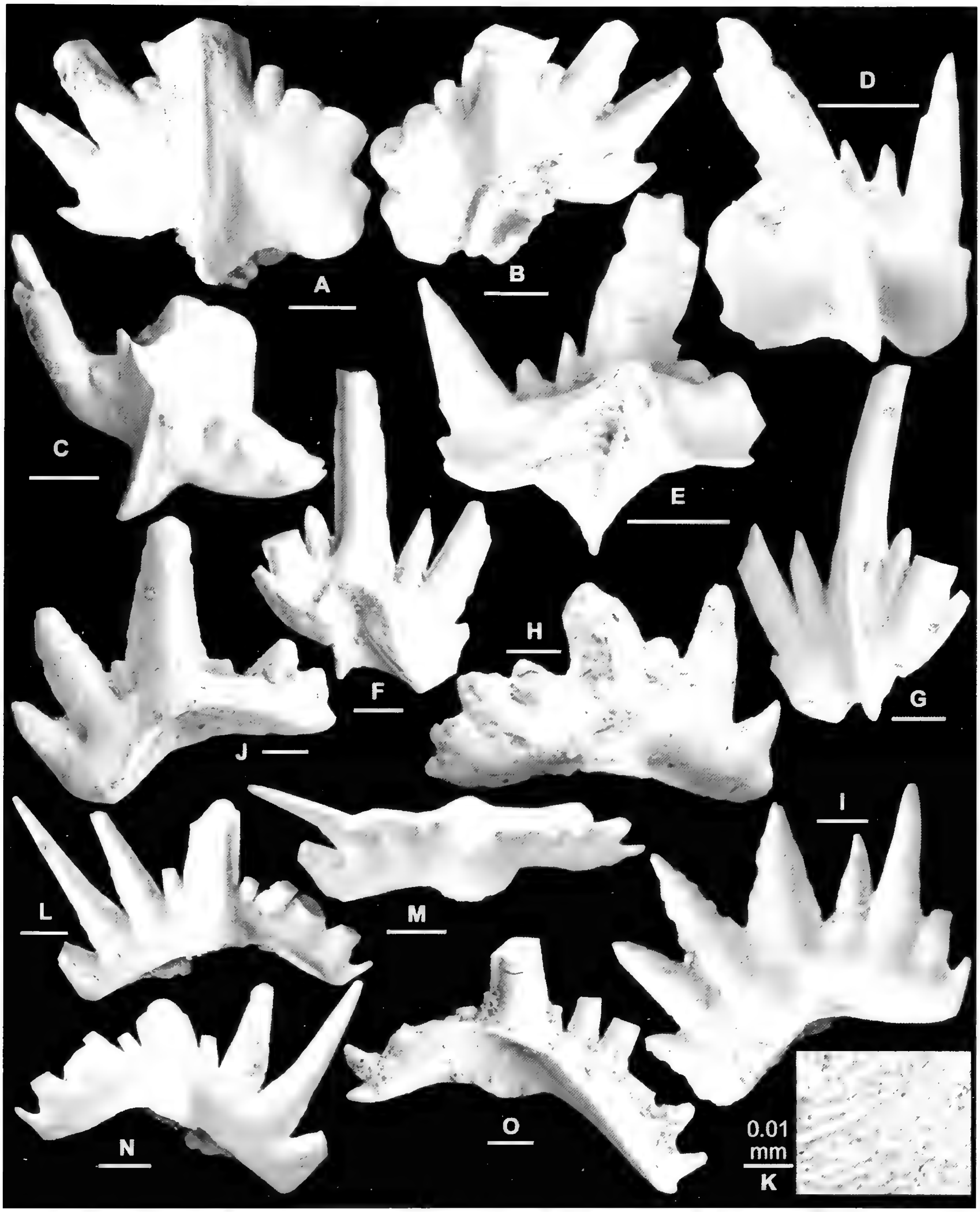

Figure 5. ***Chirognathus tricostatus*** **sp. nov. A-G, Sd element; A-C, AM F.136496, Holotype, YYF5, A, anterior view (IY135-034), B, posterior view (IY142-028), C, upper view (IY135-033); D-E, AM F.136497, paratype, C137c, D, anterior view (IY142-025), E, posterior view (IY138-027); F-G, AM F.136498, paratype, C137c, F, posterior view (IY138-024), G, anterior view (IY142-026). H, Pa? element; AM F.136499, paratype, JRC 2, outer lateral view (IY142-018); I-K, Pa element, I, AM F.136500 =UTG96866, paratype, JRC 2, outer lateral view (IY141-026); J-K, AM F.136501, paratype, JRC 2, J, inner lateral view (IY142-020), K, basal view, close up showing the zone of recessive basal margin (IY142-022). L-O, Pb element; L-N, AM F.136502, paratype, YYF1, L, posterior view (IY136-30), M, upper view (IY136029), N, anterior view (IY142-029); O, AM F.136503, paratype, YYF4, basal-posterior view (IY135-026). Scale bars 100 μm.**

Fig. 6. A-I, *Panderodus gracilis* (Branson and Mehl, 1933). A, falciform, AM F.136504, JRC 2, outer-lateral view (IY139-033). B-C, truncatiform element, AM F.136505, JRC 2, B, posterior view (IY139-026); C, inner-lateral view (IY139-024). D-G, graciliform element; D-F, AM F.136506, JRC 2, D, inner-lateral view (IY139-017); E, outer-basal view of the basal part (IY139-022); F, outer-lateral view (IY139-020); G, AM F.136507, JRC 2, outer-lateral view (IY139-023). H-I, falciform element; H, AM F.136508, JRC 2, inner-lateral view (IY139-035); I, AM F.136509, YYF2, outer-lateral view (IY140-25). J-N, Protopanderodus? nogamii (Lee, 1975). J, Sb element, AM F.136510, YYF4, outer-lateral view (IY136-027). K-N, Pa element; K-L, AM F.136511, YYF4, K, outer-lateral view (IY136-025), L, outer lateral view, closer up showing the furrow weaken and disappeared before researching basal margin (IY136-026). M-N, AM F.136512, YYF3, M, outer-lateral view (IY140-021), N, basal view (IY140-019). Scale bars 100 µm unless otherwise indicated.

anterior process typically slightly curved inward and extending downward forming a gently arched basal margin in lateral view (Fig. 5I-J); basal cavity shallow and open, often with zone of recessive basal margin preserved (Fig. 5K).

Pb element digyrate with a prominent cusp and denticulate lateral process on each side (Fig. 5L-O); cusp curved posteriorly with costate lateral margins; lateral processes bearing four or more denticles of variable sizes; basal cavity shallow and open with gently arched basal margins in anterior or posterior view (Fig. 5L, N-O).

Discussion

Chirognathus tricostatus sp. nov. was initially reported by Burrett (1979) as *Chirognathus monodactyla*, one of the 23 form species recognized by Branson and Mehl (1933). One of the syntypes of *Tasmanognathus careyi* (AM F.136494 =UTG 96872) is re-assigned herein to *C. tricostatus* to represent the Sb position (Fig. 4G; also see Burrett 1979, pl. 1, fig. 12). *C. tricostatus* from Tasmania differs from two currently known multi-element species of *Chirognathus*, *C. duodactylus* from the Upper Ordovician (Sandbian) of North American Mid-continent faunas and *C. cliefdenensis* from the Upper Ordovician (Katian) of central New South Wales, in having distinctive tricostate Sb, Sc and Sd elements.

Sweet (1982, 1988) recognized the M element for the type species, *C. duodactylus*. A comparable element has also recognized in the Tasmanian material of *C. tricostatus*, but has been assigned to the Sd position to form a symmetry transitional series with other S elements. One of the illustrated specimens of the Pa element (Fig. 5H) shows a nearly straight basal margin and posteriorly curved cusp, and may possibly represent the M element of this species. However, as only one specimen is available in the current material, it is tentatively assigned to the Pa element.

Genus PHRAGMODUS Branson and Mehl, 1933

Type species

Phragmodus primus Branson and Mehl, 1933.

Phragmodus undatus Branson and Mehl, 1933
Figs 7-8

Synonymy

Phragmodus undatus Branson and Mehl, 1933, p. 115-116, pl. 8, figs 22-26; Zhen and Webby, 1995, p. 284, pl. 4, fig. 5; Leslie and Bergström, 1995, p. 970-973, fig. 4.1-4.14 (*cum syn.*); Zhen et al., 1999, p. 90, fig. 9.1-9.5 (*cum syn.*); Zhen et al., 2003a, fig. 6N, O; Pyle and Barnes, 2002, figs 14.11-14.12, 15.31-15.32; Percival et al., 2006, fig. 4A-E.

Material

116 specimens from six samples (see Table 1).

Description

M element makellate, geniculate coniform with a robust cusp and a short base triangular in outline (Fig. 7A-B); cusp strongly antero-posteriorly compressed forming sharp lateral edges and broad anterior and posterior faces; inner-lateral corner triangular in outline, and outer-lateral proto-process short with a gently arched upper margin; basal cavity shallow with weakly wavy basal margins.

S elements ramiform bearing a long multi-denticulate posterior process with one or two enlarged denticles, but none of the Tasmanian specimens have the posterior process completely preserved. Sa element symmetrical or nearly symmetrical with a prominent costa on each side (Fig. 7C-D); posterior process long with one denticle (typically the third or fourth from the cusp) about twice as wide as the adjacent denticles, and larger and longer than the cusp; in some specimens a costa also developed on each side of the larger denticle (Fig. 7D); basal cavity shallow with strongly arched basal margins; anterior (or antero-inner lateral) costa typically only weakly developed (Fig. 7D). Sb element modified quadriramate, like Sa but asymmetrical with the sharp costate anterior margin curved inward (Fig. 7F-G). Sc element modified bipennate, like Sb but strongly asymmetrical with a sharply costate anterior margin curved inward and with smooth inner and outer lateral faces (Fig. 7H-L). Sd element tertiopedate, like Sb, but with a broad anterior face and with one of the larger denticles on the posterior process curved inward and the other outward (Fig. 8A-C).

Pa element pastinate with long denticulate posterior and inner lateral processes, and a suberect cusp (Fig. 8D-G); cusp laterally compressed with sharply costate anterior and posterior margins, outer lateral face more convex; posterior process long, bearing six or more denticles; inner lateral process shorter, bearing five or more denticles and strongly bending anteriorly forming an angle of nearly 180 degree with the posterior process (Fig. 8E, G); costate anterior margin extending downward and not forming a prominent anterior process (Fig. 8D); basal cavity shallow, forming a wide and open groove along the posterior and inner lateral processes, and flared anteriorly and inner laterally (Fig. 8G). Pb element pastinate, like Pa but with a more robust cusp and less anteriorly curved inner lateral process (Fig. 8H-I).

Discussion

Leslie and Bergström (1995) suggested a seximembrate apparatus for *P. undatus*, including adenticulate makellate M, alate Sa, tertiopedate Sb, bipennate Sc, pastinate Pa and Pb elements. All six elements have been recovered from the Tasmanian samples (Figs 7-8); they are identical with those described and illustrated by Leslie and Bergström (1995, fig. 4) from the Joachim Dolomite and Kings Lake Limestone of Missouri, except that an additional tertiopedate element was recognized in the Tasmanian material (Fig. 8A-C). This latter element is similar to the Sb element, but has the cusp and the larger denticles on the posterior process strongly twisted towards different sides in respect to the antero-posterior axis. It is assigned herein to represent the Sd position.

Fig. 7. *Phragmodus undatus* Branson and Mehl, 1933. A-B, M element; A, AM F.136513, YYF4, posterior view (IY136-005); B, AM F.136514, YYF4, anterior view (IY136-006). C-D, Sa element, AM F.136515, C137c, C, basal view (IY138-014); D, lateral view (IY138-015). E-G, Sb element; E, AM F.136516, YYF4, outer-lateral view (IY136-015); F, AM F.136517, YYF4, inner-lateral view (IY136-014), G, AM F.136518, YYF4, inner-lateral view (IY136-016). H-L, Sc element; H, AM F.136519, YYF4, inner-lateral view (IY136-013); I-J, AM F.136520, YYF4, I, outer-lateral view (IY136-009), J, inner-lateral view (IY136-010); K-L, AM F.136521, C137c, K, basal view (IY138-016), L, outer-lateral view (IY138-017). Scale bars 100 μm.

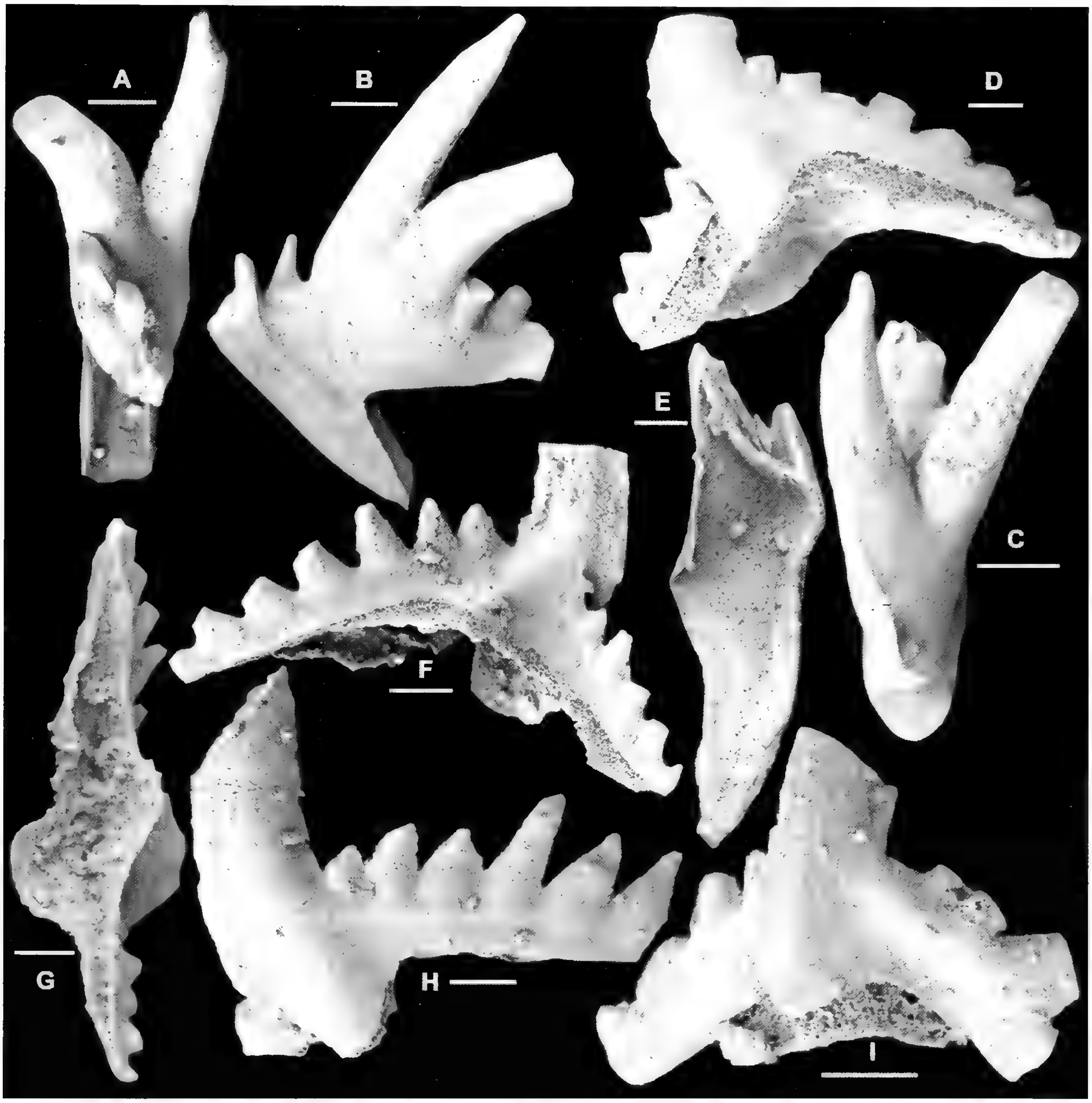

Fig. 8. *Phragmodus undatus* Branson and Mehl, 1933. A-C, Sd element; AM F.136522, JRC 2, A, upper view (IY138-028), B, outer-lateral view (IY138-029), C, posterior view (IY138-030). D-G, Pa element; D-E, AM F.136523, YYF4, D, outer-lateral view (IY136-001), E, basal view (IY136-011); F-G, AM F.136524, YYF4, F, inner-lateral view (IY136-003), G, basal view (IY136-012). H-I, Pb element; H, AM F.136525, YYF4, outer-lateral view (IY136-004); I, AM F.136526, YYF4, antero-outer lateral view (IY136-017). Scale bars 100 μm.

Genus PROTOPANDERODUS Lindström, 1971

Type species

Acontiodus rectus Lindström, 1955.

Protopanderodus? *nogamii* (Lee, 1975)
Fig. 6J-N

Synonymy

Scolopodus nogamii Lee 1975, p. 179, pl. 2, fig. 13.

?*Panderodus nogamii* (Lee); Cantrill and Burrett 2004, p. 410, pl. 1, figs 1-16.

Panderodus nogamii (Lee); Zhang et al. 2004, p. 16, pl. 5, figs 1-5.

Protopanderodus nogamii (Lee); Watson 1988: p. 124, pl. 3, figs 1, 6; Zhen et al. 2003b, p. 207-

209, fig. 23A-P, ?Q (*cum syn.*); Zhen and Percival 2004a, p. 104-105, fig. 18A-K (*cum syn.*).
Protopanderodus? *nogamii* (Lee); Zhen and Percival 2004b, p. 170-172, fig. 11P, Q (*cum syn.*).

Material

69 specimens from four samples (see Table 1).

Discussion

Recent review of this species by Cantrill and Burrett (2004) suggested a geographical distribution restricted to Gondwana and peri-Gondwanan terranes. Morphologically *P. nogamii* is rather conservative over its long stratigraphic range from the upper Floian (*evae* Zone, Zhen et al. 2003b) to upper Sandbian (*undatus* Zone, this study). Generic assignment of this species has been debated in the literature (see synonymy list). Most elements of this species bear a non-panderodontid furrow on each side, suggesting that it might be more closely related to *Protopanderodus* rather than to typical *Panderodus*.

Genus TASMANOGNATHUS Burrett, 1979

Type species

Tasmanognathus careyi Burrett, 1979.

Diagnosis

Septimembrate apparatus with a ramiform-pectiniform apparatus structure including makellate M, ramiform S (including alate Sa with a denticulate lateral process on each side, digyrate Sb, bipennate or modified bipennate Sc, and tertiopedate Sd), carminate Pa, and angulate Pb (some species with an additional modified angulate or pastinate Pb2) elements.

Discussion

Following Burrett's (1979, p. 32) original view that *Tasmanognathus* might be closely related to *Rhipidognathus*, Aldridge and Smith (1993) doubtfully included it in the Rhipidognathidae. Affinities with other genera remain conjectural, although greatest similarities appear to be with *Yaoxianognathus* (see discussion below).

Tasmanognathus was established on a single species, *T. careyi* Burrett, 1979 from the Lower Member of the Benjamin Limestone in the Florentine Valley and Everlasting Hills of central Tasmania. Subsequently, *Tasmanognathus* has been reported from the mid Darriwilian to upper Katian of eastern Australia, North China (An et al. 1985, An and Zheng 1990, Pei and Cai 1987), Qinling Mountains in the Kunlun-Qinling Region (Pei and Cai 1987), Tarim Basin (Zhao et al. 2000; Jing et al. 2007), South Korea (Lee 1982; An and Zheng 1990), ?Siberia and northeastern Russia (Domoulin et al. 2002), and possibly North America (where it was referred to as *Yaoxianognathus abruptus*). It is represented by nine named species and several additional unnamed forms, the latter included herein in *Tasmanognathus* although some are poorly known or inadequately documented. Following is a brief review of the known species (with our interpretation of element notations in parentheses):

Tasmanognathus careyi Burrett, 1979 from the Lower Limestone Member of the Benjamin Limestone in the Florentine Valley and Everlasting Hills of central Tasmania; a seximembrate apparatus was originally recognized, but based on re-examination of original topotypes and additional new material, it has been revised herein as having an septimembrate apparatus (including M, Sa, Sb, Sc, Sd, Pa, and Pb elements).

Badoudus badouensis Zhang in An et al., 1983 from the Fengfeng Formation (Sandbian) of Handan, Hebei Province in North China (considered by An et al. 1985, p. 102, to represent a species of *Tasmanognathus*); this is a poorly defined form species with only two specimens illustrated (An et al. 1983, pl. 25, figs 5, 6, text-fig. 12.17), both of which are carminate, bearing an indistinctive cusp and a long denticulate anterior process and a short denticulate posterior process. This element is comparable with the Pa element of *Tasmanognathus* defined herein.

Tasmanognathus borealis An in An et al., 1985 from the upper part of the Yaoxian Formation (late Sandbian) of Yaozhou District (formerly Yaoxian) of Tongchuan City, Shaanxi Province in North China; originally defined as having a quinquimembrate apparatus, including trichonodelliform (= Sa element; see An et al. 1985, pl. 1, fig. 20), zygognathiform (= Sb element; see An et al. 1985, pl. 1, fig. 13), cordylodiform (= Sc element; see An et al. 1985, pl. 1, fig. 15), ozarkodiniform (= Pa element; see An et al. 1985, pl. 1, fig. 14), and prioniodiniform (= Pb element; see An et al. 1985, pl. 1, fig. 16).

Tasmanognathus gracilis An in An et al., 1985 from the upper part of the Yaoxian Formation (late Sandbian) of Yaozhou District (formerly Yaoxian) of Tongchuan City, Shaanxi Province in North China; originally defined as having a seximembrate apparatus, including cyrtoniodiform (= M element; see An et al. 1985, pl. 1, fig. 8), trichonodelliform (= Sa element; see An et al. 1985, pl. 1, fig. 12), ligonodiniform (= Sb element; see An et al. 1985, pl. 1, fig. 11), cordylodiform (= Sc element; see An et al. 1985, pl. 1, fig. 10), ozarkodiniform (= Pa element;

see An et al. 1985, pl. 1, fig. 7), and prioniodiniform (= Pb element; see An et al. 1985, pl. 1, fig. 9).

Tasmanognathus multidentatus An in An and Zheng, 1990 (p. 20, 95, text-fig. 9, pl. 11, fig. 4); the only figured specimen (pl. 11, fig. 4) is a Pa element from the Yaoxian Formation of Yaozhou District (formerly Yaoxian) of Tongchuan City, Shaanxi Province in North China, which is identical with the Pa element of *T. borealis* An in An et al., 1985. In fact, the figured Pa element (pl. 11, fig. 4) of *T. multidentatus* and the holotype and a figured paratype of *T. borealis* (An et al. 1985, pl. 1, figs 13, 16) were recovered from the same sample (Tp13y2). It is unclear why An and Zheng (1990) tried to replace *T. borealis* with *T. multidentatus*. However, as the latter is a *nomem nudum*, *T. borealis* remains the valid name for this Yaoxian species.

Tasmanognathus planatus Pei in Pei and Cai, 1987 from the Sigang Formation of Xichuan and Neixiang Counties, Henan Province in the Qinling Mountains (Pei and Cai 1987; Chen et al. 1995; Wang et al. 1996); the type material was represented by Pa (Pei and Cai 1987, pl. 13, fig. 12), Pb (Pei and Cai 1987, pl. 13, figs 8, ?13), and Sb (Pei and Cai 1987, pl. 13, fig. 9) elements.

Tasmanognathus shichuanheensis An in An et al., 1985 from the lower part of the Yaoxian Formation (mid Sandbian) of Yaozhou District (formerly Yaoxian) of Tongchuan City, Shaanxi Province in North China; originally defined as having a seximembrate apparatus, including cyrtoniodiform (= M element; see An et al. 1985, pl. 1, fig. 3), trichonodelliform (= Sa element; see An et al. 1985, pl. 1, fig. 4), ligonodiniform (= Sb element; see An et al. 1985, pl. 1, fig. 1), cordylodiform (= Sc element; see An et al. 1985, pl. 1, fig. 5), ozarkodiniform (= Pa element; see An et al. 1985, pl. 1, fig. 2), and prioniodiniform (= Pb element; see An et al. 1985, pl. 1, fig. 6).

Tasmanognathus sigangensis Pei in Pei and Cai, 1987 from the Shiyanhe Formation (late Sandbian-early Katian) of Neixiang County, Henan Province in the Qinling Mountains; a quinquimembrate species apparatus was recognized including trichnodelliform (= Sa element; Pei and Cai 1987, pl. 13, fig. 4), zygognathiform (= Sb element, Pei and Cai 1987, pl. 13, fig. 11), cordylodontiform (= Sc element; Pei and Cai 1987, pl. 13, fig. 7), prioniodiniform (= Pa element; Pei and Cai 1987, pl. 13, figs 1-2), and ozarkodontiform (= ?Pb element; Pei and Cai 1987, pl. 13, fig. 3).

Tasmanognathus sishuiensis Zhang in An et al., 1983 reported from the upper Fengfeng Formation (early Sandbian) of Shandong and Hebei provinces in North China; defined as consisting of a quinquimembrate apparatus including trichonodelliform (= Sa element, see An et al. 1983, pl. 29, figs 7, 9, 10), zygognathiform (= Sb element, see An et al. 1983, pl. 29, figs 4-6, 8, ?11), cordylodontiform (= Sc element, see An et al. 1983, pl. 29, figs 1-3), ozarkodiniform (= Pa element, see An et al. 1983, pl. 29, figs 14-15), and prioniodiniform (= Pb element, see An et al. 1983, pl. 29, figs 12-13) elements. This species is characterized by its widely spaced peg-like denticles on the S elements.

Tasmanognathus sp. described by Pei and Cai (1987) from the Sigang and Shiyanhe formations of Neixiang County, Henan Province in the Qinling Mountains; represented by cordylodontiform (= Sc element; Pei and Cai 1987, pl. 13, figs 5-6) and prioniodiniform (= ?Pb element; Pei and Cai 1987, pl. 13, fig. 10) elements.

Tasmanognathus sp. from the Fossil Hill Limestone (early Katian) of the Cliefden Caves Limestone Subgroup, central New South Wales was only represented by the Pa element (Zhen and Webby 1995, p. 289, pl. 5, fig. 23), which showed close resemblance to the Pa element of *T. borealis* from the Yaoxian Formation.

Tasmanognathus sp. cf. *T. borealis* An in An et al., 1985; only the Pa element known from unnamed limestone of Late Ordovician (late Sandbian) age intersected in drillcore in the Marsden district of south-central New South Wales (Percival et al. 2006).

The three species of *Tasmanognathus* (*T. borealis, T. gracilis* and *T. shichuanheensis*) erected by An in An et al. (1985) from the Yaoxian Formation (Darriwilian-Sandbian) of Yaozhou District (formerly Yaoxian) of Tongchuan City, Shaanxi Province in North China exhibit similar species apparatus and closely related morphological variations of constituent elements. An et al. (1985) established two conodont zones in the Yaoxian Formation, namely the *T. shichuanheensis* Zone in the lower part of the formation (Bed 1 to Bed 3, see An et al. 1985, fig. 2), and the *Tasmanognathus borealis-T. gracilis* Zone spanning the upper part of the Yaoxian Formation (Bed 4 to Bed 8) into the basal part of the overlying Taoqupo Formation (Bed 9). An and Zheng (1990, p. 95, text-fig. 9) suggested that *T. sishuiensis* from the Fengfeng Formation might be the direct ancestor of the species from the Yaoxian Formation, and indicated an inferred lineage from *T. sishuiensis* to *T. shichuanheensis* and then to *T. multidentatus* (= *T. borealis*). They showed the morphological changes of the three species, mainly from widely spaced denticles on the processes of the S and Pb elements and a prominent cusp on the Pa element of *T. sishuiensis*, to closely spaced denticles in the S and Pb elements and an indistinctive cusp in the Pa element of *T. multidentatus* (= *T. borealis*). However, these species from the Yaoxian Formation and Fengfeng Formation show some detailed differences in composition of the apparatus in comparison with *T. careyi* from Tasmania. In particular, they seem to lack makellate M and tertiopedate Sd elements, and have a "dolabrate" Sc element with a long denticulate posterior process. Morphologically, such features support a closer relationship with *Yaoxianognathus yaoxianensis* An in An et al., 1985. However, these species lack hindeodellid denticles on the processes of the S elements, which was the major character that An (in An et al. 1985) employed to distinguish *Yaoxianognathus* from *Tasmanognathus*. As revision of An's species of *Tasmanognathus* from the Yaoxian Formation and the Fengfeng Formation of North China is beyond the scope of the current study, they are retained in *Tasmanognathus* for the time being, although they show some significant differences in morphology and apparatus composition in comparison with the type species of *Tasmanognathus* as revised here.

Based on the concept of *Yaoxianognathus* employed by An (in An et al. 1985) and others (e.g. Savage 1990; Zhen et al. 1999), generic assignment of species previously included in *Yaoxianognathus* but which apparently lack hindeodellid denticles on the processes of the S elements, should be reconsidered. For example, *Yaoxianognathus abruptus* (Branson and Mehl, 1933), a North American Midcontinent species ranging across the *undatus* to *tenuis* zones of the Mohawkian, was initially proposed as a form species based only on a carminate Pa element (Branson and Mehl, 1933, pl. 6, fig. 11) and revised by Leslie (2000, p. 1143) as having a seximembrate apparatus. It closely resembles An's species of *Tasmanognathus* from North China; most importantly, none of Leslie's illustrated S elements of *Y. abruptus* (fig. 4.15-4.18) bears hindeodellid denticles that are characteristic of *Yaoxianognathus*, and hence we suggest this species more likely belongs to *Tasmanognathus*.

Similarly, S elements of *Yaoxianognathus? neonychodonta* Zhang, Barnes and Cooper, 2004, from the Stokes Siltstone of the Amadeus Basin in central Australia, lack hindeodellid denticles and therefore should be excluded from *Yaoxianognathus*. As Zhang et al. (2004) implied, this species may be more closely related to *Plectodina*, judging from the morphological characters of its ramiform S and pastinate Pb elements.

In comparison, the two multielement species of *Yaoxianognathus* from the Upper Ordovician of central New South Wales (*Y. wrighti* Savage, 1990 and *Y. ani* Zhen, Webby and Barnes, 1999) do exhibit well developed hindeodellid denticles on the processes of the S elements, particularly on the long posterior process of the Sc element (Savage 1990, fig. 6.7-6.12; Zhen et al. 1999, fig. 15.3-15.6, 15.9-15.12, 15.16). The apparatuses of both species include a makellate M and a modified bipennate Sc elements, which differ morphologically from corresponding elements in the *T. careyi* apparatus as defined herein.

Tasmanognathus careyi Burrett, 1979
Figures 9-15

Synonymy

Tasmanognathus careyi Burrett, 1979, p. 33-35, *partim* only text-figs 2-4, pl. 1, figs 1-7, 11, 13-19 (text-fig. 2 = Pb2 , text-fig. 3 = Pa, text-fig.4A = Sb, text-fig. 4B = Sc, text-fig. 4C, D = Sd; pl. 1, figs 1-3 = Pb2, 4-5 = Pb1, 6-7 = Pa, fig. 11 = Sc, figs 13-14= Sb, figs 15-18 = Sd, fig. 19 = Sa); *non* fig. 12 = *C. tricostatus* sp. nov., *non* figs 8-10, 20 = *T.* sp. cf. *careyi*.

? *Tasmanognathus careyi* Burrett; An and Zheng, 1990, pl. 11, fig. 2.

Material

297 specimens from nine samples (see Table 1).

Burrett (1979, p. 33, pl. 1, figs 1-7, 11-12, 17-18, 20) designated 11 figured specimens from sample JRC 2 as syntypes, ten of which (excluding UTG 96863 which was not able to be located for this study; figured by Burrett 1979, pl. 1, figs 17-18), and 225 additional specimens (including originally undesignated topotypes) from five samples (LLMB, C137, C98, JRC 2 and JRB, see Table 1) are available for the current study. AM F.136547 (=UTG 96851; Burrett 1979, pl. 1, fig. 6) representing a Pa element is selected herein as lectotype (Fig. 14A-B); and seven out of ten originally designated and illustrated syntypes were examined and illustrated herein as paralectotypes, including AM F.136557 (=UTG 96857, Fig. 15H; Burrett 1979, pl. 1, fig. 1), AM F.136559 (=UTG 96860, Fig. 15K; Burrett 1979, pl. 1, fig. 2), AM F.136560 (=UTG 96853, Fig. 15L; Burrett 1979, pl. 1, fig. 3), AM F.136553 (=UTG 96850, Fig. 15A-B; Burrett 1979, pl. 1, fig. 4), AM F.136554 (=UTG 96882, Fig. 15C; Burrett 1979, pl. 1, fig. 5), AM F.136548 (=UTG 96856, Fig. 14C; Burrett 1979, pl. 1, fig. 7), and AM F.136539 (=UTG 96876, Fig. 12A-C; Burrett 1979, pl. 1, fig. 11).

Figure 9. ***Tasmanognathus careyi*** **Burrett, 1979. M element; A, AM F.136527 =UTG96875, JRC 2, anterior view (IY141-025). B, AM F.136528, C137c, anterior view (IY138-011). C-D, AM F.136529, C137c, C, posterior view (IY138-008); D, basal view (IY138-009). E-F, AM F.136530, JRC 2, E, posterior view (IY138-035); F, basal view (IY138-034). G-J, AM F.136531, JRC 2, G, upper view (IY139-007); H, posterior view (IY139-008); I, inner-lateral view (IY139-009); J, anterior view (IY139-010). Scale bars 100 µm.**

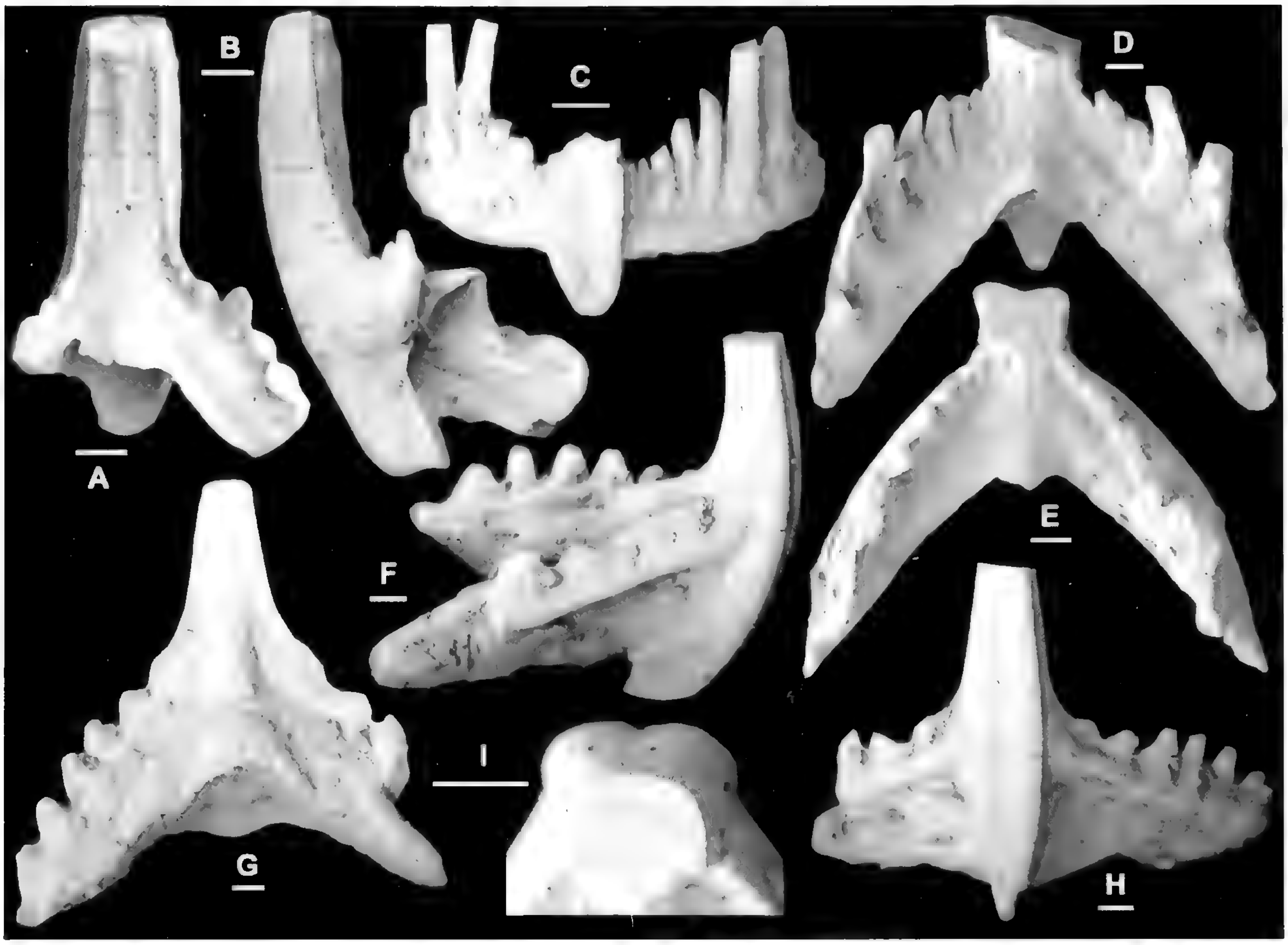

Figure 10. ***Tasmanognathus careyi*** **Burrett, 1979. Sa element; A-B, AM F.136532 =UTG96874 (Burrett 1979, pl. 1, fig. 19), JRC 2, A, posterior view (IY141-022), B, lateral view (IY141-021); C-E, AM F.136533, YYF5, C, anterior view (IY140-004), D, posterior view (IY140-003), E, upper-posterior view (IY140-001); F-I, AM F.136534, YYF4, F, lateral view (IY135-019), G, posterior view (IY135-020), H, anterior view (IY135-018), I, upper view, close up showing the cross section of the cusp (IY135-022). Scale bars 100 μm.**

UTG 96877, previously designated as a syntype (Burrett 1979, pl. 1, fig. 20) is excluded from this species and re-assigned to *T.* sp. cf. *careyi* representing the Sb position (AM F.136567, Fig. 16G herein). Another previously designated syntype UTG 96872 (Burrett 1979, pl. 1, fig. 12) is also excluded from this species and re-assigned to *Chirognathus tricostatus* sp. nov. where it represents the Sb position (AM F.136494, Fig. 4G-H herein).

Diagnosis

Septimembrate apparatus with a ramiform-pectiniform structure including makellate M, alate Sa, digyrate Sb, bipennate Sc, tertiopedate Sd, carminate Pa, angulate Pb1, and pastinate Pb2 elements. S elements with a robust cusp, an open and shallow basal cavity, and long closely-spaced denticles on the processes; Pa element with a longer anterior process, a nearly straight basal margin and a cusp varying from prominently larger (juvenile) than adjacent denticles to rather indistinctive in size (when mature). Pb1 element with a robust cusp, and a strongly curved basal margin. Pb2 element with a short adenticulate outer lateral process, long denticulate anterior and posterior processes, and a strongly laterally flared base.

Description

M element makellate with a denticulate inner-lateral process bearing three to five pointed denticles (Fig. 9), and a shorter, typically adenticulate outer lateral process (Fig. 9A-C, H); cusp robust, antero-posteriorly compressed (Fig. 9G), with a sharp costa along the inner-lateral and outer lateral margins (Fig. 9G-I), and distally curved posteriorly (Fig. 9C-D, G); denticles on the inner lateral process also antero-

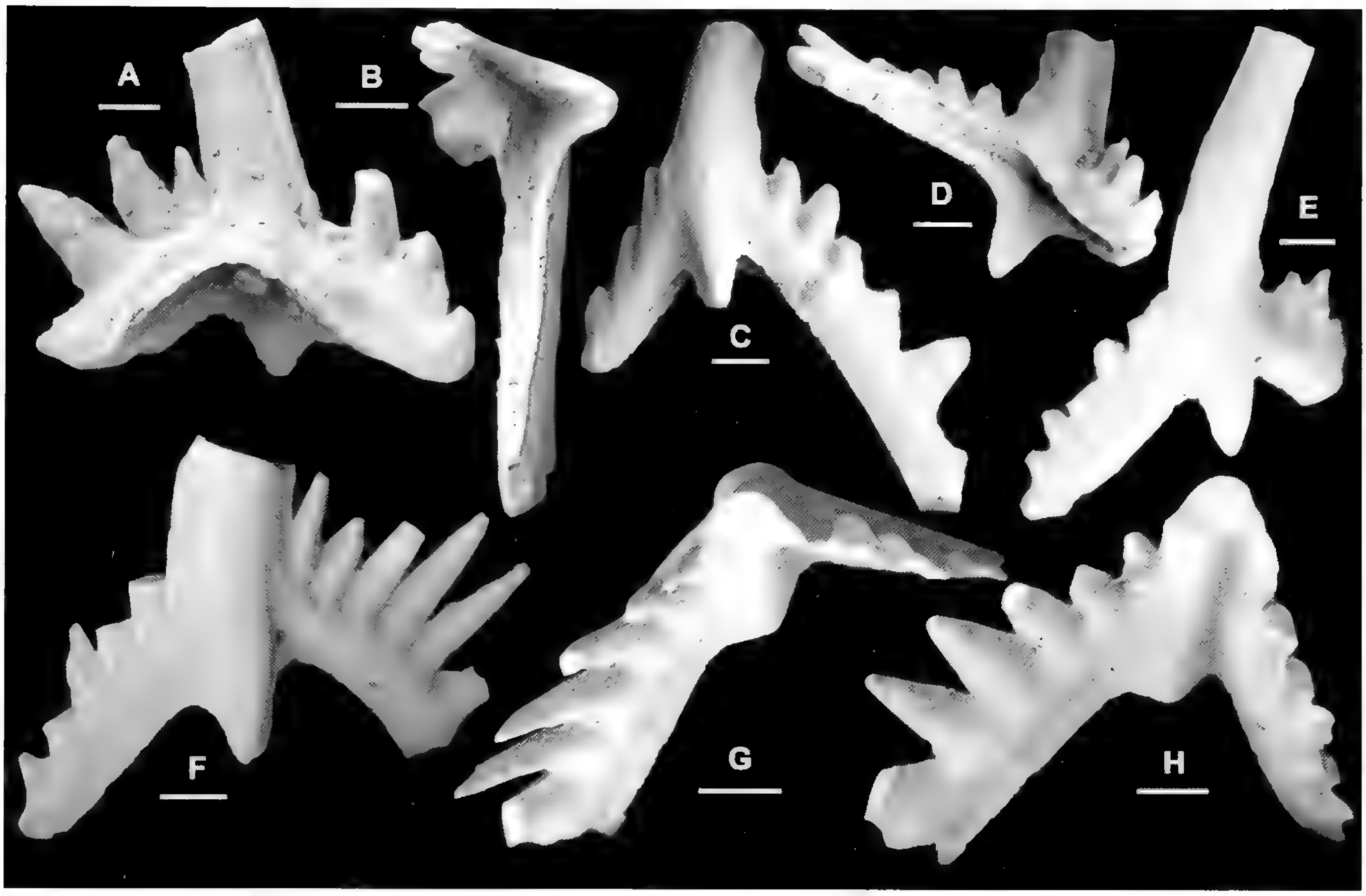

Figure 11. ***Tasmanognathus careyi*** **Burrett, 1979. Sb element; A, AM F.136535 =UTG96873, posterior view (IY141-027); B-D, AM F.136536, C98, B, basal view (IY137-039), C, anterior view (IY137-037), D, basal-posterior view (IY137-038); E, AM F.136537, C98, outer-anterior view (IY137-034); F-H, AM F.136538 =UTG96898 (Burrett, 1979, fig. 4A), C98, F, anterior view (IY137-031), G, upper view (IY137-032), H, upper-posterior view (IY137-030). Scale bars 100 µm.**

posteriorly compressed, with a sharp costa along the inner-lateral and outer-lateral margins (Fig. 9C, G-H); basal cavity shallow and open, tapering towards distal ends of the processes and flaring posteriorly (Fig. 9D, F), and often with weakly developed zone of recessive basal margins (Fig. 9F); anterior portion of basal margin nearly straight (Fig. 9B, J), but posterior portion weakly curved (Fig. 9C, E, H).

Sa element alate (Fig. 10), symmetrical with a robust cusp, a prominent tongue-like anticusp, and a long denticulate lateral process on each side; cusp proclined, subquadrate in cross section (Fig. 10E, I), with a sharp costa on each side (Fig. 10A-B) and often a weak costa along the posterior margin (Fig. 10D-E), but some specimens with a broad posterior face (Fig. 10G) or with a broad carina developed (Fig. 10A); broad anterior face bearing a shallow but prominent mid groove and a broad carina on each side (Fig. 10C, H); cusp extended downward to form a downward extending tongue-like anticusp (Fig. 10A-D, H); lateral process long, bearing up to ten or more closely spaced denticles (Fig. 10C-D, H), which are compressed antero-posteriorly; basal cavity open and shallow, flared posteriorly; basal margin arched in posterior view (Fig. 10D).

Sb element digyrate, asymmetrical, with a robust cusp, long denticulate process on each side, and a prominent downwardly extending tongue-like anticusp (Fig. 11); cusp suberect, slightly curved inward (Fig. 10A), with a more strongly convex anterior face, and a sharp costa on each side (Fig. 11G-H); outer lateral process shorter, bearing three or more denticles (Fig. 11A, D, G); inner lateral process longer, bearing five or more peg-like denticles (Fig. 11C, F), and more strongly curved posteriorly (Fig. 11B, G), forming an angle of about 100-110 degrees between the two processes in the upper or basal view (Fig. 11B, G).

Sc element bipennate, asymmetrical with a robust cusp, a long denticulate posterior process, and a short denticulate anterior process (Fig. 12); cusp suberect basally and reclined distally (Fig. 12A, F, H) with a more convex outer lateral face, and laterally compressed with a sharp costa forming anterior

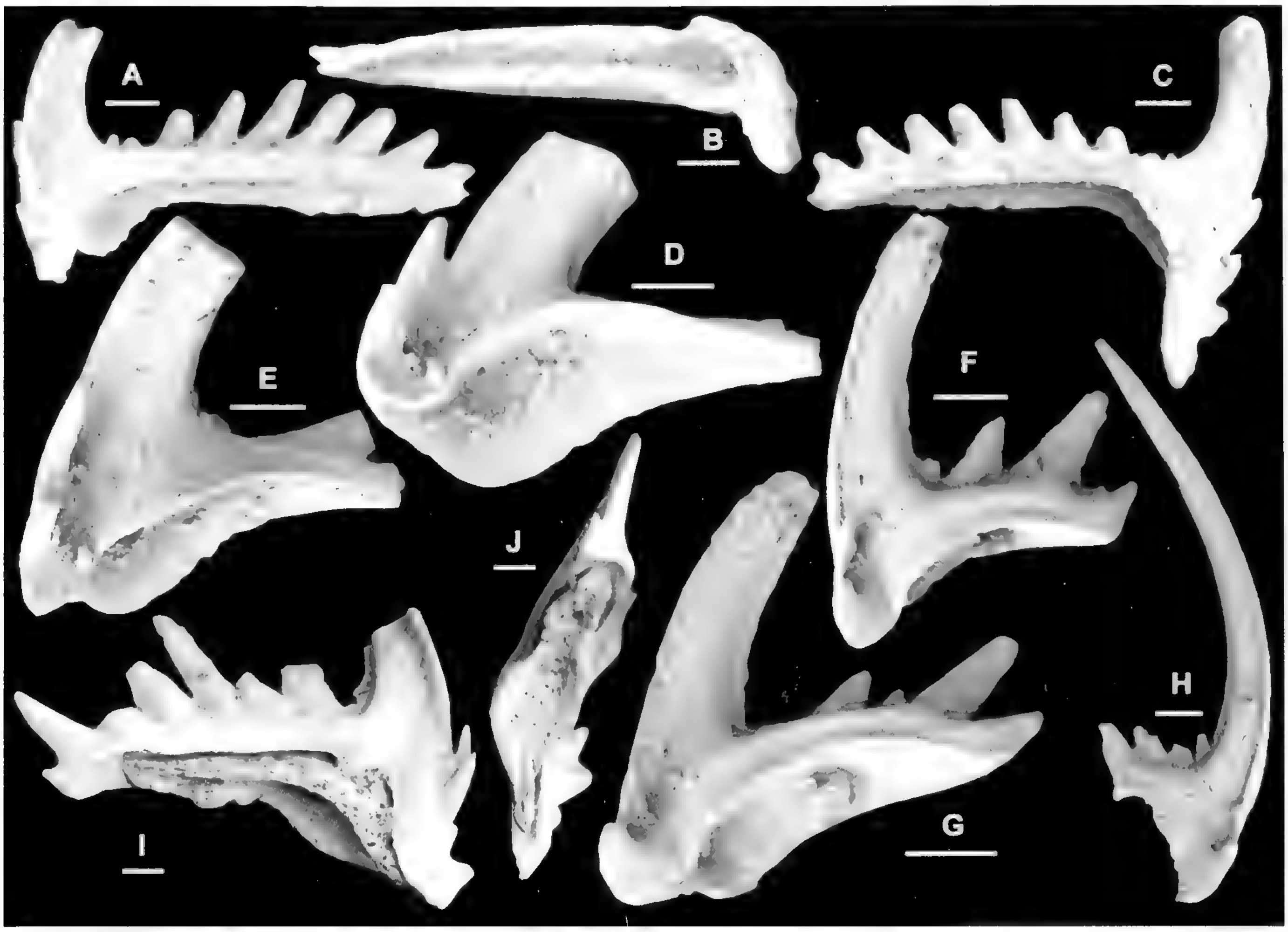

Figure 12. ***Tasmanognathus careyi*** **Burrett, 1979. Sc element; A-C, AM F.136539 =UTG96876 (Burrett 1979, pl. 1, fig. 11), JRC 2, paralectotype, A, inner lateral view (IY141-020), B, basal view (IY141-016), C, outer lateral view (IY141-015); D-E, AM F.136540, YYF5, D, inner-basal view (IY135-041); E, inner-lateral view (IY135-040); F-G, AM F.136541, JRC 2, F, inner lateral view (IY139-028); G, inner-basal view (IY139-027); H, AM F.136542, YYF5, inner-lateral view (IY140-009); I-J, AM F.136543 =UTG 96899 (Burrett, 1979, fig. 4B), C98, I, inner-lateral view (IY137-029), J, basal view (IY137-027). Scale bars 100 μm.**

and posterior margins (Fig. 12F-I); anterior margin curved inward (Fig. 12D-I); posterior process bearing three or more (up to seven) denticles, which are laterally compressed and posteriorly reclined (Fig. 11A, C, I); anterior process with upper margin curved inwards, and extending downwards bearing two to four small denticles (Fig. 12D-H); basal cavity open and shallow, slightly flared inwards (Fig. 12B, D, G), some specimens with basal funnel attached (Fig. 12I-J).

Sd element tertiopedate, weakly asymmetrical to nearly symmetrical with a robust cusp, a prominent anticusp, a denticulate posterior process and a denticulate lateral process on each side (Fig. 13); cusp with a broad anterior face (Fig. 13B-C), and with a prominent costa along the posterior margin and on each lateral side (Fig. 13D, G); anticup short and downward extending (Fig. 13C-D); posterior process long and straight, broken in most specimens, in one of the examined specimens bearing ten denticles (Fig. 13A); lateral process bearing four or more denticles (Fig. 13B-D); basal cavity open, T-shaped in basal view (Fig. 13B).

Pa element carminate (Fig. 14), laterally compressed and blade-like, with a small cusp, and with the anterior and posterior processes bearing basally confluent denticles; cusp erect (smaller specimens, Fig. 14C, E) to slightly inclined (larger specimens, Fig. 14A, D), typically larger and higher than adjacent denticles (Fig. 14C, E, F), but less distinctive in the larger specimens (Fig. 14 A, H); two processes of unequal length, anterior process longer and higher, bearing five to eight closely-spaced denticles; posterior process lower and shorter, bearing two to six denticles, with distal end slightly bent downward (Fig. 14A, D); juvenile specimens

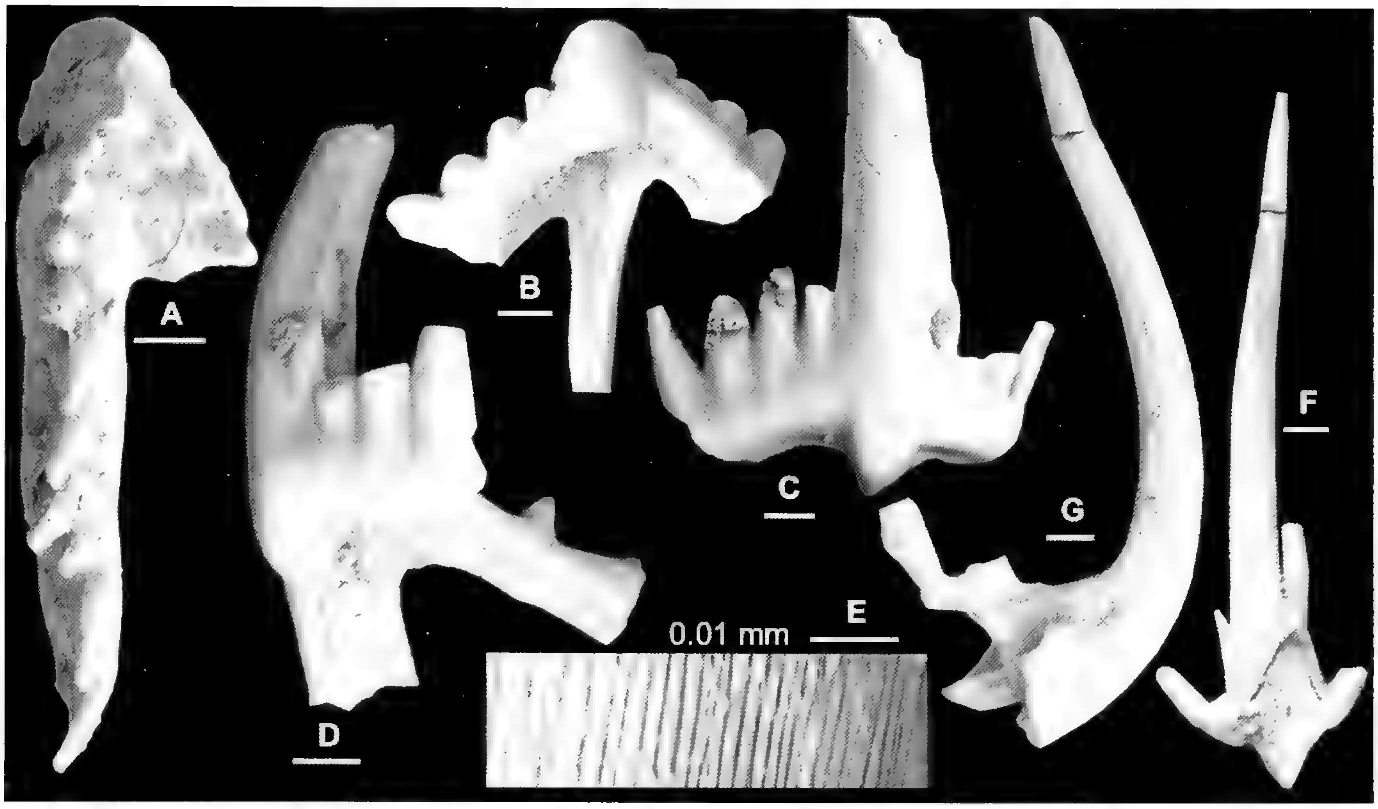

Figure 13. ***Tasmanognathus careyi*** **Burrett, 1979. Sd element; A, AM F.136544 =UTG96902 (Burrett, 1979, pl. 1, figs 15-16), LLMB, upper view (IY137-033); B-E, AM F.136545 =UTG96900 (Burrett, 1979, fig. 4C-D), B, basal view (IY137-023), C, anterior view (IY137-022), D, lateral view (IY127-024), E, close up showing fine striae on the surface of the cusp (IY137-026); F-G, AM F.136546, YYF1, G, lateral view (IY140-015), F, basal-posterior view (IY140-014). Scale bars 100 μm.**

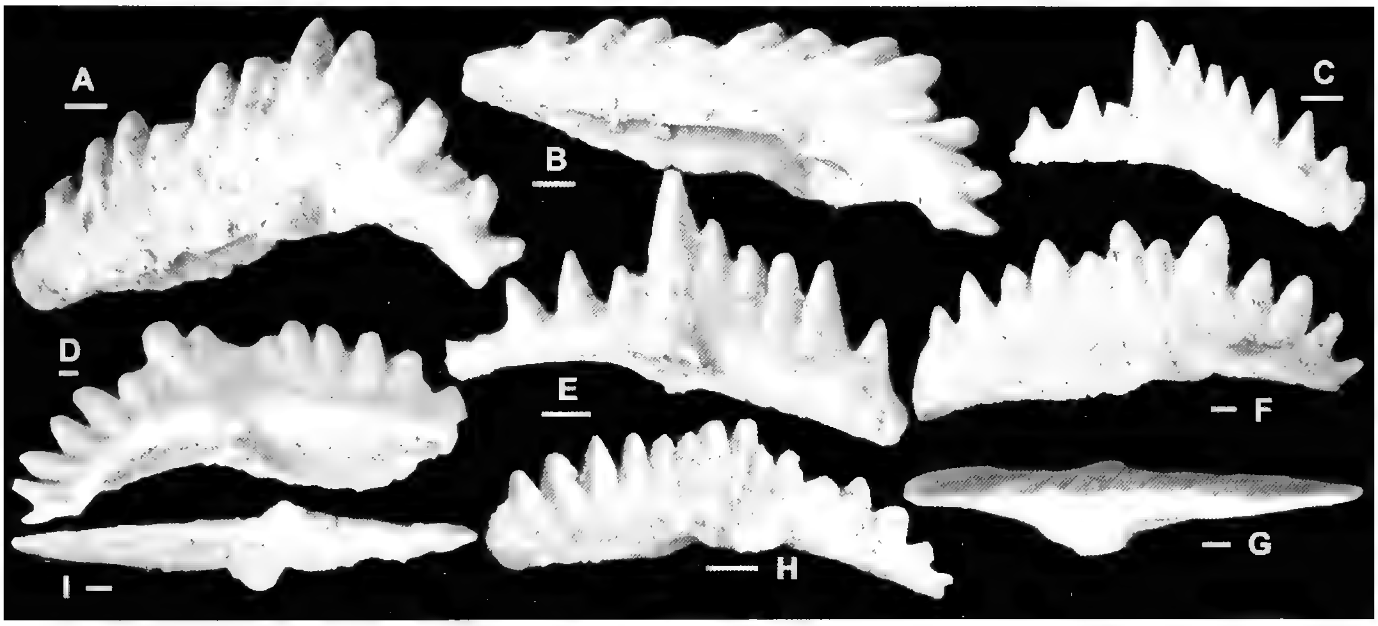

Figure 14. ***Tasmanognathus careyi*** **Burrett, 1979. Pa element; A-B, AM F.136547 =UTG96851 (Burrett 1979, pl. 1, fig. 6), lectotype, JRC 2, A, outer lateral view (IY141-002), B, basal-inner lateral view (IY141-003); C, AM F.136548 =UTG96856 (Burrett 1979, pl. 1, fig. 7), paralectotype, JRC 2, outer lateral view (IY141-004); D, AM F.136549 =UTG96893a (Burrett, 1979, fig. 3), LLM (B), inner-lateral view (IY137-001); E, AM F.136550 =UTG96893b (Burrett, 1979, fig. 3), LLM (B), outer-lateral view (IY137-003); F-G, AM F.136551, C98, F, outer-lateral view (IY137-005), G, upper view (IY137-006); H-I, AM F.136552, JRC 2, H, inner-lateral view (IY137-010), I, basal view (IY137-009). Scale bars 100 μm.**

Figure 15. ***Tasmanognathus careyi*** **Burrett, 1979. A-G, Pb1 element; A-B, AM F.136553 =UTG96850 (Burrett 1979, pl. 1, fig. 4), paralectytype, JRC 2, A, basal-outer lateral view (IY141-007), B, outer lateral view (IY141-006); C, AM F.136554 =UTG96882 (Burrett 1979, pl. 1, fig. 5), paralectotype, JRC 2, inner lateral view (IY141-008); D-E, AM F.136555, C98, D, basal view (IY137-018), E, inner lateral view (IY137-019); F-G, AM F.136556, C98, F, outer-lateral view (IY137-021), G, basal view (IY137-020). H-M, Pb2 element; H, AM F.136557 =UTG96857 (Burrett 1979, pl. 1, fig. 1), paralectotype, JRC 2, outer lateral view (IY141-009); I-J, AM F.136558, JRC 2, I, inner-lateral view (IY137-040), J, basal view (IY137-041); K, AM F.136559 =UTG96860 (Burrett 1979, pl. 1, fig. 2), paralectotype, JRC 2, outer lateral view (IY141-011); L, AM F.136560 =UTG96853 (Burrett 1979, pl. 1, fig. 3), paralectotype, JRC 2, outer lateral view (IY141-012); M, AM F.136561, JRC 2, outer-lateral view (IY137-014). Scale bars 100 μm.**

exhibiting a prominently lower and shorter posterior process with two to four less closely-spaced denticles (Fig. 14C, E); basal cavity shallow and open, flared laterally and extended toward distal end of the processes as a tapering shallow groove (Fig. 14I); basal margin nearly straight to slightly arched in lateral view (Fig. 14A, C-E, F).

Pb1 element angulate (Fig. 15A-G), laterally compressed and blade-like, with a robust cusp, and denticulate anterior and posterior processes; cusp strongly compressed laterally, more convex outer laterally, suberect and slightly curved inwards with sharp anterior and posterior margins; two processes typically sub-equal in length (Fig. 15E) or with slightly longer posterior process (Fig. 15B, C), bearing three to six short, laterally compressed and basally confluent denticles; anterior process extending downward forming an angle of about 100-120 degrees between the two processes in lateral view (Fig. 15B, F); basal cavity shallow and open, laterally flared and extended as a shallow groove underneath each process (Fig. 15D, G).

Pb2 element pastinate (likely a variant of the Pb1 element), with a robust cusp, long denticulate anterior and posterior processes, and a short adenticulate outer lateral process (Fig. 15H-M); cusp suberect (Fig. 15H), laterally compressed, with a broad smooth inner lateral face, and sharp anterior and posterior margins, outer lateral face smooth (Fig. 15L-M) or with a mid costa (Fig. 15H, K); anterior process typically longer, bearing up to seven or more denticles, which are typically closely spaced with confluent bases (Fig. 15I, M); most specimens with posterior process broken, bearing up to five denticles (Fig. 15L); outer lateral process typically represented by a prominent tongue-like basal extension (Fig. 15J-M), or as a short adenticulate process (Fig. 15H); basal cavity shallow, outer laterally flared more strongly, and tapering as a shallow groove to the distal end of anterior and posterior processes (Fig. 15I-J).

Discussion

One originally designated syntype (AM F.136567 =UTG96877 Fig. 16G; also see Burrett 1979, pl. 1, fig. 20) and an additional figured specimen (AM F.136562 =UTG96904, Fig. 16A; also see Burrett 1979, pl. 1, figs 8-10) of *T. careyi* are excluded from this species and re-assigned to represent the Sb and Pb2 elements of *T.* sp. cf. *careyi*, as they exhibit more widely spaced denticles on the processes.

The original definition of the S element given by Burrett (1979) is more or less followed herein, except that his Sa1 element (Burrett 1979, fig. 4C-D) is now assigned to the Sd position (Fig. 13), the digyrate element with a longer inner lateral process (Burrett 1979, fig. 4A, referred to as Sc) to the Sb position (Fig. 11), and the bipennate element with a shorter downwardly extended and inner laterally curved anterior process (Burrett 1979, fig. 4B, referred to as Sb) to the Sc position (Fig. 12). Burrett (1978, p. 34) further recognized an Sa2 element with the cusp exhibiting a subquadrate cross section, but illustrated it as Sa (Burrett 1979, pl. 1, fig. 19; also Fig. 10A-B herein). This symmetrical or nearly symmetrical element (Fig. 10) is confirmed as occupying the Sa position. The makellate M element (Fig. 9) described herein was not recognized in Burrett's original description of *T. careyi*. Specimens originally included in the Pa element by Burrett (1979) show two morphotypes, which are defined herein to represent the Pb1 (Burrett 1979, pl. 1, figs 4-5; Fig. 15A-G) and Pb2 (Burrett 1979, pl. 1, figs 1-3; Fig. 15H-M) elements. They can be easily differentiated from each other by having a short tongue-like outer lateral process, a costa on the outer lateral face or a short adenticulate outer lateral process in the Pb2 element (Fig. 15H-M).

Burrett (1979, pp. 33-34) discussed the considerable ontogenetic variations among the P elements, in particular the posterior process of the Pa element (referred to as the Pb element by Burrett, 1979, see p. 33, fig. 3) and the anterior process of the Pb2 element (assigned to part of the Pa element by Burrett, 1979, see p. 33, fig. 2). Juveniles of the Pa element have a larger cusp and a lower posterior process with less closely spaced denticles (Fig. 14C, E; Burrett 1979, fig. 3). It cannot presently be established whether the distinctions between the Pb1 and Pb2 elements, and within the Pa elements, represent ecophenotypic variations, or whether they reflect a high degree of morphological plasticity.

T. careyi has been widely reported from North China (Zhao et al. 1984; Wang and Luo 1984; Pei and Cai 1987; An and Zheng 1990). However, judging from the illustrations of these specimens, none can be confidently assigned to the Tasmanian species, except for one specimen figured by An and Zheng (pl. 11, fig. 2) from the lower part of the Yaoxian Formation in the Ordos Basin of Shaanxi Province that is comparable with the Pa element of *T. careyi*. Pa elements of *T. borealis* (An in An et al. 1985, pl. 1, fig. 14) and *T. multidentatus* (An and Zheng 1990, pl. 11, fig. 4; = *T. borealis*), also from the Yaoxian Formation of the Ordos Basin, similarly have an indistinct cusp that is nearly the same size as adjacent denticles, but the outline of these two illustrated specimens is shorter and higher in comparison with the Pa element of *T. careyi* (Fig. 14).

Figure 16. Tasmanognathus sp. cf. careyi Burrett, 1979. A, Pb2 element, AM F.136562 =UTG96904 (Burrett, 1979, pl. 1, figs 8-10), LLM (B), outer-lateral view (IY137-007). B, M element, AM F.136563, YYF1, posterior view (IY136-032). C-F, Sa element; C-D, AM F.136564, JRC 2, C, Posterior view (IY138-006); D, postero-basal view (IY138-005); E, AM F.136565, JRC 2, posterior view (IY139-029); F, AM F.136566, YYF1, anterior view (IY140-010). G, Sb element, AM F.136567 =UTG96877 (syntype of T. careyi; Burrett 1979, pl. 1, fig. 20), JRC 2, posterior view (IY141-024). H-I, Sd element, AM F.136568, YYF4, H, posterior view (IY135-023), I, upper view (IY135-024); J-K, Sc element, AM F.136569, YYF1, J, inner lateral view (IY140-013), K, outer lateral view (IY140-012). Scale bars 100 µm.

Tasmanognathus sp. cf. *T. careyi* Burrett, 1979
Figures 16-17

Synonymy

Tasmanognathus careyi Burrett, 1979, p. 33-35, *partim* only pl. 1, figs 8-10 (= Pb2 element), fig. 20 (= Sb element).

Material

34 specimens from four samples in the Settlement Road section of Florentine Valley area (see Table 1).

Diagnosis

A species of *Tasmanognathus* having an septimembrate apparatus, including makellate M, alate Sa, digyrate Sb, bipennate Sc, digyrate? (modified tertiopedate) Sd, carminate Pa, angulate? (bipennate) Pb1, and pastinate Pb2 elements; elements robust and large in size bearing a prominent cusp ornamented with fine striae, and small widely spaced denticles on the processes of M, S, Pb1 and Pb2 elements; most elements with basal funnel attached.

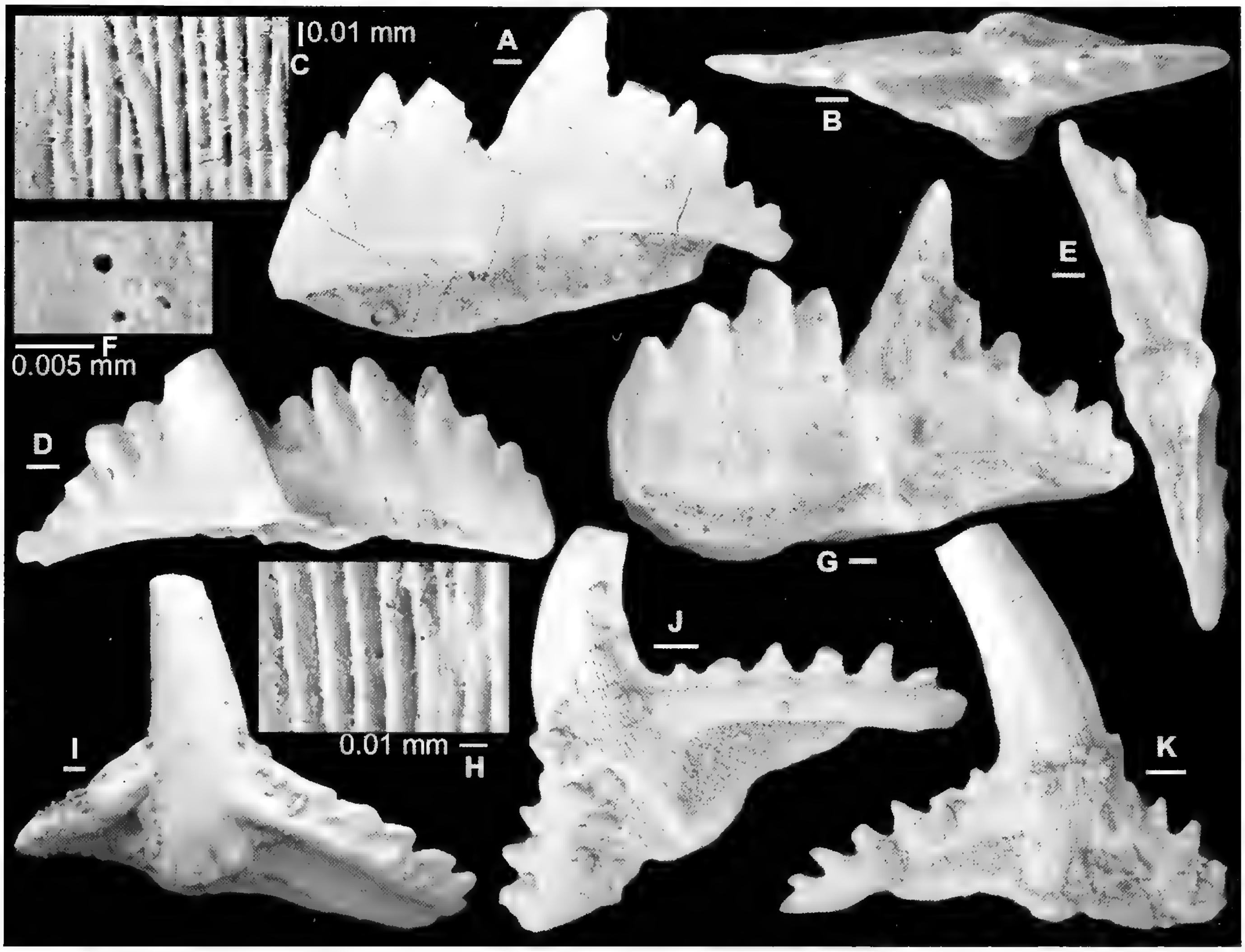

Fig. 17. *Tasmanognathus* sp. cf. *T. careyi* Burrett, 1979. A-H, Pa element; A-C, AM F.136570, YYF4, A, inner-lateral view (IY135-005), B, upper view (IY135-003), C, outer-lateral view, close up showing fine surface striae (IY135-007); D-F, AM F.136571, YYF4, D, outer-lateral view (IY135-009), E, basal view (IY135-008), F, outer-lateral view, close up showing rounded boring hole on the surface (IY135-010); G-H, AM F.136572, YYF4, G, inner lateral view (IY140-037), H, close up showing fine surface striae (IY140-038). I-K, Pb1 element; I, AM F.136573, YYF4, outer-lateral view (IY135-012); J-K, AM F.136574, YYF4, J, inner-lateral view (IY140-031), K, outer lateral view (IY140-030). Scale bars 100 µm unless otherwise indicated

Description

M element with a long, denticulate inner-lateral process bearing five short and widely spaced denticles (Fig. 16B), and a short, outer lateral process bearing two small rudimentary denticles; cusp robust, antero-posteriorly compressed with a sharp costa along the inner-lateral and outer lateral margins and distally curved posteriorly.

Sa element alate (Fig. 16C-F), with a robust cusp and a long denticulate lateral process on each side; cusp strongly compressed antero-posteriorly, with a sharp costa along the lateral margins; lateral process long, bearing three or more peg-like denticles (Fig. 16C), which are also strongly compressed antero-posteriorly, basal cavity open and shallow, flared posteriorly, isosceles-triangular in basal view (Fig. 16D-E); basal margin gently arched in posterior view (Fig. 16C).

Sb element digyrate, like Sa but asymmetrical (Fig. 16G); cusp robust and antero-posteriorly compressed with sharp lateral margins; denticulate lateral process on each side bearing two or three short widely-spaced denticles; inner lateral process longer and more downwardly extending.

Sc element bipennate, strongly asymmetrical with a robust cusp, denticulate anterior and posterior processes (Fig. 16J-K); cusp distally curved inner laterally with a more convex outer lateral face bearing a prominent costa; posterior process longer and slightly arched bearing three widely-spaced denticles; anterior process curved inward bearing two widely-spaced denticles.

Sd element digyrate? with a robust cusp, a long denticulate lateral process on each side, a sharp costa on the posterior face and a broad anterior face with a weak carina (Fig. 16H-I); cusp with a sharp costa on each side and on the posterior face, and ornamented with fine striae; inner lateral process longer bearing eight small denticles.

Pa element blade-like with a prominent cusp, and denticulate anterior and posterior processes (Fig. 17A-H); cusp suberect or slightly inclined posteriorly, laterally compressed, standing higher above the adjacent denticles, and about twice width of the adjacent denticles on the anterior process, and typically leaving a prominent notch between cusp and the first denticle on the anterior process (Fig. 17A, G); anterior process higher and longer bearing four to eight larger and basally confluent denticles (Fig. 17A, D, G); posterior process slightly shorter, triangular in outline in lateral view, with a tapering distal end and bearing five or six smaller denticles (Fig. 17A, G); basal cavity shallow, flared laterally, forming a shallow groove underneath each process (Fig. 17E), and with a straight basal margin (Fig. 17D); some specimens bearing fine rounded boring holes (Fig. 17F).

Pb1 element asymmetrical with a suberect, robust cusp and long denticulate anterior and posterior processes (Fig. 17I-K); cusp curved inward, diamond-shaped in cross section with a sharp costa along the anterior and posterior margins, a mid costa on the inner lateral face (Fig. 17J), and a broad carina on the outer lateral face (Fig. 17K); two processes bearing small, discrete denticles; posterior process longer with six or more denticles, and anterior process shorter, extending downwards (Fig. 17K).

Pb2 element pastinate, with a robust cusp and denticulate anterior, posterior and outer lateral processes (Fig. 16A); cusp laterally compressed with a sharp costa along anterior and posterior margins and on the outer lateral face; long anterior and posterior processes bearing short, widely spaced denticles; outer lateral process short, represented by a single denticle.

Discussion

This species differs from *T. careyi* in having a Pa element with shorter and higher outline bearing a prominent cusp and a notch in front of the cusp, and in having the S, Pb1 and Pb2 elements bearing small, discrete or widely-spaced denticles on the processes. Additional specimens from the Settlement Road section of Florentine Valley area confirm that it represents a separate species of *Tasmanognathus*. However, as only a small number of specimens are available for study, this species is retained herein under open nomenclature pending further collecting and study.

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Stratigraphic Revision of the Hatchery Creek Sequence (Early-Middle Devonian) Near Wee Jasper, New South Wales

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Hunt, J.R., and Young, G.C. (2010). Stratigraphic revision of the Hatchery Creek sequence (Early-Middle Devonian) near Wee Jasper, New South Wales. *Proceedings of the Linnean Society of New South Wales* **131**, 73-92.

A new formation (the Corradigbee Formation) is erected for the upper part of the previous 'Hatchery Creek Conglomerate', which is elevated to Group status, its lower part renamed the Wee Jasper Formation. The 'Hatchery Creek Conglomerate', south of Burrinjuck Dam and 50 km northwest of Canberra, was previously defined as a 2.9 km thick sedimentary sequence of conglomerate, sandstone and shale nonconformable on underlying Lower Devonian limestones. The coarser lower part (Wee Jasper Formation) is now estimated at about 1500 m thick; an additional type section is nominated for its upper part, which was not included in the original type section, and lithologies, subdivision, and contacts with underlying and overlying formations are described. The upper sequence of dark shales and mudstones (Corradigbee Formation) has an estimated thickness of about 260 m, with 15 fining-upward cycles in which 50 new fossil sites have been found. Repetition of lower strata of the Hatchery Creek sequence in the west, due to an unrecognised syncline axis through the central part of the outcrop area, had suggested a much greater thickness than interpreted in this study. The relatively high topography of the softer shales and mudstones in the core of the syncline is a transient inverted topography resulting from recently eroded Tertiary basalts. The whole sequence is interpreted as conformable on underlying limestones, and of Emsian-Eifelian age.

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KEYWORDS: Corradigbee Formation, Emsian-Eifelian, Hatchery Creek Group, Wee Jasper Formation.

INTRODUCTION

The previously named 'Hatchery Creek Conglomerate' is a thick sedimentary sequence of Devonian non-marine strata located 50km NW of Canberra (Fig. 1a). It is exposed over an area of about 70 km², with most of its outcrop on the Brindabella 1:100 000 sheet, about 4 km² of which is covered by remnant Tertiary basalt (Owen and Wyborn 1979), and a small northern extension on the Yass 1:100 000 sheet (Cramsie et al. 1978). Underlying marine limestones of the Murrumbidgee Group, in the Goodradigbee valley near the village of Wee Jasper (Fig. 1b), contain an abundant invertebrate fauna, including conodonts, brachiopods, and corals (see Pedder et al. 1970, and references therein). These provide a late Early Devonian (Emsian) maximum age limit for the Hatchery Creek sequence.

The 'Hatchery Creek Conglomerate' was originally assumed to be Upper Devonian in age, based on lithological similarity with the Hervey Group of central New South Wales (Pedder 1967, Conolly, in Packham 1969, Pedder et al. 1970). However a fossil fish assemblage discovered during geological mapping by Owen and Wyborn (1979) was described by Young and Gorter (1981) as probably late Eifelian (Middle Devonian) in age.

Previous authors, when referring to the 'Hatchery Creek Conglomerate', commented on the most accessible lower section, formed predominantly of cycles of massive conglomerate and sandstone. The measured section of Owen and

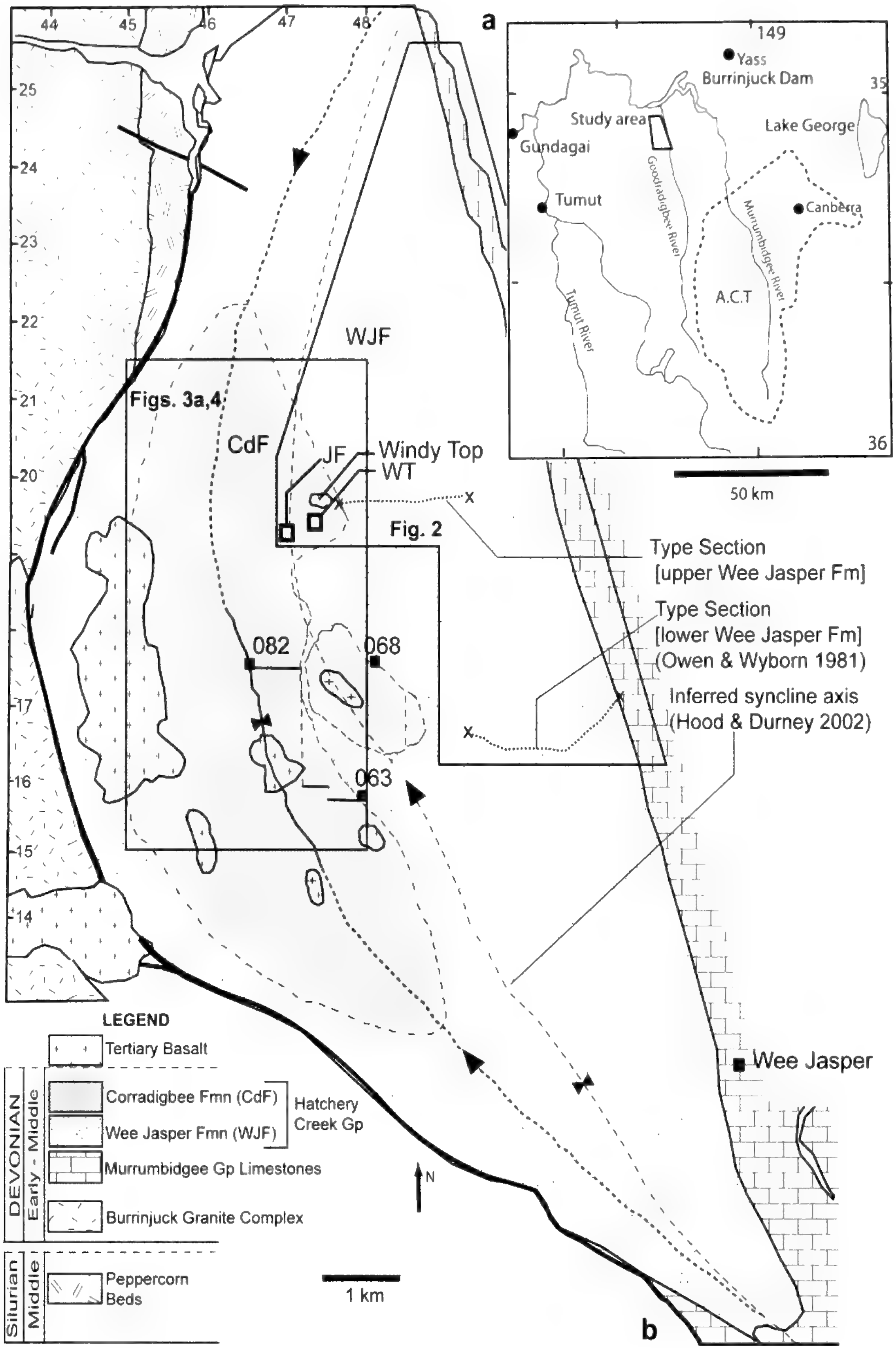


Figure 1. a. Regional locality map showing the study area. b. Generalised geological map showing the outcrop area of the Hatchery Creek Group, based on the Owen and Wyborn (1979) Brindabella 1:100 000 geological map, updated by detailed field mapping (e.g. eastern areas of basalt; large area to west not remapped). Previous fossil localities are the original fish locality at Windy Top (WT) described by Young and Gorter (1981), and a second fish-plant locality (JF) studied by Francis (2003). The syncline axis as identified in this study (on the left) is compared with the position of this structure inferred by Hood and Durney (2002). Boxed study areas are shown in more detail in Figs. 2-4 as indicated.

Wyborn (1979) did not reach into the upper sequence above the lower massive conglomerates (Figs. 1b, 2a). The fossil fish assemblage of Young and Gorter (1981) occurs within the upper finer sequence of siltstones and mudstones, in which almost no conglomeratic horizons are seen. In this paper this upper sequence is separated out as the new Corradigbee Formation, described below, and the lower coarser sequence is renamed the Wee Jasper Formation, both formations included in the Hatchery Creek Group.

A second fossil locality (plants) was recorded on the geological map of Owen and Wyborn (1979). In 1988 an ANU student excursion located fish remains about 4 km south of the original fossil fish locality (locality 59, Fig. 3a), and apparently higher in the sequence. However the faunal composition seemed identical to that from the original fish locality, suggesting problems with the stratigraphy and structure. The plant locality of Owen and Wyborn (1979) was investigated by Francis (2003), where fish were found in association, this locality (JF, Figs. 1b, 2a, 3a, 4b, 5a) being only slightly higher in the sequence than the original fish locality, now called 'Windy Top' (WT, Fig. 1b). Hunt (2005, 2008) conducted a detailed field study of the upper fine-grained sequence (Corradigbee Formation), and discovered many additional fossil localities (Fig. 3a), mainly fish and plant remains, but with a few invertebrates (gastropods, and probable arthropods; see Appendix). New fish taxa in these assemblages (Table 1) include several osteichthyans (bony fish), and a new placoderm genus probably belonging to the arthrodires (Hunt and Young, in press; Young et al. 2010, fig. 4A). Fifteen fining-upward sedimentary cycles were identified, comprising about 260 m of the Corradigbee Formation. The cycles were mapped on both sides of the axis of a broad syncline, a major structure not shown on the geological map of Owen and Wyborn (1979). As a result their estimated total thickness of at least 2900 m for the entire sequence is erroneous. The results presented here conform closely with the first geological investigation of the area, in an unpublished honours thesis by Edgell (1949).

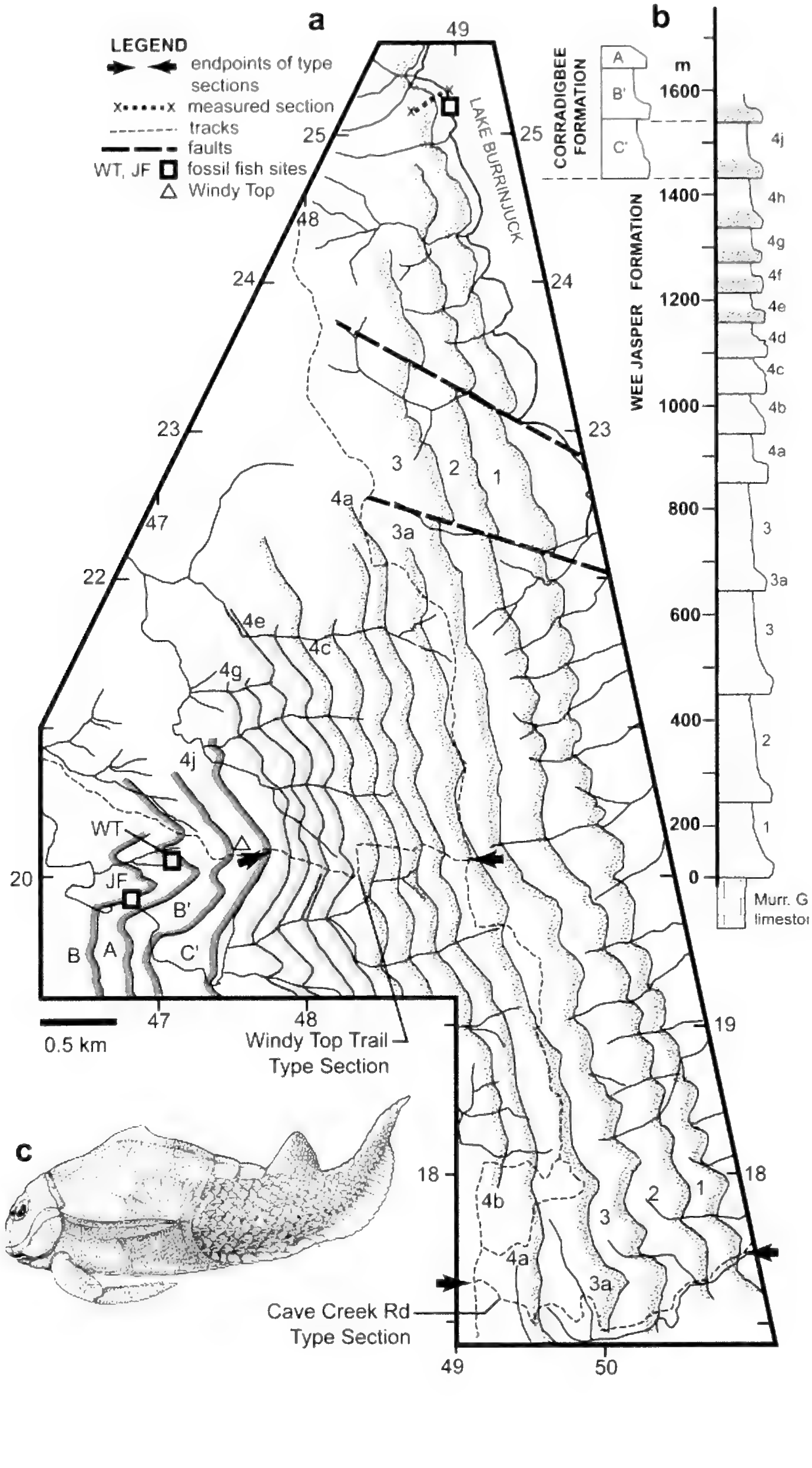
The original fish locality was estimated at about 1.9 km above the base of the sequence, and it was suggested that any disconformity with the underlying limestones was of short duration (Owen and Wyborn 1979; Young and Gorter 1981). Previously, Edgell (1949) had interpreted a conformable boundary between the Hatchery Creek sequence and the underlying limestones, an interpretation now followed here (see below).

Physiographically, the Hatchery Creek area of outcrop is part of the 'Bimberi-Brindabella Upland' of Owen and Wyborn (1979, fig. 5), across which Miocene basalts spread into the mapped area from the 'Kiandra Tableland'. The higher relief of the softer mudstone sequence in the 'middle ridge' of the mapped area of Hunt (2005, 2008; Fig. 3a) probably results from inverted topography. It coincides with the syncline axis, the topographic expression of which has evidently been masked by recent erosion of the cover of Tertiary basalt. Probably the basalt flowed down a previous valley representing the eroded core of the syncline, the basalt cover then inhibiting further erosion until it was eventually stripped off. A small residual cap of basalt remains adjacent to the original fossil fish locality at 'Windy Top' (~700 m elevation, Fig. 1b), with larger outcrops 3-5 km to the south and west (Owen and Wyborn 1979). A flagstone quarry at about 760 m elevation is located in the basalt that forms the highest part of the middle ridge of the mapped area, including Goodradigbee Hill (803 m; Fig. 3a). The area of finer sedimentary rocks was cleared for grazing many years ago, in contrast to the timbered ridges to the east in the coarser sandstone and conglomerates lower in the Hatchery Creek sequence, but since completion of this study has been revegetated as plantation pine forest.

Original access to the main outcrop was up the Cave Creek Road (locked from 2008) and along the 'Main Ridge Trail' to the north, then west along the 'Windy Top Trail' to the original fish locality. Access to 'Corradigbee' homestead (Fig. 3a) is off the access road to the 330kv power transmission line, from the south via the Tumut Road.

METHODS

Reconnaissance mapping of the lower part of the Hatchery Creek sequence by Young (1969) has been reinvestigated during many excursions to collect fossils following the research of Young and Gorter (1981), and associated with the honours project of Francis (2003). The detailed study of Hunt (2005) involved about 30 days field work on the Corradigbee Formation, covering about 20 km^2 in the upper section of the Hatchery Creek sequence (rectangle, Fig. 1b). The softer mudstone sequence is deeply eroded by two north-flowing tributaries of MacPhersons Swamp Creek, here termed 'eastern creek' and 'western creek', separated by the prominent 'middle ridge' (Fig. 3a). Erosion gullies give many good exposures of the softer sediments, and improved exposure and accessibility was a result of the 2003 bushfires in the Wee Jasper area, which burnt blackberry infestations.


a
b
c
LEGEND
endpoints of type sections
measured section
tracks
faults
WT, JF fossil fish sites
Windy Top
LAKE BURRINJUCK
CORRADIGBEE FORMATION
WEE JASPER FORMATION
Murr. G limestone
m
Windy Top Trail Type Section
Cave Creek Rd Type Section
0.5 km

Only some of the more significant fossil material collected from many new localities has been prepared and identified. The original description (Young and Gorter 1981) documented such forms as the placoderm *Sherbonaspis hillsi* (Fig. 2c), which closely resembled the 'winged fish' first described by Hugh Miller (1841) from classic Middle Devonian Old Red Sandstone fish faunas of Scotland. This was the first discovery of such an assemblage from the Southern Hemisphere. An updated faunal list for the Hatchery Creek fish assemblage is given in Table 1; formal fossil descriptions will be presented elsewhere.

For the Corradigbee Formation, various field sites were examined as to the bedding type, dip, strike, lithology and sedimentary structures (see Appendix). Many fining-upward sedimentary cycles could be seen on air photographs by their more resistant basal sandstones, and were traced out on a 90x90 cm photo enlargement. Some identified beds were walked along strike to establish correlations between different exposures for the detailed stratigraphy (Figs. 2a, 4a). Sedimentary strata with good exposure were selected for measured stratigraphic sections using either a tape or 150 cm Jacobs staff and abney level. The cycle containing the original 1981 fossil fish locality (WT) was called Cycle A, with overlying cycles labelled up through the sequence as B, C, etc., and underlying cycles down the sequence labelled B'-F'. The thickness of the Wee Jasper Formation was estimated using aerial photographs and data plotted from the lowest beds of the Corradibee Formation and measured off the maps and photos.

Numbered localities are shown in Fig. 3a and listed in the Appendix. For different field investigations the locality numbers are: 1-24, 59-159 (Hunt 2005); 160-161, 062-082 (Hunt 2008); prefix GY (Young 1969); prefix JF (Francis 2003). All grid references refer to the Wee Jasper 1:25 000 topographic map 8627-4N (second edition, 2003). Full grid references (as in appendix) are abbreviated in the text (e.g. 646385 611805 shortened to GR46385 1805). Fossil material is registered in the ANU palaeontological collection, Canberra (Building 47, Research School of Earth Sciences).

PREVIOUS STRATIGRAPHY

The 'Hatchery Creek Conglomerate', named by Joplin et al. (1953), consists of cyclothems of terrestrial conglomerates, sandstones and mudstones. These fine upwards and the beds are laterally extensive, some being traceable over several kilometres along the length of the outcrop (Young 1969). These beds can be classified as red beds according to the definition of Van Houten (1973).

Owen and Wyborn's (1979) estimated thickness of about 2.9 km for the Hatchery Creek Conglomerate was followed by other authors (Young and Gorter 1981; Branagan and Packham 2000; Packham 2003). With the subdivision of this sequence into two formations as proposed here (the Wee Jasper Formation and the Corradigbee Formation), and the recognition that the previously interpreted upper ~300 m of coarse sandstones and conglomerates is in fact a repetition of the lower strata (Wee Jasper Formation) on the western limb of a syncline, a significantly reduced total thickness estimate of 1760 m for the Hatchery Creek Group is based on the following: thickness for the lower formation (Wee Jasper Formation) estimated from air photos (average dip 40°) at about 1500 m; thickness for the upper Corradigbee Formation (as defined below) estimated at 260 m.

HATCHERY CREEK GROUP (UPGRADED FROM FORMATION)

WEE JASPER FORMATION (NEW NAME)

The first published description (as 'Hatchery Creek Conglomerate') recorded numerous fining-upward conglomeratic cycles (Owen and Wyborn 1979: microfiche M314-M320). A type section comprising about 1200 m of almost continuous exposure of cycles of 'conglomerate, sandstone and siltstone typical of the lower part of the formation' was nominated along the Cave Creek Road (see Fig. 1b), from the basal contact with the underlying carbonates at their stated grid reference (GR509 176), to the top at the T-junction of the Cave Creek

Figure 2 (LEFT). a. Detailed geological map of the Wee Jasper Formation (previously Hatchery Creek Conglomerate, lower part) between the original type section (Cave Creek Road) for the lower part defined by Owen and Wyborn (1979), and the new type section for the upper part (Windy Top Trail) described in the text. Coarser basal part of each fining-upward unit indicated by stippling or shading. b. Summary section for the lower 1600 m of the Hatchery Creek Group, showing correspondence between the upper cycles of the Wee Jasper Formation and lower cycles of the Corradigbee Formation. c. Reconstruction of the placoderm fish *Sherbonaspis hillsi* Young and Gorter (1981), which established a probable Eifelian age for the Hatchery Creek sequence.

Road and Main Ridge Trail (their GR491 172; Fig. 2a). Owen and Wyborn (1979) noted a change at about 1500 m above the base of the formation to a lithology dominated by fine buff sandstone and red siltstone with root casts. They considered but did not follow the stratigraphic subdivision first proposed by Edgell (1949), who separated off this finer upper sequence as the 'Middle Ridge Shales' from the lower 'Wee Jasper Creek Conglomerates' (also overlooked by Packham 1969; Pedder et al. 1970).

Young (1969) had previously subdivided the lower 1550 m of the Hatchery Creek Conglomerate into four units, the lower Units 1 and 2 forming the eastern slope of the main ridge along the western margin of the Goodradigbee valley, and the upper Units 3 and 4 mainly outcropping in the western drainage of Macphersons Swamp Creek. The top of the formation was left undifferentiated. This subdivision has been checked in the field since 2003, supported by air photo interpretation using new colour air photos, and more recently Google Earth images, as summarised in Figure 2a. Estimated thickness from the base for these four units was 250, 200, 400 and 700 m (Young 1969). Owen and Wyborn (1979) stated that the cycles as defined by the beds of conglomerate rarely extend beyond about 1 km, but some of the units mapped by Young (1969), for example the prominent basal conglomerates of Units 1 and 2, can be traced on air photos nearly 10 km along the western escarpment of the Goodradigbee valley (Fig. 2a). The basal conglomerates of Unit 2 form a row of conspicuous outcrops about one third of the distance up the slope of each spur between about GR495 210 and GR492 220. Both horizons can be traced north (with two slight fault displacements at about GR495 222 and GR492 232) at least to GR490 245. Unit 3 crops out near the top and over the ridge to the west.

To the south, prominent outcrops of three ridges north of the road in the Cave Creek Road type section of Owen and Wyborn (1979) can be assigned to the basal coarse beds of Units 1-3 (between GR509 174 and 504 171). The basal conglomerate of Unit 3 can be readily traced on air photos from GY52 (GR499 193) to a prominent knoll on the spur at GR497 197, and then to the crest of the main ridge between GR492 208 and 489 219. Farther north a sharp bend to the west in the track crosses the basal conglomerate of Unit 4 at GR4855 221. This basal conglomerate is readily traced along strike to the south as a series of prominent outcrops between valleys (e.g. GR487 2125, 487 208), and forms the first outcrop of conglomerate encountered after the turnoff into the eastern end of the Windy Top track, at GR489 2015.

Since the existing type section finishes well below the lithological change to much finer sediments (the base of our new formation), we nominate an additional type section for the upper part of the renamed Wee Jasper Formation, along the Windy Top Trail from its junction with the main track at GR491 201, to the vicinity of the locked gate at Windy Top (GR477 2016), about 1.4 km to the west. This is accessible by 4-wheel drive vehicle, and the valleys to the north and south display a thick section of alternating coarse and fine beds as mapped by Young (1969). From the eastern end of this type section, down the spurs into the Goodradigbee valley, air photos clearly show the base of Unit 3 at GR494 201, the base of Unit 2 at GR496 2065, and the base of the Hatchery Creek Group (and Unit 1 of the Wee Jasper Formation) on the edge of the treeline at GR5012 202.

Owen and Wyborn (1979) recorded a fine-grained sequence between about 1500-2600 m above the base of their Hatchery Creek Conglomerate, then a return to cyclic conglomerates about 300 m thick at the top of the sequence. However our more detailed mapping has shown this interpretation to be incorrect, these 'upper' conglomerate cycles in fact representing a repetition of the contact between the Wee Jasper Formation and the Corradigbee Formation on the western limb of the syncline. The western contact (running beneath the largest basalt outcrop; Fig. 1b) was not mapped in detail, but approximates to the corresponding formation boundary of Edgell (1949). The most westerly discovered fossil site (Fig. 3a, locality 160; with fish and plants) is still in the Corradigbee Formation. Further west, light yellow sandstones of the Wee Jasper Formation were observed in the vicinity of GR449 174, but to the north similar horizons are more conglomeratic where they emerge from beneath the basalt (near GR450 203). A similar increase in coarseness to the north was observed on the eastern limb of the syncline (see below). The uppermost coarse layers of the Wee Jasper Formation are exposed within the main outcrop of the Corradigbee Formation, in the creek bed along a section of the Western Creek (dashed line, Fig. 5a), but too narrow to be shown on the geological map (Fig. 1b). Here, the lower levels of the Corradigbee Formation beneath measured section 2 (see Fig. 3) are inaccessible with a steep drop down to the creek bed.

Lower and Upper Contacts

Various authors have commented on the nature and significance of the contact between the Hatchery Creek sequence and the underlying marine limestones, but only some of these were based on actual field investigations. Young (1969, p. 47) discussed the upper limestone boundary, noting that the uppermost Unit 6 of his 'Upper Reef Formation' was generally poorly exposed because of high clay content, and was covered by scree from the much more prominent overlying 'Hatchery Creek Conglomerate' (now Wee Jasper Formation). Where Unit 6 had continuous exposure on the western shore of Lake Burrinjuck, north from about GR491 243 around to the mouth of Hatchery Creek, the beds were highly sheared in the vicinity of the fold axis. The same applies at the southern fold closure in the vicinity of the Long Plain Fault south of Wee Jasper, obscuring sedimentary changes at the boundary.

Young (1969) noted there was no change of strike across the boundary, and no limestone clasts were observed in the basal conglomerate. However, in four measured sections across this interval there was a marked difference in thickness of the uppermost Unit 6, from 80 m in the south at GY39 (GR520 136), 210 m at GY40 (GR508 183), 140 m at GY43 (GR499 210), and 110 m at GY44 (GR494 230). This thickness variation was attributed to slight warping (less than 1°) before deposition of the conglomerate, indicating a disconformable contact. Pedder et al. (1970, p. 210) independently provided similar evidence for a disconformable contact, noting that the 'Hatchery Creek Conglomerate' (Wee Jasper Formation) on the eastern limb 'rests more than 250 feet above the highest assemblage zone of the Taemas Formation, whereas on the western limb it may rest less than 100 feet above the *Hexagonaria smithi smithi* Teilzone'. They also noted that 'the lithologies of the two formations belong to entirely distinct megafacies'. Owen and Wyborn (1979, M320) also favoured a disconformable contact on the evidence of thickness variation in the uppermost unit of the Taemas Limestone, but suggested, from the age evidence of the overlying fish assemblage (subsequently published by Young and Gorter 1981), that a 'disconformity – if present – represents a short time duration'.

Subsequent to these field investigations a new track was cut around the western shore of the lake at the northern end of the Goodradigbee valley. This gave much improved exposure of this contact in the vicinity of GR488 252, an important fossil fish locality in the limestone (Fig. 2a). Here, Campbell and Barwick (1999) measured a section through the contact, the uppermost beds of the Taemas Limestone comprising about 110 m of thin-bedded limestones and shales 'interpreted as an intertidal zone carbonate deposit consistent with the fact that the overlying unit is the fresh water Hatchery Creek Formation' (p. 125). Lindley (2002, fig. 4) presented a revised version of this section, with the uppermost unit beneath the conglomerate assigned to Unit 6 of the 'Upper Reef Formation' of Young (1969), and Campbell et al. (2009, p. 62) noted that the top of carbonate sequence with shallow marine algal mats was 'transitional into the overlying fresh water Hatchery Creek Formation'.

Although uncertainty about this boundary was indicated in stratigraphic sections of Basden et al. (2000, fig. 2) and Young and Turner (2000, fig. 3B), the new evidence just summarised is accepted as indicating a conformable contact at the base of the Hatchery Creek Group. The thickness variations in the uppermost limestone units noted above must therefore be interpreted as a depositional feature. This complies with the original opinion of Edgell (1949, p. 10) that interbedded lithologies at the contact indicated continuous deposition.

The upper contact of the Wee Jasper Formation (and base of the new Corradigbee Formation as defined below) is at the top of Cycle D' of Hunt (2005). This is the highest cycle observed with conglomerate/coarse pebbly sandstone forming the basal unit, all higher cycles having sandstone at the base (the rare thin conglomerates described below for the Corradigbee Formation were within a cycle, not at the base). It is noted that coarse beds persist to the top of the Wee Jasper Formation in the vicinity of localities 062 and 068 (Fig. 2a), but farther south the equivalent beds seem less coarse, the contact being less clearly defined, and recognised by a change in colour rather than grainsize (discussed below).

Subdivision

The general outcrop of the Wee Jasper Formation is indicated in Figure 1b, and a refined version of Young's (1969) subdivision into four units is detailed in Figure 2. As noted above, the coarser basal unit of each cycle (normally about 30-40 m thick), can generally be traced with confidence on air photos, although individual beds may pinch out along strike. For example a prominent ridge just west of the Main Ridge Trail at GR495 190 (Fig. 2a) is the next resistant set of beds above the base of Unit 3, it forms the main ridge for about 1 km along the track to the south, but is less clearly differentiated in the Cave Creek type section (Unit 3a, Fig. 2a). To the north it is traceable to a similar prominent ridge immediately east of the track at GR492 199, and it also crosses the track at the Windy Top Trail turnoff. It forms prominent outcrops immediately west of the track between GR490 208 and 4895 213, before it is crossed by the track again at about GR488 219, where it is less distinct. This is a distance of about 3 km along strike for what

Table 1. Faunal list for the Hatchery Creek fish assemblage (updated from Young and Gorter 1981).

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

Gnathostomata
Acanthodii
2. climatiid gen. et sp. indet.
3. ?diplacanthiform gen. et sp. indet.
4. *Tareyacanthus* sp. cf. *T. magnificus* Valiukevicius (Burrow 2002)
5. *Watsonacanthus*? sp.

Osteichthyes (Sarcopterygii)
6. *Gyroptychius*? [new genus] *australis* Young & Gorter, 1981
7. osteolepiform gen. et. sp. nov. 2 (Hunt 2008)
8. osteolepiform gen. et. sp. nov. 3 (Hunt 2008)
9. ?onychodontid indet.

Placodermi
Arthrodira
10. *Denisonosteus weejasperensis* Young & Gorter, 1981
11. cf. *Denisonosteus* sp. nov. (Hunt 2005)
12. coccosteomorph cf. *Coccosteus* (Hunt 2008)
13. ?arthrodire gen. et. sp. nov. Hunt and Young, in press.
14. Arthrodira incertae sedis

Antiarcha
15. *Sherbonaspis hillsi* Young & Gorter, 1981
16. cf. *Sherbonaspis* sp. nov. (Hunt 2005)
17. *Monarolepis verrucosa* (Young & Gorter 1981) Young, 1988

is interpreted as a laterally discontinuous coarser interval in the middle part of Unit 3.

The overlying recessive zone, representing the top of Unit 3 at its boundary with the basal conglomerate of Unit 4, is more persistent along strike, being traceable over about 5 km back to the Cave Creek Road type section. In the north it is crossed at a sharp turn in the Main Ridge Trail at GR4855 221, it can be followed south to GR4893 2015 (Windy Top Trail), GR490 1955 (next valley south), GR4955 180 (east-west section of Main Ridge Trail), and GR4955 1705 (Cave Creek Road type section).

Above this in the Cave Creek Road type section, the coarse basal part for the overlying Unit 4 as mapped by Young (1969) corresponds to a sharp bend in the Cave Creek road at GR495 170. Unit 4 is subdivided into 9 fining upward cycles (4a-j), the upper parts of which correspond to the five 'thin zones of low weathering resistance' mapped by Young (1969). These are readily identified on recent air photos in the valleys to the north and south of the Windy Top Trail, designated here as type section for the upper part of the Wee Jasper Formation. The basal conglomerate/pebbly sandstone of Unit 4 (cycle 4a) is about 40-50 m thick, fining up into a poorly outcropping interval of similar thickness, the latter clearly visible on air photos as a continuous less resistant zone from GR4845 224 south to the Windy Top Trail type section. Here it separates the basal conglomerate of Unit 4 at GR489 2015, and the basal coarse beds of the second cycle, encountered at the first bend in the track (GR488 202). This is the lowest of three similar fining upward cycles (4b-d) crossed by the track before a sharp southerly bend at GR4935 202. Each cycle is estimated at about 70 m thick, with the coarse resistant beds comprising more than half the thickness (4b, c), or about half (4d). These three units are well exposed in the next creek to the south, between about GR485194 and 490 196.

On air photos (and 'Google Earth') the E-W sections along the valleys of the three creeks to the north of the Windy Top Trail clearly show the alternating resistant and five recessive beds of Unit 4 as mapped by Young (1969). The undifferentiated upper part of the 'Hatchery Creek Conglomerate' of Young (1969) approximates to the Corradigbee Formation as defined below. The upper part of cycle 4c is the lowest of the five 'less resistant mudstones' mapped by Young (1969), and can be traced to the north at least as far as the vicinity of GR478 222.

The recessive upper part of cycle 4d thickens along strike to the north of the Windy Top Trail, in the vicinity of GR483 205. The overlying four cycles (4e-h) in this valley (the first creek north of the track, between GR490 205 and GR475 206) are seen as narrow ridges separated by less resistant bands of equal or greater width. Most can be traced farther north to the valley section of the creek between GR476 216 and GR487 216, where the resistant bands are thinner and recessive bands correspondingly thicker. The base of cycle 4e is traceable to the south to cross the Windy Top Trail immediately west of the sharp bend at GR483 200. Where the northern creek turns to the north-west at GR476 216 the creek has eroded along the upper recessive bed mapped by Young (1969). This is the upper part of cycle 4f, traceable back to GR481 2005 on the Windy Top Trail. The basal coarse bed of cycle 4g is the lowest of three apparently thicker fining-upward cycles (4g,h,j) along the Windy Top Trail, their finer upper parts forming gullies immediately to the south. However further south between about GR475 194 and GR482 194 these beds are more differentiated, and the less weathered outcrop along the track may be due to relatively recent exposure by removal of the overlying basalt. The uppermost of these units (4j) passes beneath the remnant basalt cap of Windy Top (Fig. 4b).

The correspondence between the uppermost cycle 4j in the Windy Top Trail type section, and Cycle C' of the Corradigbee Formation as mapped in the area farther south by Hunt (2005), is indicated in Figure 2b. Cycle C' is the lowest horizon in which fish remains were found to the south, and in the gully just south of the locked gate at Windy Top some arthrodire fish fragments (ANU V2270) were found at about GR476 200 by G. Young and A. Warren in 1986, the equivalent lowest fish horizon in this section. The interpreted correspondence between the uppermost cycles identified are summarised in Fig. 2. Figure 4b shows a view from the south towards Windy Top, outlining the constituent units representing uppermost cycles of the Wee Jasper Formation, and the lowermost cycles of the Corradigbee Formation.

Lithologies and sedimentary structures

Owen and Wyborn (1979: M314-M320) noted numerous fining-upward conglomeratic cycles in their type section. These varied in thickness from 1 to 20 m, partly due to upper beds in many cycles being truncated by erosion such that one conglomerate rested directly on the conglomerate of the preceding cycle. A complete cycle was described in terms of three lithologies. At the base they described a reddish brown conglomerate, showing scoured contact with the top of the preceding cycle, and including subrounded to rounded pebbles and cobbles of quartzite, quartz, chert, rhyolite and minor granitic rock, with clay clasts and pellets. This was overlain by reddish purple sandstone, usually thin-bedded and flat-bedded, with local foreset cross-bedding (at about 20°). At the top of each cycle an upper red siltstone/mudstone was described, with round whitish mottles, containing root casts which bifurcate downwards, extensively bioturbated in the upper part with bedding sometimes completely destroyed, colour bleached around numerous root casts; and rare wood tissue.

These cycles in turn make up the larger fining-upward units mapped by Young (1969). The lowest Unit 1 was described as 1-2 m thick conglomerates interbedded with coarse lithic arenites for the lower 70 m, fining upwards into interbedded yellow sandstones and red siltstones and mudstones. Unit 2 (thickness ~200 m) and Unit 3 (thickness ~400 m) are similar fining upwards units, the basal conglomerate of the latter exhibiting large scour and fill structures at GY52 (GR499 1935), large scale cross-bedding was recorded in overlying sandstones, and mudcrack polygons in the upper part of Unit 3. Unit 4 (~700 m) is generally finer grained, comprising more resistant intervals 40-100 m thick separated by at least nine thin zones of less resistant material summarised in Figure 2b. In outcrop the more resistant strata are pebbly sandstones up to 3 m thick interbedded with red mudstone of similar thickness, although considerable variation was observed (Young 1969, p. 50). The thin less resistant intervals, where examined at two localities (GY50, 51, GR484 208, 4795 209), are very distinct zones of no outcrop and sparse vegetation about 10 m across, forming well defined saddles on the crest of each ridge, with poor soil of coarse red mudstone gravel presumably derived from a friable red mudstone.

CORRADIGBEE FORMATION (NEW FORMATION)

The change in lithology at about 1500 m recorded by Owen and Wyborn (1979) was described as follows: the conglomerate portion of each cycle becomes less important, contains smaller pebbles, and in places is absent, and the sequence is dominated by fine buff sandstone and red siltstone with root casts. This finer upper part approximates to the upper formation of Edgell's (1949) stratigraphic subdivision, and to the new formation defined here, named after the property (*Corradigbee*; GR64699 61166 on the Wee Jasper 1:25 000 topographic map 8627-4N, 2nd edition) that encompasses much of its outcrop. Previous studies referred to this unit as the 'upper Hatchery Creek Formation' (Young and Gorter 1981; Francis 2003; Hunt 2005), or 'upper beds of the Hatchery Creek Conglomerate' (Owen and Wyborn 1979).

Detailed mapping in the study area of Hunt (2005) revealed at least 18 sedimentary cycles in this finer upper part, of which 15 are assigned to the Corradigbee Formation. The base of its type section (Figs. 1b, 3a) is at locality 063 (GR47598 17285), and the top is at locality 082 (GR46644 18456). The 231.5 m section was measured in three parts, and the composite section is given in Figure 3b.

Lower and upper contacts

The boundary between the Wee Jasper Formation and the overlying Corradigbee Formation is defined at the base of the fourth lowest cycle (Cycle C'). Cycles D' - F' of Hunt (2005) correspond to the upper cycles of the Wee Jasper Formation as described above (Fig. 2). The base of Cycle C' is a fine sandstone, which is a marked sediment change from the basal conglomerates or coarse pebbly sandstones of all lower cycles. This lithological change was observed in the northern part of the field area at locality 068 (GR47793 18228), extending to the north in the gullies immediately south of the Windy Top type section. However, in the southern part of the mapped area of Hunt (2005) the underlying Wee Jasper Formation appears generally less coarse than in the north, although these upper beds were not mapped in detail. Along the access track into *Corradigbee* homestead south of Goodradigbee Hill (Fig. 3a) yellow sandstones predominate, and conspicuous conglomerate or coarse sandstone strata were not seen. The first conglomerates observed were farther to the east (lower in the sequence) along the main road (under the transmission line) in the vicinity of GR475 155. In the vicinity of locality 063 (base of the Corradigbee Formation type section), the formation boundary was identified as a consistent colour change, the underlying sediment (assigned to the Wee Jasper Formation), including coarse grained sandy-mudstone (containing root casts, bioturbation), with a general very light yellowish brown colour. In contrast, the overlying interbedded red and grey mudstones containing fossil fish and plant material (assigned to the Corradigbee Formation) is generally much darker in colour. As a general impression the grey mudstones seem to become darker in cycles towards the middle part of the formation.

The uppermost horizons of the Corradigbee Formation (K–M; see Fig. 4a) are exposed at localities only in the core of the syncline, and only in the southern part of the study area where erosion has been impeded by the basalt cover. Another section was measured on the western limb of the syncline to include these upper cycles (Section 2, Fig. 3b). The uppermost cycle M is inferred from a basal sandstone overlain by about 2 m of mudstone before cover by basalt scree. Thus the estimated thickness of the Corradigbee Formation (260 m) is a minimum estimate, because erosion before the basalt was deposited is unknown.

Subdivision

Owen and Wyborn (1979) recorded at least three grey sandstone – mudstone cycles in the upper fine-grained part of the sequence, said to be less than 30 m thick and of limited lateral extent, each comprising several sedimentary cycles. With more detailed mapping, 15 sedimentary cycles are now identified in the Corradigbee Formation, labelled from the base to the top C′ to M (Fig. 3b), the original 1981 fossil fish locality (WT) being in the third cycle from the defined base of the formation (Cycle A). These cycles are interpreted as cyclothems (i.e. an asymmetrical repetition of sedimentary layers; Weller 1960). They were first identified on air photographs by their basal sandstones, which had a thickness greater than 20 cm. Two part sections were measured (sections 1a, 2, Fig. 3b), and compared with the type section to demonstrate a similar sequence of cycles on both sides of the syncline axis.

Cycle thickness varies, many being 12-15 m thick, with an increase in thickness in the middle part of the formation (Fig. 3b). This indicates either variation in the period of time represented by each cycle, or more likely variation in sediment supply, with the thicker upper cycles reflecting increasing fine over coarse material. These cycles indicate a repetitive sequence of climatic or depositional conditions over the area, presumably representing considerably longer time intervals than annual cycles.

Lithologies and sedimentary structures

Owen and Wyborn (1979) described each fining upwards cycle in terms of three lithologies: i) thin basal medium grey coarse sandstone which contained

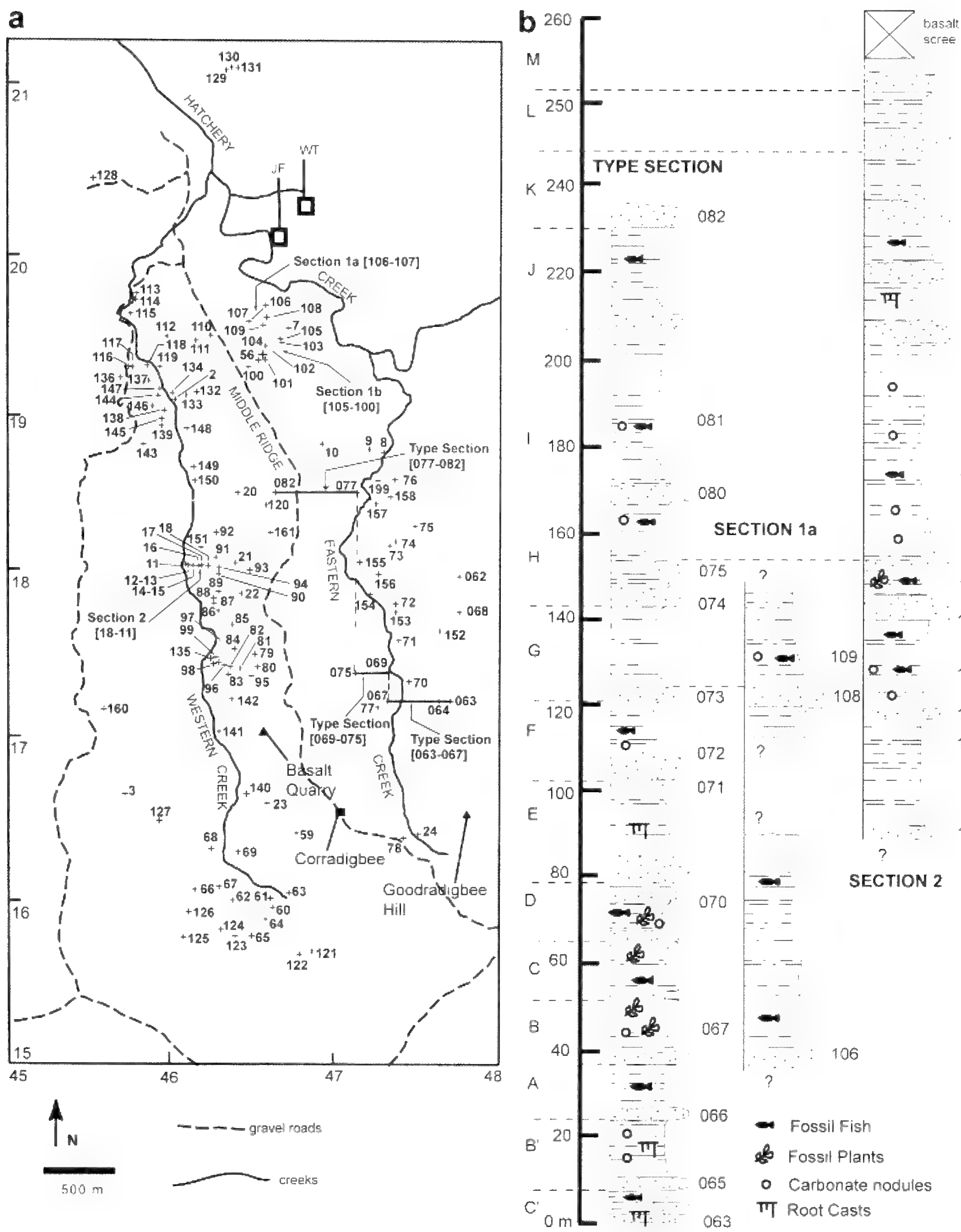
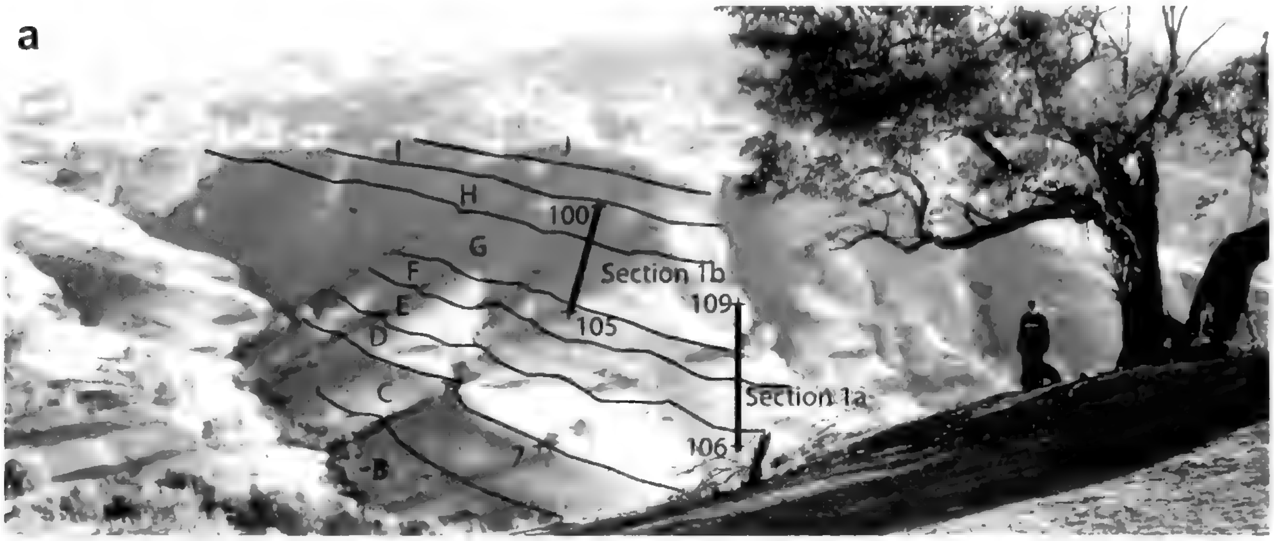


Figure 3. a. Locality map for the study area of the Corradigbee Formation (base map Wee Jasper 1:25000 topographic map 8627-4N [second edition]). Previous fossil localities (JF, WT) and measured sections indicated. For locality details see Appendix. b. Three measured sections through the Corradigbee Formation and suggested correlations. Locality numbers shown on the right of each section.



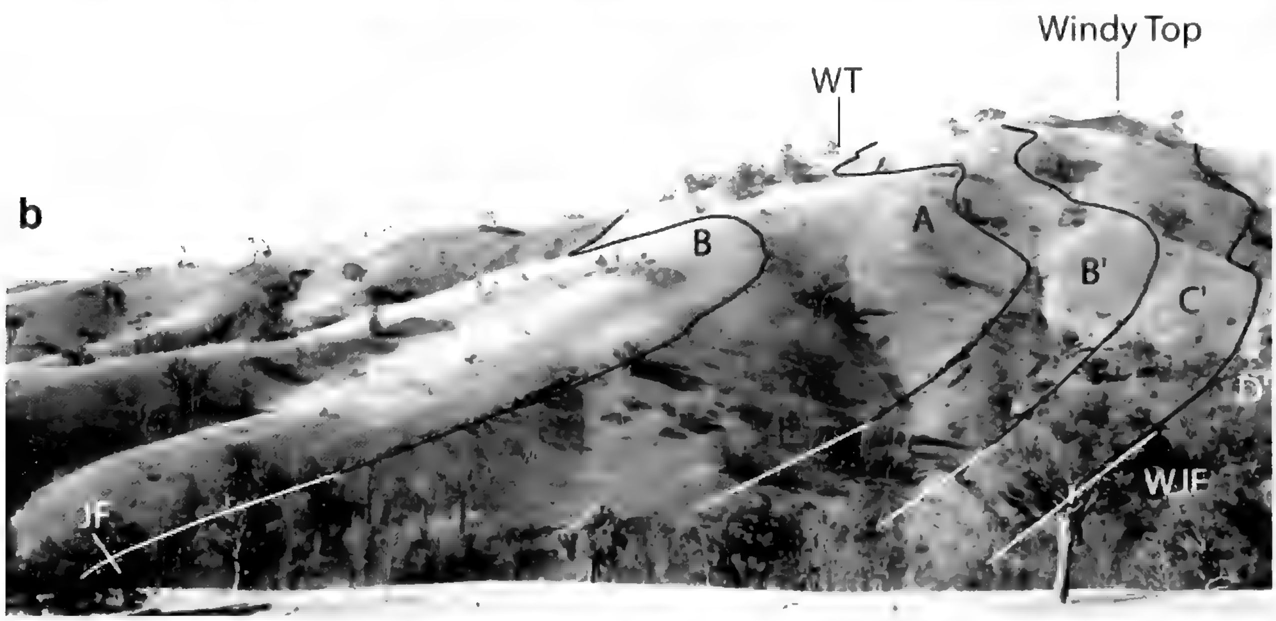


Figure 4. a. View to the southwest from near the original fish locality at Windy Top, showing main cycles of the Corradigbee Formation and position of measured sections. b. View to the north showing the original fish locality (WT) to the west of the basalt cap at Windy Top, in the lower part of Cycle A. The second fossil locality (JF, lower left) is in the upper part of the same cycle. Upper beds of the Wee Jasper Formation (WJF) in the Windy Top type section shown to the right of the figure.

small subangular to subrounded pebbles; ii) thin fine to medium-grained sandstone also including small pebbles, and fish and plant fossils in one of the cycles showing little evidence of abrasion, with fish plates apparently not parallel to bedding, indicating that the sandstone formed as a single bed; iii) an upper dark grey to black massive mudstone up to 2 m thick, containing vascular plant remains, rare fish remains at the base, and grey-white limestone nodules in the upper part, some containing microscopic fish remains, and with mud cracks on upper bedding surfaces.

In the present study, lithologies can be described in more detail for Cycle G of Section 2 as a typical cycle (Fig. 3b). The base at locality 14 is a fine sandstone (grain size <0.3 mm) approximately 3m thick. Above the sandstone six mudstone/siltstone units were identified by variation in colour. The first 3 m thick unit is a grey mudstone containing small carbonate nodules (up to 5 cm diameter), in which no fossils were found. This is overlain by another grey mudstone about 7 m thick, containing both fossil fish fragments and calcareous nodules. Above this is a 3 m orange mudstone layer, overlain by 1.5 m of dark red mudstone, both lacking fossil material, followed by a 5 m thick light grey mudstone producing osteolepid and arthrodire fish material at locality 17. Above this, another grey mudstone layer about 4.5 m thick contains large plant material (stems up to 30

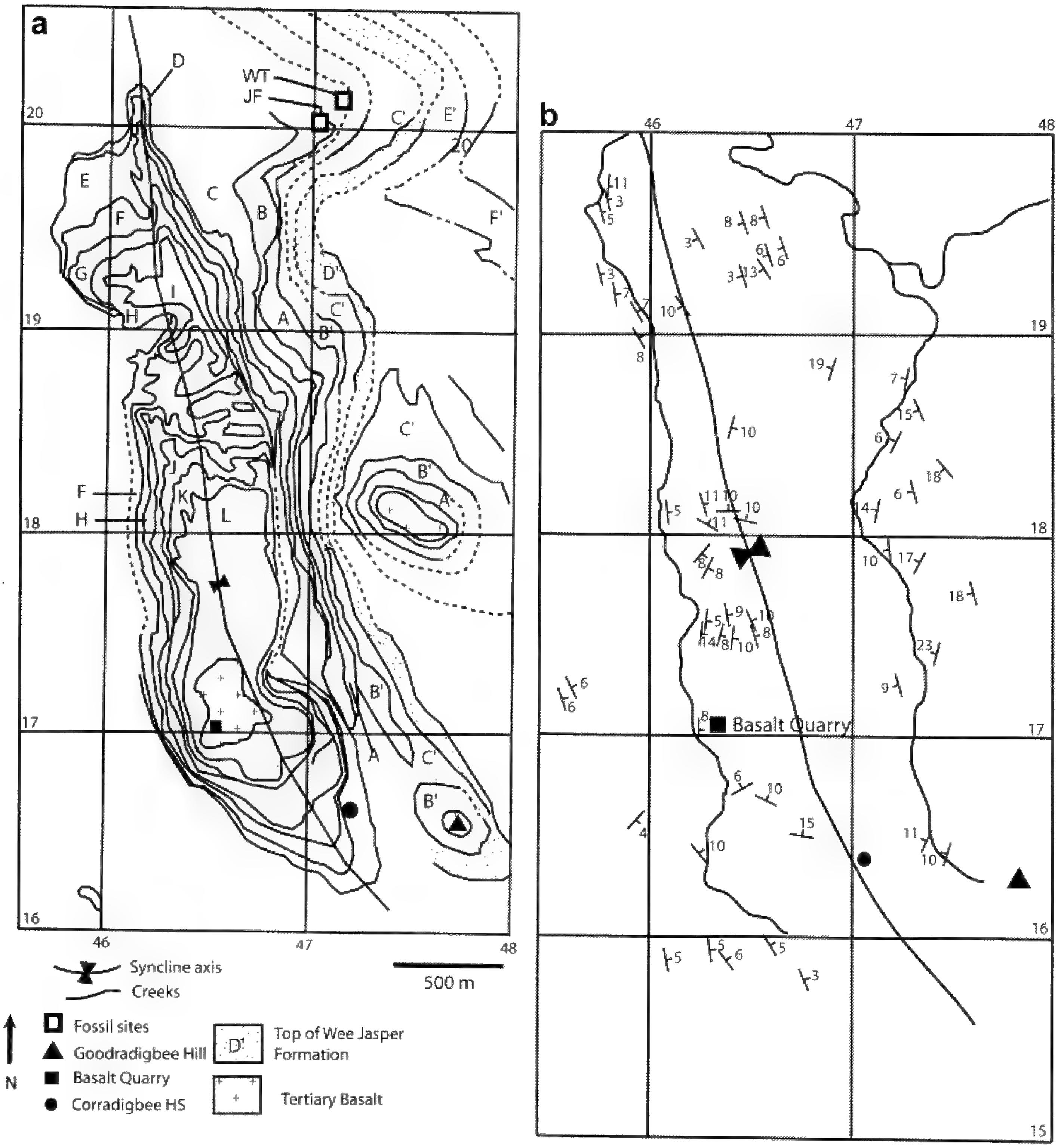


Figure 5. a. Outcrop map for the study area of the Corradigbee Formation. Cycles represented as alternating shaded and clear units to indicate outcrop pattern. b. Measured dips and strikes in relation to the syncline axis identified in this study.

cm in length) at the base, with fossil fish material and scattered plants above. The next sandstone layer marks the start of cycle H in this section (but correlated only approximately with an additional sandstone in cycle H of the type section).

Conglomerate

Conglomerates are very rare in the Corradigbee Formation. One thin (~ 8 cm) bed of pebbly red conglomerate was observed at locality 70 (near the middle of Cycle C). This contained small quartz pebbles, mudclasts, and mudballs generally less than 10 mm diameter, with generally rounded quartz pebbles and grains, although some of the smaller grains (<0.5 mm) were subangular. No fish fossils were observed in the conglomerate bed, but these occur immediately below in the mudstones (e.g. ANU V3171). Another thin (up to ~5 cm) bed of grey conglomerate was seen in erosion gullies at localities 98 and 138 (both probably in Cycle F), with quartz pebbles up to 20 mm diameter, and much fragmented fossil fish material giving the grey colour.

Sandstone

The sandstone layers at the base of each cycle vary in thickness, over 3 m thick in cycle F (Fig. 3b), but most are about 1.5 m thick. Sandstones within the cycles vary in the size of the sand grains but grain size is uniform within the bed itself. Grain size ranged from around <0.2 mm in each layer of sandstone, with some beds being finer than others. None of the sandstones in the formation were noted to be very coarse grained. Good exposures of the basal sandstones observed at localities 11, 14, 64, and 154 showed no cross-bedding, scour marks, mudclasts or other evidence of a river deposit. At only one locality (108, Cycle D) was some cross-bedding observed. Fish material found in the sandstones was disarticulated and fragmented (identified at only three localities 134, 138, JF).

Siltstone/Mudstone

Siltstones and mudstones in the formation vary in colour, from predominantly grey-black, to less common orange, red, dark purple and light grey lithologies. These colours are identified as primary on the evidence that the colour terminated with the bedding plane. In general, the red-purple colour phases are assumed to have formed in well-drained conditions, and the grey-black mudstones to indicate poorly drained swampy conditions.

Sedimentary structures

In the mudstones of the Corradigbee Formation calcareous nodules (up to 5 cm diameter) are abundant at many levels (common at localities 62, 97, 109, 128, 137 and 158, but noted at many other localities). They occur in both the red-purple and grey-black colour variations (largest examples were seen at locality 158, in Cycle B). In the Devonian Aztec Siltstone of Antarctica, common calcareous nodules were taken to indicate lengthy subaerial exposure (4,000-10,000 years) for pedogenic processes to operate (McPherson 1979). The same can be assumed here, except that the nodules are equally common in the red-purple and grey-black colour phases, the latter representing poorly drained swampy conditions, which would preclude pedogenesis. Cubic pyrite crystals were identified near fossil locality 161 (ANU 46692), consistent with the idea that the black mudstones formed under stagnant, anaerobic conditions.

Although laminar bedding was reported by Young and Gorter (1981) and Francis (2003) to indicate lacustrine conditions, only one occurrence of laminar bedding was observed in this study, in grey green mudstones at locality 24. Ripple marks were identified at localities 129, 130 and 131. Rather than lake deposits, the sedimentary structures indicate predominantly swampy conditions for the Corradigbee Formation, the whole Hatchery Creek sequence being interpreted as a humid alluvial fan.

Root casts were noted at various levels in the red and dark purple mudstones (Fig. 3b), in these cases indicating sub-aerial exposure and soil formation as do associated calcareous nodules. Apart from rain drop impressions at locality 80, no other dessication structures or mud crack horizons were observed in this study.

STRUCTURE

Young (1969) recorded measurements from the western side of the Goodradigbee valley indicating a fairly consistent dip in the limestones and overlying Hatchery Creek sequence, averaging 40° west with a strike of about 338°. A plot of bedding/axial plane cleavage intersections indicated a fold axis plunging 20-30° to the NW (315°). The uppermost limestone beds forming the contact with the northernmost exposure of the Hatchery Creek Conglomerate along the edge of Burrinjuck Dam (on the Yass 100K sheet) swing round a northern synclinal closure which limited data suggested plunged about 35° to the southwest (250°).

Owen and Wyborn (1979) showed only one anomalous easterly dip on the Brindabella 1:100 000 geological map for the upper part of the Hatchery Creek Conglomerate, interpreting the entire sequence as dipping to the west, the basis for their estimated 2.9 km total thickness. They suggested renewed uplift in the source area to explain a return to coarse conglomeratic cycles at the top of the sequence, but this can now be discounted (see above).

Their published cross sections (on the 1979 geological map) show the Hatchery Creek Conglomerate as a thick westerly-dipping section across the middle part of its outcrop (section A-B), and tightly folded in the southeastern extremity of the outcrop, with a steep to overturned western limb against the Long Plain Fault Zone (section E-F). Wyborn (1977) attributed this to thrusting of the rigid Goobarragandra Block over the Hatchery Creek Conglomerate, and no fold axis was indicated on the geological map. However, Edgell (1949) and Pedder et al. (1970) had previously shown a syncline axis running to the northwest towards the central part of our Corradigbee Formation. This structure, named the Wee Jasper Syncline by Hood and Durney (2002), runs through the area mapped in detail by Hunt (2005). New dip and strike measurements were recorded from 69 localities in and around the area of detailed mapping (see Appendix), and on both sides of the syncline axis, which was identified in the mapped area running through locality 21 and under the basalt cap of the central ridge (Fig. 1b), which is somewhat further to the west than the extrapolated position shown by Hood and Durney (2002, fig. 1). On the western side of the axis only easterly dips were measured, conforming to the one anomalous easterly dip of Owen and Wyborn's map, and in the same area Edgell's (1949) map shows 10° and 13° easterly dips. However, all measured dips were on the eastern side of the Western creek (representative measurements shown on Fig. 5b). We assume that the westerly dips previously shown on the Brindabella 1:100 000 geological sheet for the upper part of Corradigbee Formation outcrop must have been based on cleavage masking the bedding.

SUMMARY

Type sections are proposed for a new Corradigbee Formation, representing the upper fine-grained part of the Hatchery Creek sequence, comprising about 15 fining-upward cycles of sandstones, dark shales and mudstones in which 50 new fossil sites have been found.

The lower coarse-grained part of the Hatchery Creek sequence is renamed the Wee Jasper Formation, within a revised Hatchery Creek Group (total thickness about 1760 m). Thickness of the Wee Jasper Formation is estimated at about 1500 m, it is subdivided into four main fining upward cycles, and an additional type section is nominated for the upper part of the formation.

The Hatchery Creek Group is conformable on Lower Devonian limestones of the Murrumbidgee Group, thickness variations in the upper tidal flat deposits of the carbonate sequence being interpreted as depositional features.

Sedimentary structures indicate predominantly swampy rather than lacustrine conditions for the upper Corradigbee Formation, the whole Hatchery Creek sequence being interpreted as a humid alluvial fan.

The axis of a major syncline was identified, with previously unrecognised repetition of the lower coarse strata in the western part of the outcrop area resulting in a considerable over-estimate of total thickness in published literature. The relatively high topography of the softer shales and mudstones in the core of the syncline is a relatively transient topography resulting from recently eroded Tertiary basalts.

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APPENDIX

Abbreviations:
f = fish, p = plants, n =nodules, a = arthropods, r= root casts.
b = bioturbation, g = gastropods, impr = rain drop impressions.
x = cross bedding, lam = laminar bedding

2005 Localities	GRID REFERENCE	Horizon	Dip/Strike	Fossils and Structures
1	55 H 645457 6117228		6°E/345°	f
2	55 H 646000 6119045	G		
3	55 H 645626 6116656	F		p
4	55 H 646151 6118053			f
5	55 H 646519 6119415			f
6	55 H 646535 6119428		13°W/106°	f.p
7	55 H 646646 6119620	C		f
8	55 H 647280 6118881	D'	7°W/25°	x
9	55 H 647194 6118825	C'		
10	55 H 646906 6118728	B	19°W/10°	
11	55 H 646062 6118133		5°E/345°	
12	55 H 646093 6118127	F		
13	55 H 646125 6118108	F		
14	55 H 646121 6118105	G		
15	55 H 646154 6118073	G		f
16	55 H 646149 6118087	G		
17	55 H 646170 6118087	H		f.p.n
18	55 H 646179 6118060	H		f
19	55 H 646542 6118600	H		
20	55 H 646426 6118514	H	10E°/295°	
21	55 H 646418 6118061	K	10N/310°	
22	55 H 646455 6117973	L		
23	55 H 646600 6116644	D		p
24	55 H 647449 6116390	C	10°N/285°	f. lam
59	55 H 646709 6116402	E	15°N/95°	f
60	55 H 646585 6115979	E		p
61	55 H 646570 6116005	E		f
62	55 H 646552 6116007	E		n
63	55 H 646655 6116134	E		p
64	55 H 646543 6115914	E	5°E/120°	
65	55 H 646450 6115880	G		p
66	55 H 646199 6116092	E		
67	55 H 646261 6116124	E		
68	55 H 646237 6116362	E	10°E/120°	
69	55 H 646517 6116499	E		f
70	55 H 647411 6117304	C'	23°W/5°	f
71	55 H 647306 6117767	B'		r
72	55 H 647331 6117878	B'	17°W/210°	
73	55 H 647310 6118258	B	6°W/138°	
74	55 H 647373 6118281	D		p

75	55 H 647458 6118317	D	18°W/135°	r.b
76	55 H 647754 6117945	B	15°W/130°	
77	55 H 647465 6116410	A	9°W/148°	
78	55 H 647452 6116390	B	11°W/65°	
79	55 H 646479 6117559	M		f
80	55 H 646475 6117509	M	8°W/345°	f. impr
81	55 H 646432 6117481	L	10°E/185°	f
82	55 H 646408 6117475	J		f
83	55 H 646410 6117566	J	8°E/15°	
84	55 H 646404 6117569	J	9°E/140	f
85	55 H 646309 6117780	L		
86	55 H 646280 6117839	J	8°E/30	f
87	55 H 646238 6117838	L	8°E/30	f
88	55 H 646226 6117873	J		f
89	55 H 646218 6117934	J	8°E/50°	f
90	55 H 646224 6118003	J	11°N/70°	f
91	55 H 646235 6118092	J	11°E/180	f.a
92	55 H 646250 6118240	I		f
93	55 H 646422 6118054	I	10°N/110°	
94	55 H 646398 6118027	J	8°E/120°	
95	55 H 646433 6117488	L		
96	55 H 646342 6117551	I		p
97	55 H 646316 6117507	H		f
98	55 H 646279 6117544	I	14°E/310°	f
99	55 H 646207 6117646	G	5°E/310°	
100	55 H 646489 6119386	H	3°W/325°	f
101	55 H 646505 6119399	F		f
102	55 H 646506 6119407	E		f
103	55 H 646522 6119419	D	6°W/315°	f
104	55 H 646544 6119454	E		
105	55 H 646572 6119474	D	6°W/335°	f
106	55 H 646509 6119660	D		f.p
107	55 H 646487 6119618	D	8°W/335°	
108	55 H 646382 6119535	D	8°W/340°	p
109	55 H 646368 6119522	D		f.n
110	55 H 646218 6119567	H	3°W/310°	
111	55 H 646118 6119555	J		
112	55 H 645876 6119708	H		
113	55 H 645773 6119735	D	11°E/45°	
114	55 H 645727 6119736	D	3°E/325°	
115	55 H 645738 6119686	D	5°E/345°	
116	55 H 645779 6119398	C		
117	55 H 645788 6119395	C	3°E/335°	
118	55 H 645824 6119392	H		f
119	55 H 645914 6119367	J		
120	55 H 646583 6118459	I		f
121	55 H 646753 6115769	H		p
122	55 H 646740 6115768	G	3°E/330°	
123	55 H 646371 6115865	G	6°E/335°	
124	55 H 646453 6115883	E	5°E/356°	p

125	55 H 646090 6115893	E	5°E/355°	n
126	55 H 646011 6115953	F		
127	55 H 645950 6116511	G	4°E/30°	
128	55 H 645483 6120425	.	6°E/350°	n.b
129	55 H 646315 6121384	.	11°W/330°	b
130	55 H 646380 6121374	.	20°W/345°	b
131	55 H 646394 6121386	.	34°W/350°	b
132	55 H 646141 6119126	I		n
133	55 H 646036 6119138	F	10°E/335°	
134	55 H 645968 6119128	F		f
135	55 H 646244 6117558			f
136	55 H 645697 6119296	G		n
137	55 H 645734 6119219	G	7°E/350°	n
138	55 H 645965 6119015	F	8°E/315°	f
139	55 H 645848 6118845	F	6°E/310°	f.p
140	55 H 646434 6116715		6°E/40°	
141	55 H 646297 6117036	H	8°E/315°	f
142	55 H 646318 6117284			f
143	55 H 645979 6118978	H		f
144	55 H 645936 6119145	F	7°E/320°	f
145	55 H 645938 6119144	F		f
146	55 H 645947 6119148	F		f
147	55 H 645923 6119179	F		
148	55 H 646075 6118902	F		
149	55 H 646113 6118668	F		f
150	55 H 646115 6118654	H		p
151	55 H 646172 6118227	G		
152	55 H 647697 6117736	B'	18°W/350°	
153	55 H 647329 6117876	B'	10°W/310°	
154	55 H 647197 6117955	A	10°W/345°	n
155	55 H 647126 6118159	B	14°W/10°	
156	55 H 647090 6118284	D		p
157	55 H 647262 6118401	B	6°W/35°	
158	55 H 647375 6118448	B		n
159	55 H 647245 6116898	B		p

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2007/08 Localities	GRID REFERENCE	Horizon	Dip/Strike	Fossils and Structures
160	55 H 645457 6117228		6°E/345°	
161	55 H 646597 6118044	I		
062	55 H 647714 6118047	C'		p.g
063	55 H 647598 6117285	C'		
064	55 H 647328 6117162	C'	11°W/320°	b
065	55 H 647280 6117140	C'		b
066		A	14°W/352°	
067	55 H 647188 6117113	B		n
068	55 H 647793 6118228	C		
069	55 H 647766 6118251	B		f.p
070	55 H 647173 6117114	D		p.n.b
071	55 H 647155 6117111	E	14°W/320°	f
072	55 H 647114 6117413	F		
073	55 H 646093 6117410	G	6°W/340°	n
074	55 H 647073 6117404	H		
075	55 H 647068 6117404	H		
076	55 H 647031 6117389	H		
077	55 H 647006 6118570	H		
078	55 H 646982 6118563	H	14°W/40°	
079	55 H 646946 6118572	H		
080	55 H 646905 6118579	I	14°W/350°	
081	55 H 646851 6118549	J		f
082	55 H 646644 6118456	K		

Reproductive Phenology of White Box (*Eucalyptus albens* Benth.) in the Southern Portion of its Range: 1997 to 2007

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The abundance of reproductive structures (buds, flowers and capsules) in individual *Eucalyptus albens* trees at four sites was monitored for up to 11 years. Average abundance values for a stand of trees often masked individual differences, e.g. abundant budding (a surrogate for flowering) in consecutive years was never recorded in a stand but it was common in individuals. On average, floral buds appeared in November and flowers were produced between March and November the following year but some trees produced buds as early as March, and in others flowering extended to January. Though summer-flowering was uncommon in this study, some observations from the 1970-80s reported a flowering period of, for example, January to June, suggesting that flowering is now later. Except for peak flowering years, e.g. at three sites in 2006, when virtually all trees flowered, flowering was individualistic suggesting that previous rainfall was not the sole driver. Correlations between bud abundance and previous rainfall suggested that individual trees, or groups of trees, responded to different rainfall events. For example, budding in some trees at all sites (particularly those in the two northern-most sites) was positively correlated with winter rainfall three years previously whereas at the most southerly site, budding in many of the trees was correlated with autumn rainfall four years previously. Such variability may be genetically determined and have positive benefits for seedling recruitment in a variable climate such as Australia's.

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KEY WORDS: capsules, *Eucalyptus albens*, floral buds, flowers, rainfall, seedling recruitment, variability

"*All around Sydney, and particularly in our bushland suburbs, the Angophora costata (Sydney Red Gum) are in exceptionally heavy flower. So heavy that the white honey scented blossoms weigh the branches down to give the trees an uncharacteristic domed shape. Why are they busily preparing for such a profusion of seeds to drop this year? What do they know that we don't?*"
Letter to the editor, *Sydney Morning Herald*, 27 November 2006

INTRODUCTION

Woodlands dominated or co-dominated by white box (*Eucalyptus albens*) once extended almost continuously from southern Queensland, along the inland slopes of New South Wales (NSW) into north central Victoria with outliers in the Snowy River area, western Victoria and the Southern Flinders Ranges of South Australia. The woodlands occur on several soil types that, at least for those with a grassy understorey, are relatively fertile and are now used for wheat-growing (Beadle 1981). Consequently the woodlands now occupy a lesser area than they once did. Nevertheless *E. albens* trees are still relatively common across their range and contribute to the aesthetics of the roadsides and farmlands where they occur. However, intact grassy woodlands, i.e. those with relatively undisturbed overstorey and groundstorey, are rare and poorly conserved in the formal reserve system (Prober 1996). They are listed nationally as an endangered ecological community under the *Environment Protection and Biodiversity Conservation Act 1999*.

Natural recruitment of seedlings of *E. albens* is uncommon, at least in the southern part of its range, and has been attributed (Semple and Koen 1997, 2003) to the seedling's inability to compete with exotic species that are now dominant in many groundstoreys of these woodlands. Exotic dominance is probably due to enhanced soil fertility, particularly nitrogen (Prober et al. 2002) and/or phosphorus (Allcock 2002). Other potential limitations to successful seedling recruitment include: reduced seed quantity and quality produced by isolated trees in cleared environments (Burrows 1995), the unlikely coincidence of suitable rainfall for both germination and survival, browsing of seedlings by wingless grasshoppers and domestic and feral animals, minimal seed reserves in the soil due to predation by ants and ready germination of non-dormant seed following rainfall events. A consequence of the last-mentioned is a reliance on an aerial seedbank from which seed is shed intermittently (Semple et al. 2007).

The amount and occurrence of seed fall is primarily determined by a range of prior factors that affect the production of buds and in turn, flowers and fruits. In the case of eucalypts, the inflorescence commences as a bud that differentiates into a cluster of 'bud initials' ('inflorescence buds') that are enclosed by a cap of fused bracts. After the cap is torn and shed, buds develop through 'pin', 'cylindrical' and 'plump' stages until anthesis (Boland et al. 1980). Each bud consists of a basal hypanthium, in which the ovary is wholly or partially embedded, and the calyptera (operculum), which encloses the stamens. In species of the *Symphomyrtus* sub-genus, the operculum is double-layered and the outer calyptra is shed early or, as in the case of *E. albens*, fuses with the inner, which is shed at anthesis (Hill 1991). Following pollination (by insects, birds, small mammals) and fertilization of ovules, seed and fruit development commences. Fruits (capsules) expand, change colour from 'green' to 'brown' and become increasingly woody. Dehiscence is initiated by twig death or the formation of an abscission layer that cuts off the sap flow to the capsules. Fertilised ovules are shed as seed and unfertilised ones (the majority) and ovulodes as 'chaff'.

In an earlier study of *E. albens* trees near Cowra, NSW, Semple et al. (2007) reported that seed fall was highly variable between trees as was the occurrence and abundance of flowers. Moderately abundant flowering occurred every second year on average and appeared, at least in the period 1996 to 1999, to be associated with above-average rainfall in winter and spring the previous year. Whether biennial flowering was usual or whether it was associated solely with previous above-average rainfall could not be determined from data that was limited to scattered paddock trees at one site and only four years of observations.

The study reported below formed a component of a broader study investigating the role of various factors (seedbed, rainfall, seed fall, etc.) in the seedling recruitment of woodland eucalypts. It aimed to (a) document the seasonality, frequency and abundance of floral buds, flowers and capsules in individual trees within stands that were distributed across the southern range of *E. albens*; and (b) examine the relationship between rainfall and the production of floral buds over a longer period than was the case at Cowra.

METHODS

Site selection

The basic requirements were for stands containing at least 12 trees of variable size, as indicated by diameter at breast height (DBH), that were readily (and safely) accessible. The latter was satisfied by occurrences beside roads that were travelled regularly in the course of normal business or recreation. Small trees that were unlikely to flower were ignored but these were only evident at one site (Molong). An additional requirement was that stands were distributed relatively evenly across the southern distribution of the species, viz. from central western NSW to north-eastern Victoria. There were no requirements with respect to aspect, altitude or condition of the stand though those with unhealthy, e.g. dieback-affected, trees were avoided. Four sites, located to the north and south of the earlier study site near Cowra, were selected (Fig. 1). All stands were parts of 'corridor communities' (e.g. Fig. 2) except at Molong where the stand extended into the adjacent paddock. None was located near a supplementary source of water, such as a dam or watercourse, and spatially variable run-on (with associated nutrients) from the roadside or adjacent land appeared unlikely. An unintended consequence of the selection procedure was that as latitude increased, altitude and mean annual rainfall generally decreased (Table 1).

Monitoring

Trees were observed with binoculars by the same observer [WS] at regular intervals – ideally monthly during bud formation and flowering (usually mid/late autumn to late spring, when new floral buds also become evident). At each observation the abundance

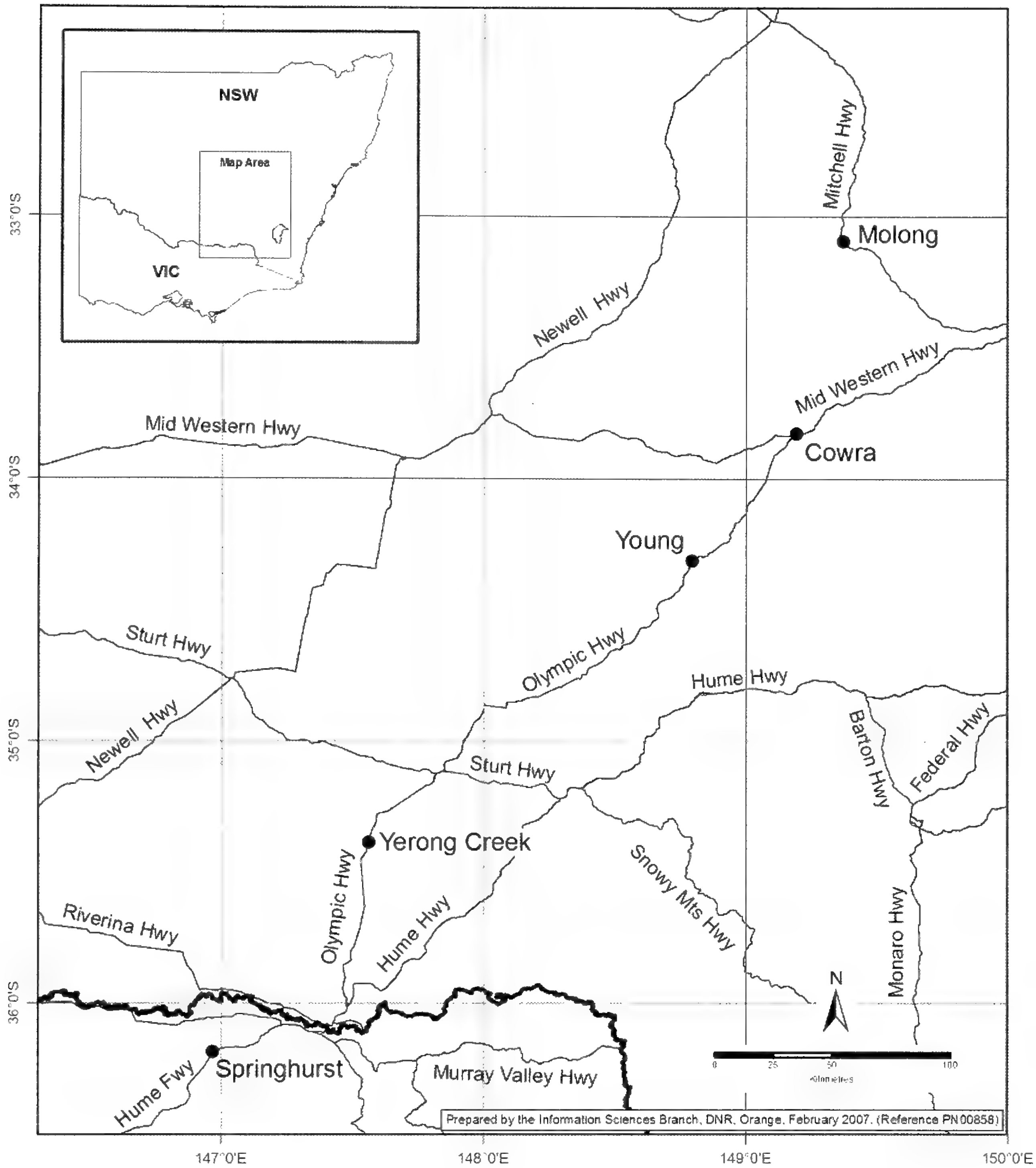

Figure 1. Location of towns nearest the four *E. albens* sites in the present study and an earlier one near Cowra.

of reproductive structures across the canopy of each tree was assessed on a 6-point integer scale: 0 (none), 1 (one to very few), 2 (scattered or a few small clumps), 3 (obvious and dispersed across most of the canopy), 4 (very abundant), 5 (maximum possible). Structures assessed were: pin buds, buds ('cylindrical' and 'plump' stages were not distinguished), flowers (up to withering of anthers) and capsules (= all post-flowering structures with no distinction made between fruits at different stages of maturity). Initial attempts at assessing 'inflorescence buds' were abandoned as they could not be distinguished reliably from the vegetative buds that were produced each autumn and spring with the latter period often coinciding with the presence of inflorescence buds. Observations were less frequent over summer and also during periods when bud production was nil or minimal (and hence, flowering was unlikely to occur). Inevitably over a monitoring period of up to 10 years, there were periods when bud and/or flower activity were missed.

Figure 2. A typical roadside stand of *E. albens*. The monitored stand at Yerong Creek in November 2006 [photo 245/6].

Table 1. Brief details on the monitored roadside stands of *Eucalyptus albens* listed in order from north to south.

Stand name	Locality and latitude	Tree nos. at start (end [A])	DBH [B] (m): mean and range	Altitude (m a.s.l.)	Mean annual rainfall (mm)	Period of regular monitoring [C]
Molong	6 km SW of Molong 33° 7′ 12″ S	13 (12)	0.62 (0.11–1.53)	600	700	Mar. 2000 – Nov. 2006
Young	Rest area, 7.2 km N of Young 34° 17′ 12″ S	12 (11)	0.67 (0.41–1.15)	550	650	July 1997 – Nov. 2006
Yerong Creek	3.6 km S of Yerong Creek 35° 25′ 00″ S	19 (18)	0.52 (0.14– 0.99)	230	530	Jan. 1997 – Nov. 2006
Springhurst	Rest area, 6 km S of Springhurst 36° 14′ 30″ S	19 (18)	0.54 (0.18– 2.08)	180	610	Dec. 1996 – Nov. 2006

A Tree decline was due to deliberate removal associated with roadworks (Molong and Springhurst), ringbarking (Young shortly after observations commenced) and tree fall (Yerong Creek).
B Diameters of any multi-trunked trees have been summed.
C All stands were revisited in early 2007 to assess the size of the 2007 bud crop though Molong observations were ignored because of the confounding effects of a wildfire in November 2006.

Regular monitoring ceased in November 2006 though the bud crop for 2007 was assessed on number of occasions at all sites except at Molong where most of the trees were severely burnt in November 2006 [though monitoring at this site was maintained so as to document the effects of fire on the trees and the groundstorey (see Semple and Koen 2008)].

Data analysis and presentation

Data for all types of floral bud have been amalgamated for presentation purposes. Where trees were not observed as frequently as desired (i.e. missing monthly observations), the abundance of reproductive structures has been interpolated when little change was known to have occurred. However, where new structures appeared between these extended observation periods, the periods of unobserved activity have been shown as 'missing data' on graphs of abundance of structures.

Averaging the abundance ratings of flowers across all trees at a site at each time of observation was misleading because individual trees flowered over varying periods of time (or failed to flower at all) and times of maximum flower abundance in individual trees did not always coincide. Hence, average values across the flowering season implied lower abundance than was the case. Conversely, floral buds usually developed synchronously in trees; and averages of maximum values prior to flowering provided an indicator of potential flowering in a stand in any one season. Bud abundance has generally been used as a surrogate for overall flower abundance in the analyses presented here.

The suggestion that larger/older eucalypts flower more frequently and heavily than smaller ones (various authors cited by House 1997) was examined via correlations between DBH and the frequency of abundant budding (abundance rating ≥ 3) of trees at each site. Two sets of DBH values were used – averaged and summed DBHs for multi-trunked trees.

Associations between rainfall and bud abundance were examined for each site and for each tree. The interpolated monthly rainfall (Jeffrey et al. 2001) at each site was summed in various periods: calendar year, warm (September to February of following year) and cool (March to August) season, and actual season (autumn, winter, etc) for each year of data, 1986 to 2006. Linear correlations were calculated between each of these rainfall periods and the maximum bud abundance (usually in summer each year) for (a) each site (mean values), and (b) for each tree.

RESULTS

Abundance of buds and flowers in stands

Average abundance ratings for floral buds and flowers over time at the four sites are presented in Fig. 3. Low abundance ratings (<3) generally indicated very low numbers of structures and can largely be ignored – apart from cases of flowering at low levels over an extended period. The occurrence of abundant budding (mean rating of ≥ 3) was uncommon at most sites: three in seven years at Molong, three in nine years (ignoring incomplete data for 1997) at Young, two in 10 years at Yerong Creek and Springhurst. Between these abundant budding years, at least some of the trees produced buds and flowers, sometimes at very low levels, except at Springhurst in 1997, 1998, 2000 and 2001 when no buds or flowers were observed (though very low level budding and flowering may have been missed).

Periods of abundant budding tended to occur every second or third year but were less frequent at Springhurst. Some stands budded abundantly in the same years (e.g. 2001 and 2006) but the sequence of budding in the two southerly stands, particularly at Springhurst, was usually different from those in the north. Years of high average bud abundance were followed by at least one year of low abundance. Abundant budding levels in each stand were positively associated with the proportion of trees producing abundant buds in that year (compare Figs. 3 and 4).

Times of bud formation and flowering in stands

Pin buds were usually evident between October and December. Buds were at a maximum by early summer and abundance ratings rarely declined prior to the commencement of flowering.

During peak flowering periods when most trees flowered abundantly, flowering in some trees was usually evident in March (though as early as February in some trees at Young in 2003; Fig. 5a) with the latest commencing in June or July. Flowering was usually complete in all trees by October or November. Some trees flowered for a long period between March and November but most trees flowered for only a few months. In non-peak flowering years when only some trees flowered, some trees, usually those with very few buds, did not commence flowering until August or September.

Some of the Molong trees did not follow these trends. For example, the main flowering period for tree M194 in 2003 was from November to January 2004. Some trees produced pin buds very early in the season: two trees (M181 and M192) during March/August 2000 and one tree (M181 again) in May 2002;

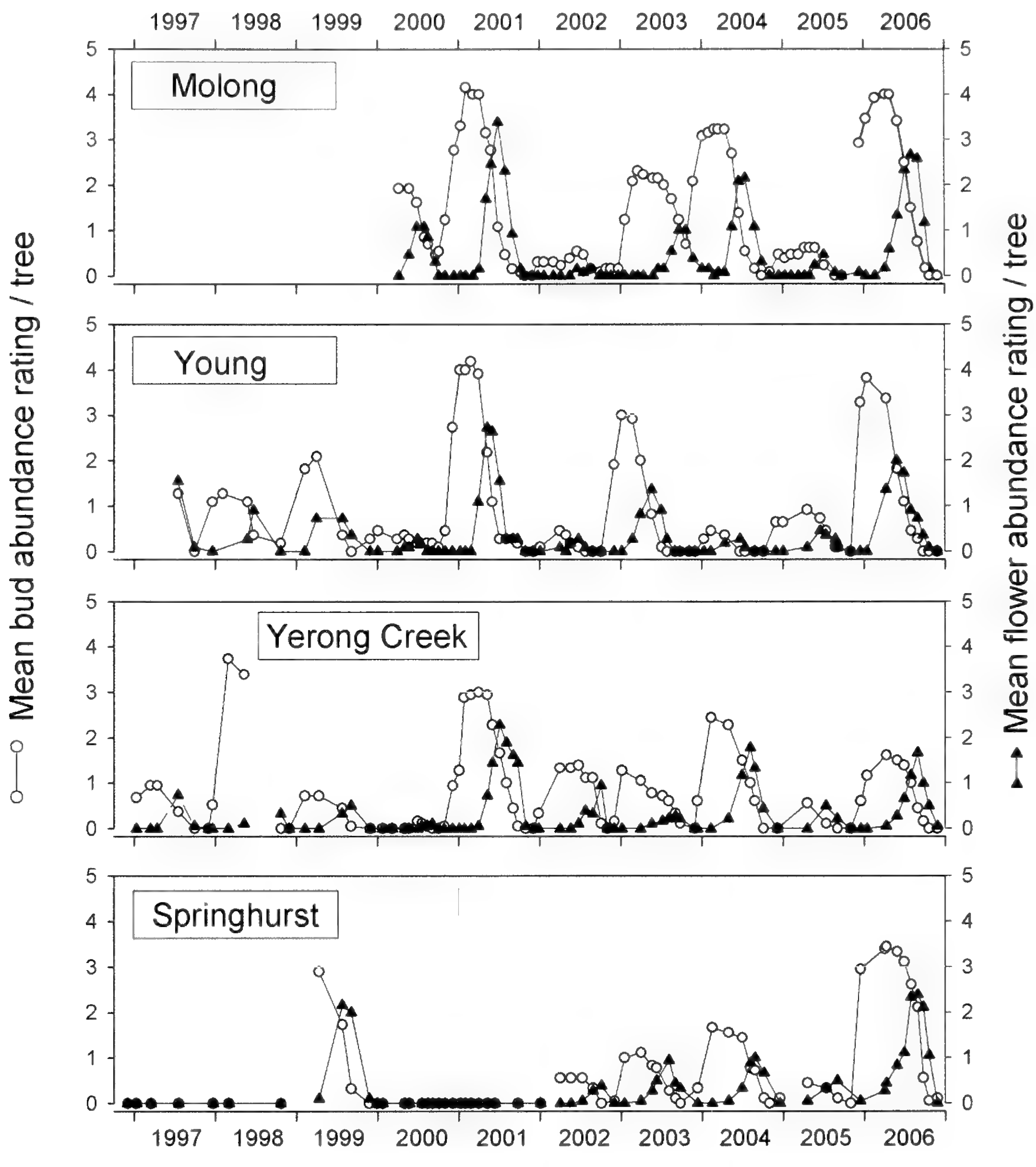

Figure 3. Mean abundance ratings (0-5) for floral buds (o) and flowers (▲) over varying periods of times at four stands of *E. albens*. Sites are presented in order from north to south. Periods of missing data have generally been smoothed over except when bud initiation, or a major flowering event (i.e. Yerong Creek in 1998), were missed.

but these buds matured slowly and were eventually indistinguishable from buds produced at the normal time (~November). Small quantities of early pin buds were also produced by a few other trees at Molong, and one at Young, but they apparently failed to develop. Unusually, a small number of buds that became evident in October/November at Molong produced flowers in November/January. This occurred at trees M177, M192 and M181 in 2003, 2004 and 2005 respectively (Fig. 5b)

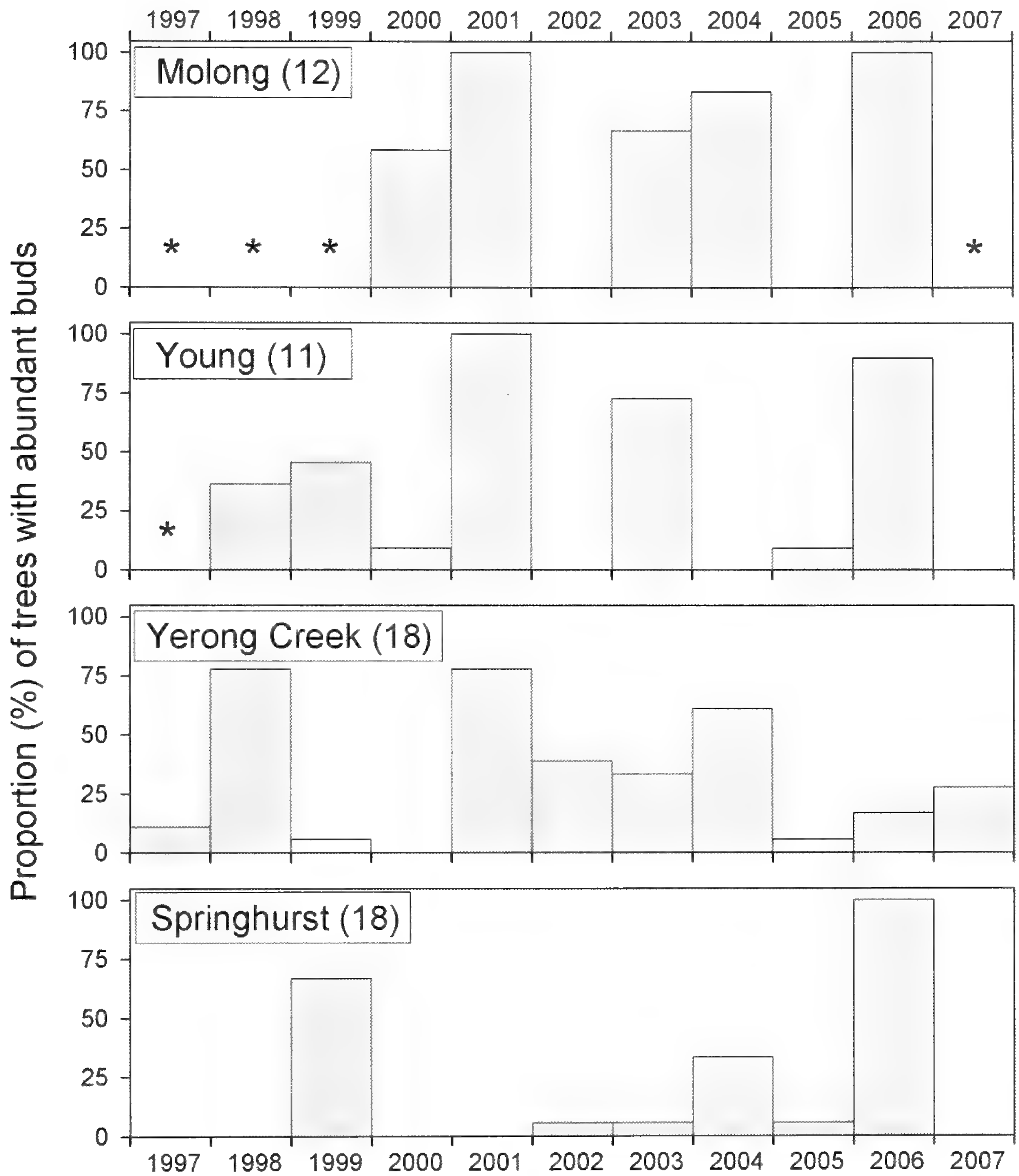

Figure 4. Proportion (%) of trees in each stand that produced abundant (rating ≥ 3) floral buds in any one year. * = nil or incomplete data. Numbers of trees monitored for the full period at each site are shown in parentheses. Bud abundance in 2007 was determined from a few strategically-timed observations.

Budding and flowering of individual trees within stands

Frequency, abundance and duration of flowering varied between trees at all sites, particularly in years when flowers were not abundant. Space prohibits the presentation of all data. Young and Molong are presented as examples in Figs. 5a and 5b. During the 'big' budding/flowering years at Molong (2001, 2004, 2006 and to a lesser extent 2003), Young (2001, 2003 and 2006), Yerong Creek (1998 – presumably as the main flowering period was missed, 2001 and to a lesser extent 2004) and Springhurst (1999 and 2006), all trees flowered – except for one or two trees at Springhurst in 1999 and Yerong Creek in 2004 – though with varying levels of intensity.

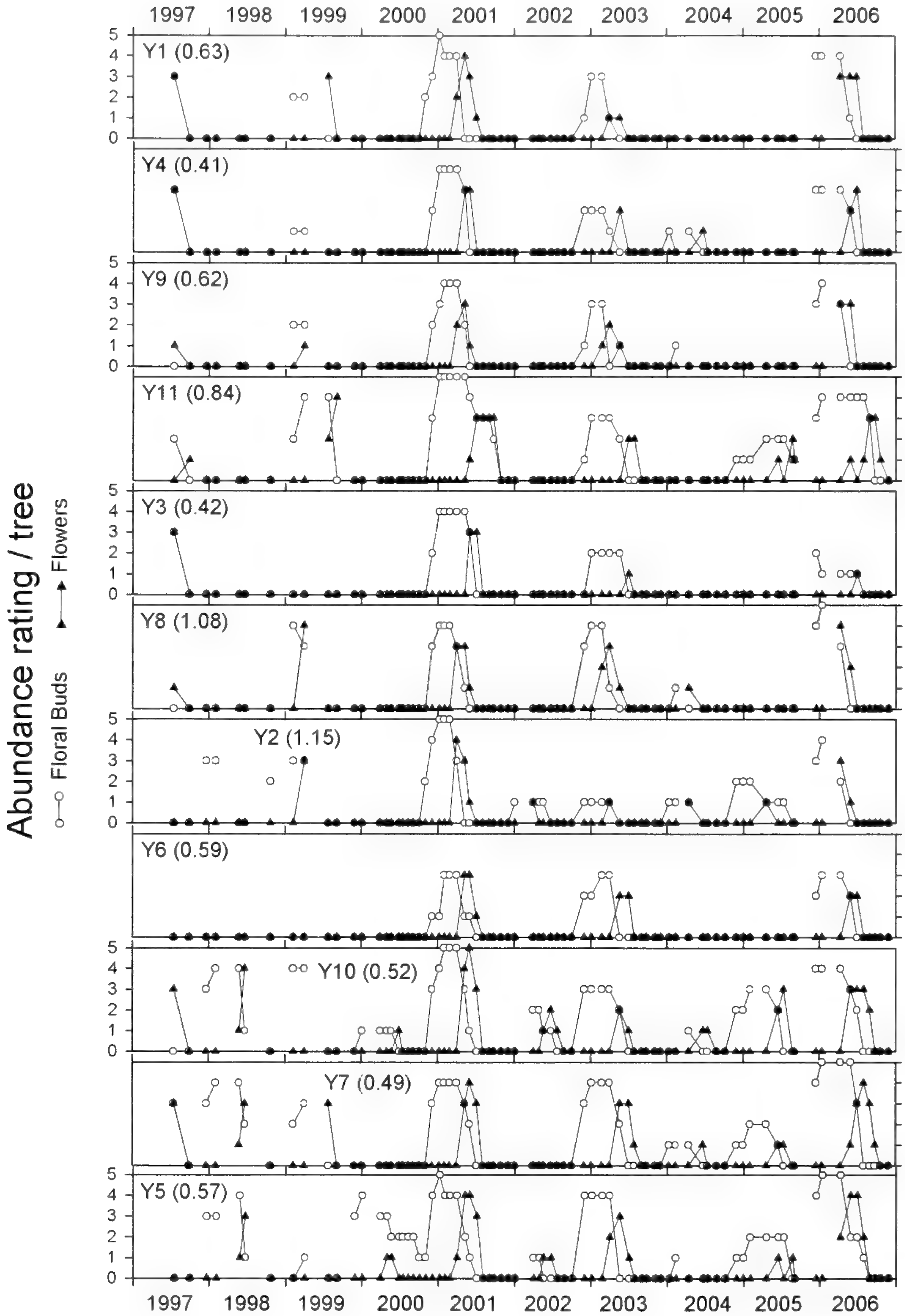

Figure 5a. Floral bud (o) and flower (▲) abundance ratings (0-5) for eleven *E. albens* trees on a roadside near Young: July 1997 to November 2006. Tree identification numbers are preceded by the letter Y, and have DBH (m) in parentheses.

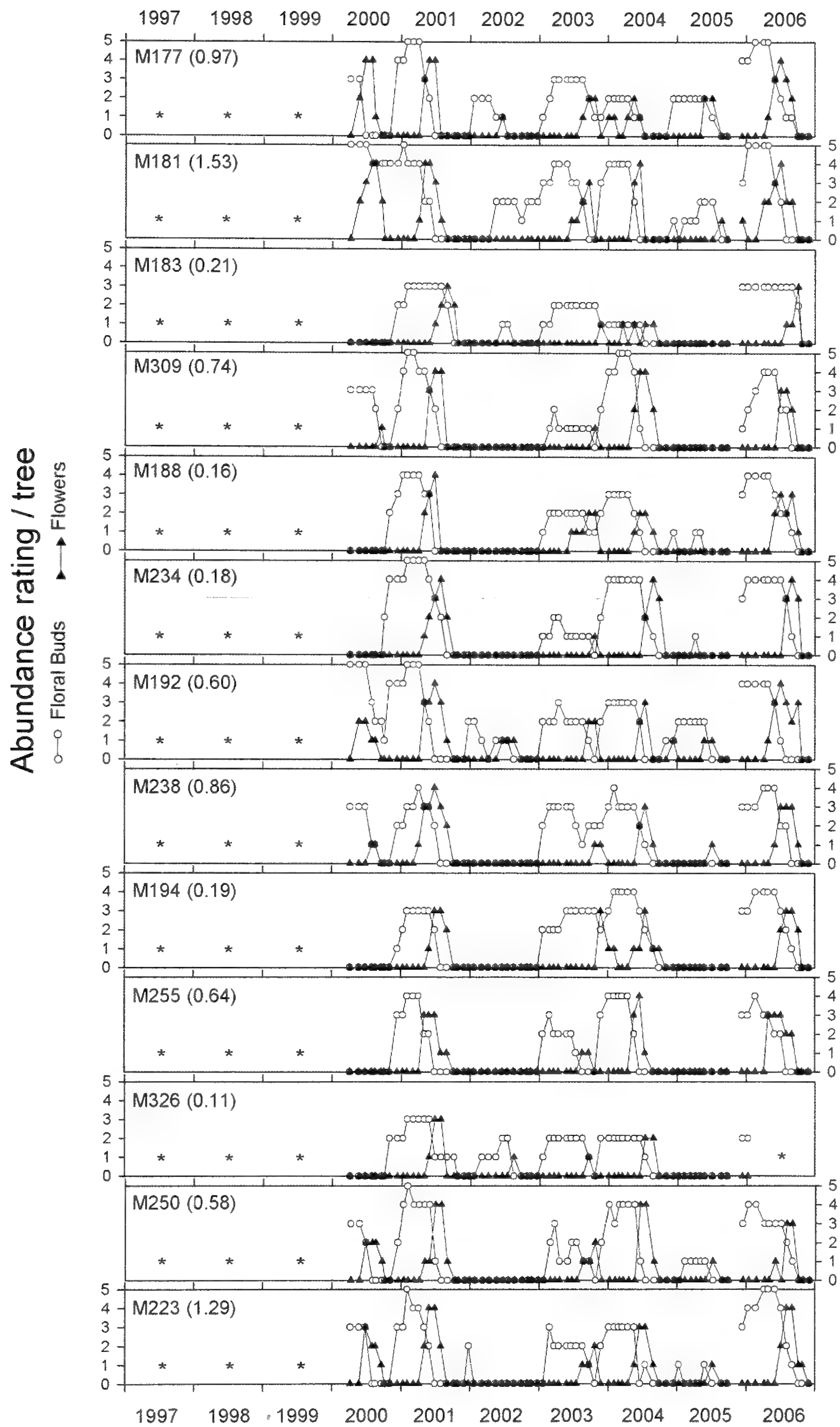

Figure 5b. Floral bud (○) and flower (▲) abundance ratings (0-5) for thirteen *E. albens* trees on a roadside near Molong: March 2000 to November 2006. Tree identification numbers are preceded by the letter M, and have DBH (m) in parentheses. * = no data.

Abundant budding (mean rating ≥3) in consecutive years across a stand was rare (Fig. 3) but it was often recorded in individual trees. At Young, three trees (Y2, Y5, Y7) budded abundantly in consecutive years on one occasion, and another (Y10) on two occasions (Fig. 5a). Abundant budding in consecutive years was less frequent in trees at Springhurst (two trees on one occasion each) but considerably higher at Yerong Creek: eight trees on one occasion and four trees on two occasions but in the case of two of the latter trees, the second occasion extended over four years, 2001 to 2004. Despite the shorter period of observation at Molong, four trees (M177, M309, M194, M255) produced abundant buds in consecutive years on one occasion and five trees (M181, M192, M238, M250, M223) on two occasions – though in some cases buds declined prior to flowering, e.g. at M255 in 2003 (Fig. 5b).

Some trees budded abundantly more often than other trees at all sites (Fig. 6). This was particularly evident at Molong where five (41%) trees budded abundantly in five of the seven years observed. At the other extreme, six trees at Springhurst produced abundant buds in only one of the 11 years observed. Larger trees tended to produce abundant buds more frequently than smaller ones, at least for the range of DBHs shown in Table 1, but the overall association was low, ranging from $r = 0.23$ at Young to $r = 0.70$ at Molong.

Production and decline of capsules

The abundance of capsules in individual trees over time reflected the varying flowering patterns, and minor flowering events (bud abundance ≤2) generally had an imperceptible effect on the crop of capsules.

Though peak flowering events (Fig. 3) were important in replenishing the capsule crop in stands (Fig. 7), even minor flowering events (mean bud abundance ≤2) played a role because some trees flowered abundantly during these periods. Though the crop consisted mainly of immature capsules following each peak flowering, for much of the time crops of different ages were present in the canopies – except at Springhurst where flowering was infrequent. For most of the time at this site, average capsule abundance was low (≤2) and any fruits present were likely to have been over-mature, i.e. dehisced.

Relationship between the occurrence of budding and preceding rainfall

Linear correlations were examined primarily for significant correlations between bud abundance and recent (≤ 5 years previously) rainfall that the site (i.e. mean values) shared with many of the individual trees. A subset of the rainfall data, cool-season and warm-season, is presented in Fig. 8.

Mean maximum bud abundance at Molong was significantly correlated ($r = 0.81$) with winter rainfall three years previously (Fig. 9a) and warm-season rainfall five years previously ($r = 0.82$); and negatively correlated with cool-season ($r = -0.76$) and/or winter ($r = -0.78$, Fig. 9b) rainfall four years previously. Only three trees exhibited all correlations but most showed one or two. Bud abundance at four trees (M181, M192, M238, M250) was not significantly correlated with recent rainfall.

At Young, mean maximum bud abundance was also significantly correlated ($r = 0.69$) with winter rainfall three years previously (Fig. 9c) and negatively with winter rainfall four years previously ($r = -0.64$, Fig. 9d) but also with summer rainfall one year previously ($r = 0.72$). None of the individual trees showed all three correlations. Bud abundance for the first five trees in Fig. 5a was correlated with winter rainfall three years previously and summer rainfall one year previously. Figure 5's last three trees, which tended to produce abundant buds in most years, were not consistently associated with these lagged rainfall series but bud abundance at two of them (and also Y2) was significantly negatively correlated with winter rainfall four years previously.

Mean maximum bud abundance at Yerong Creek was significantly correlated with spring ($r = 0.62$) and/or warm season ($r = 0.64$) rainfall three years previously. Budding at seven of the 18 trees with a complete set of data showed a similar pattern. Unlike Molong and Young, the positive correlation with winter rainfall three years previously and the negative correlation with winter rainfall four years previously were evident at only one or other of four trees, and across all trees these correlations were weak (Figs. 9e and 9f).

At Springhurst, mean bud abundance was significantly negatively correlated with rainfall two years previously: calendar year ($r = -0.72$) and cool-season ($r = -0.66$). One or both of these correlations were evident for 13 of the 18 trees with a complete data set but budding at nine trees was also significantly positively correlated (r values ranging from 0.60 to 0.74) with autumn rainfall four years previously. Correlations with winter rainfall three and four years previously were weak (Figs. 9g and 9h).

Across all 59 trees, bud abundance at 24 was significantly positively correlated with winter rainfall three years previously. Such trees were present at all sites, particularly at Molong and Young. At Yerong Creek, seven trees were correlated with rainfall three years previously: one with winter rainfall,

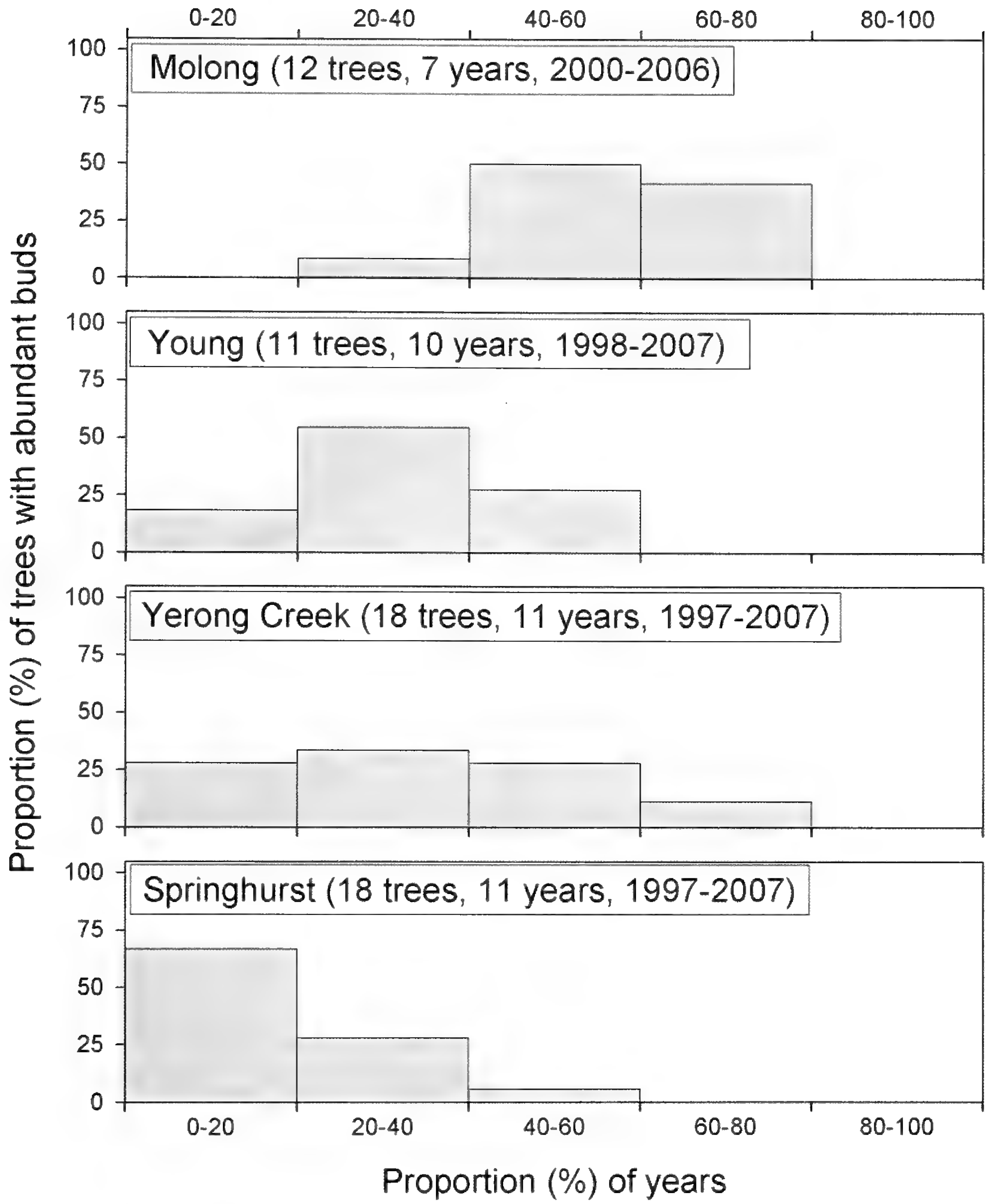

Figure 6. Proportion (%) of trees in each *E. albens* stand that produced abundant floral buds (rating ≥ 3) grouped by the proportion of years of observation (years with incomplete data excluded). For example, 12 trees (67% of 18 trees) at Springhurst were observed to produce abundant buds on just two or fewer occasions (18% of 11 years). Except for Molong, bud assessments for 2007 are included.

three with winter and spring rainfalls and three with spring rainfall. (Budding at a few other trees was also correlated with warm-season rainfall but it was most apparent at Young where six of the 11 trees were positively correlated with summer rainfall one year previously.) Only a few trees were correlated with rainfalls two and four years previously and for most it was negative. Contrary to all the other sites, nine of the 18 trees at Springhurst were positively correlated with autumn rainfall four years previously. Budding in most (but not all) trees therefore seemed to be dependent on cool-season (either winter or autumn) rainfall three or four years previously.

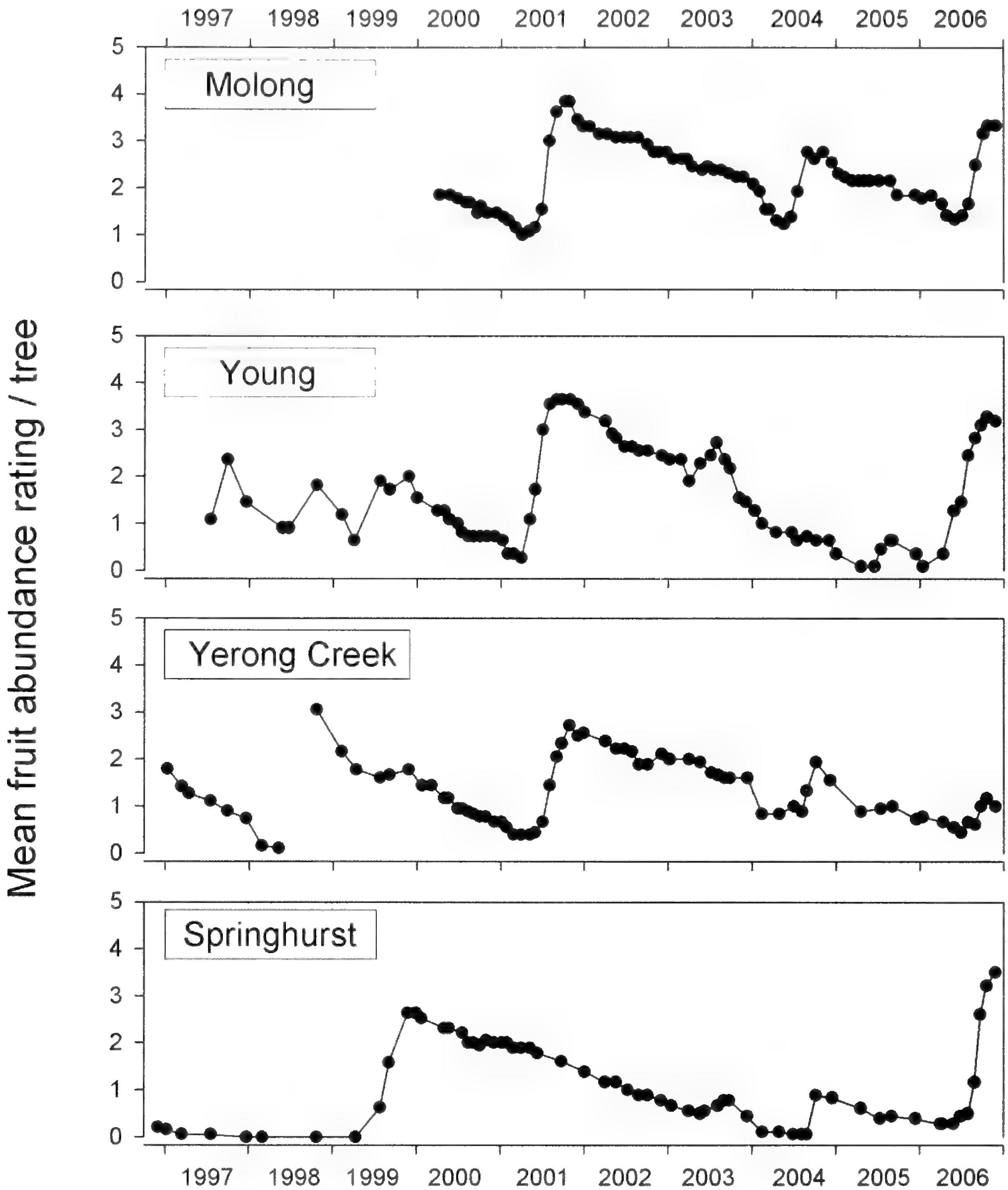

Figure 7. Mean abundance ratings (0-5) for capsules over time at four stands of *E. albens*. No distinction is made between immature (usually the main component on peaks and steeply rising limbs on the graphs) and over-mature capsules (usually the main component towards the ends of falling limbs on each graph).

DISCUSSION

Budding and flowering times

Floral (pin) buds were usually first evident around November – apart from some unusual occurrences of early budding at a few trees at Molong (and again in March 2007 and 2008; Semple and Koen 2008). Buds were at a maximum by early summer and bud abundance ratings rarely declined prior to the commencement of flowering. Even so, bud shedding

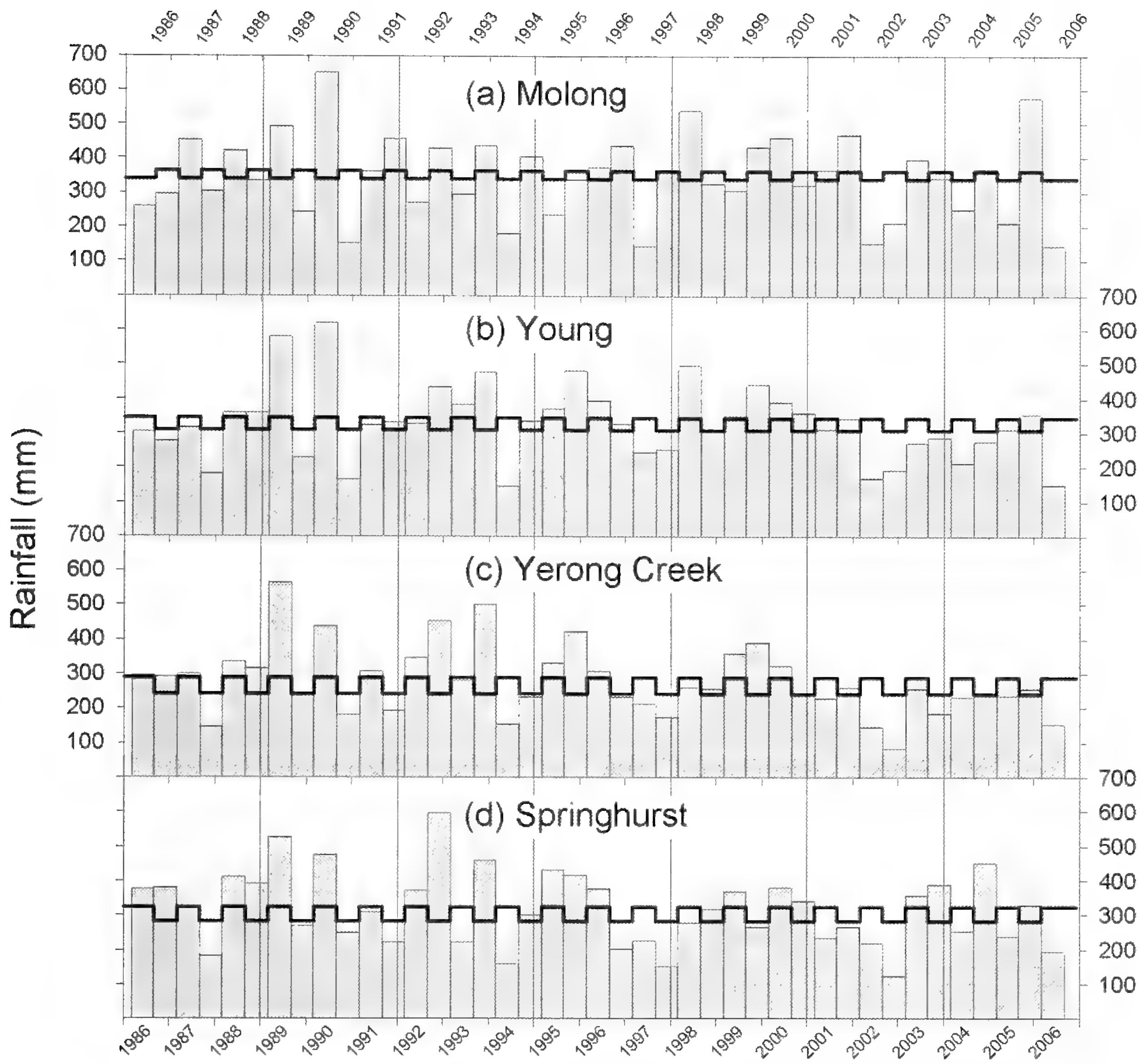

Figure 8. Cool (March to August) and warm (September to February of the following year) season rainfall from stations near the four *E. albens* monitoring sites. Seasonal data derived from monthly interpolations (as per Jeffrey et al. 2001) and long term means (thickened lines) from incomplete Bureau of Meteorology data: Molong (1884-2006), Young (1871-1991), Yerong Creek (1885-2007), Springhurst (1900-2007).

was probably common as has been reported for eucalypts (Florence 1996) and for *E. albens* at Cowra (Semple et al. 2007) but was not usually detected by the relatively coarse abundance rating scale used in this study. Flowering generally occurred from March to November in the year following budding.

The first occurrence of buds and the flowering period were consistent with previous observations by Clemson (1985) and Semple et al. (2007) but the flowering period was inconsistent with observations by others, e.g. mid/late summer to winter, or autumn to winter (see Table 2). Summer flowering is possible as was demonstrated by a few trees at Molong (though few flowers were produced and flowering did not extend beyond January) and for two trees at Young in 2003 (when their main flowering period commenced in February). As some of the reports of an earlier flowering period, i.e. between summer and winter, predate the early 1990s, is it possible that the flowering period has changed since *c.*1990 – perhaps in response to increased frequencies of years of below-average rainfall (e.g. Fig. 8) or even higher temperatures in recent times. Without access to the original observations, it is difficult to establish but the possibility of a later and longer flowering period in recent times cannot be ruled out.

Leigh's (1972) report of a longer flowering period in NSW compared to southern Queensland

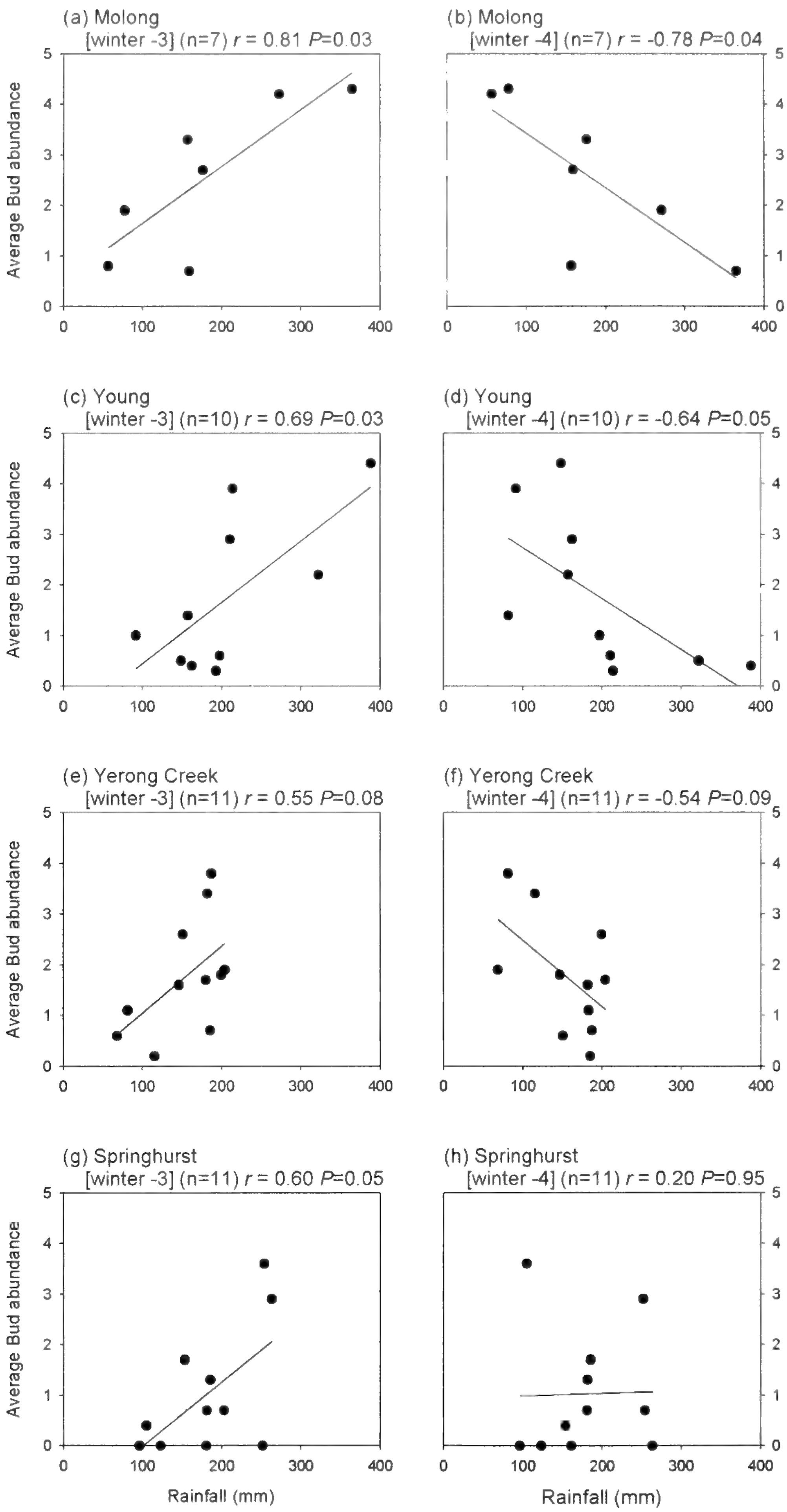

Figure 9. Correlations between maximum mean annual bud abundance and winter (June-August) rainfall 3 and 4 years previously at four *E. albens* monitoring sites. Number of years of data indicated by 'n'.

suggested that it may be longer in the south, e.g. at Springhurst, but this was not evident in the data, albeit limited by only two peak flowering periods in that stand. Nor was it evident in Stelling's (1998a, b) report for southern NSW (Table 2).

Temporal and spatial variation in flowering

Variable flowering periods and intensities between individual eucalypts in a stand in any one year is well known and has been attributed variously to tree age/size, health and probably genotype as well as local variations in elevation, soil types and moisture availability (House 1997, Wilson and Bennett 1999). As indicated by the ranges of DBHs (Table 1), trees of variable size and presumably age were present in each stand but the association between DBH and the frequency of abundant budding was generally weak. Elevation, soil type and moisture availability appeared to be relatively uniform in each stand, except for the hilltop stand at Young where elevation varied by ~2 m. As budding intensity varied (a) between trees in each stand in the one year and (b) between individuals across years, e.g. some budded abundantly in consecutive years whereas others did not, prior rainfall alone cannot explain flowering in a stand. If it did, then all trees would flower (or produce buds) in a similar manner each year.

Nevertheless prior rainfall is important for tree health and its varying occurrence and abundance would be expected to have varying effects on the production of new leaves and reproductive structures. For example, Porter (1978) in attempting to explain correlations between previous rainfall (and temperature) and honey production (= flowering intensity in a stand) from *E. tricarpa* (with similar phenology to *E. albens*), noted that leaf growth was favoured by wet summers but not by cool wet winters - though stored water from the latter favoured growth of floral buds in the following spring.

The data presented here indicate that individual (and sometimes groups of) trees responded differently to the same rainfall cues – except perhaps in those years when most trees budded abundantly (e.g. Fig. 4). This was supported by the examination of correlations between bud abundance and previous rainfall: bud abundance in some trees was not correlated with prior rainfall (at least in the previous five years) whereas other trees in the same stand were correlated with differing rainfall events. Even so, there were some broad correlations between mean bud abundance in a stand and previous rainfall e.g. between winter rainfall three years previously (positive) and four years previously (negative) in the two northern-most stands but these associations

Table 2. Flowering periods of Eucalyptus albens as reported by various authors.

Flowering period	Area	Source
Late summer and sometimes into winter	SE Australia	Kelly *et al.* 1977
January to June	SE Australia	Costermans 1983
February to July	central western NSW	Schrader 1987
March to May	SE Australia	Brooker and Kleinig 1990; Boland *et al.* 1992; Nicolle *et al.* 1994
April to July (Qld) or August (NSW)	SE Australia	Leigh 1972
May to September	southern NSW	Stelling 1998a, b
Autumn to late spring	near Cowra, NSW	Semple et al. 2007
April to November	SE Australia	Clemson 1985

did not extend to stands further south (Fig. 9) where mean bud abundance was correlated with other previous rainfall occurrences. Varying genotypes within and between stands would seem to be the mostly likely explanation for these results; though phenotypic variation due to (undetected) fine-scale variation in resource availability cannot be ruled out. Nevertheless, the presence of such variation would increase the likelihood of floral bud and hence, seed production in at least a few trees in each stand in most years.

The role of flowering (and seeding) in seedling recruitment of woodland eucalypts

The availability of a seedbank is only one of a number of factors that affect seedling recruitment. The success of seedbed-manipulation experiments over a number of years in the eucalypt woodland belt (e.g. Semple and Koen 1997, Lawrence et al. 1998, Geeves et al. 2008) suggests that sufficient and timely rainfall for germination and seedling establishment is not a rare occurrence. However, unlike parts of Victoria, seedling recruitment of woodland eucalypts is rarely observed in NSW. For the most part, this is probably due to the absence of a seedbed that provides exposed mineral soil and reduced herbaceous competition – a consequence of relatively high fertility soils (Beadle 1981) and groundstoreys that are often dominated by exotic species (Prober 1996) in the box (e.g. *E.albens* and *E. melliodora*) woodlands of central and southern NSW. Though appropriate seedbeds can be deliberately (or accidentally) prepared, e.g. by applying herbicides or cultivating near trees, their 'natural' occurrence is largely dependent on high intensity grazing (e.g. Curtis and Wright 1993), drought (e.g. Curtis 1990) or fire (e.g. Cluff and Semple 1994, Semple and Koen 2001) though in the latter case, exotic species if present, rapidly recolonise negating any initial benefits for the eucalypt seedling. Nevertheless, when rainfall, seedbed and other favourable conditions do coincide, the on-going availability of seed, even if in small amounts in a few trees, is critical for successful recruitment. A case in point is the Molong site that was burnt in late 2006. Though the developing 2006 seed crop was destroyed, a small amount of seed was present from earlier (2004?) flowerings (Fig. 7) and this yielded some seedlings beneath a few trees (Semple and Koen 2008). Despite suboptimal rainfall, most of these seedlings were still alive in early 2009 – probably due to the localised absence of competition from exotic herbage.

Predicting the future?

The view expressed by the letter-writer at the start of this paper implies that flower abundance is an indicator of some future meteorological event. Such views are not uncommon, e.g. as reported by Duff (2007) for observations of box trees near Jeparit in Victoria. Results presented above suggest that bud (or flower) abundance did not provide much information on past, leave alone future rainfall events.

CONCLUSIONS

In general, floral (pin) buds appeared in November and flowers were produced during the following March to November. Flowers were produced by at least a few trees in each stand each year except for the southern-most stand. However, the frequency of abundant budding, when most or all of the adult trees flowered abundantly, declined from about 4.3 years in 10 in the northern-most stand to two years in 10 in the south. For each tree stand, these occurrences were important for maintaining its aerial seedbank. Without replenishment, capsule abundance was low after two to three years.

However, the production of reproductive structures in individual trees was often at variance to the stand 'average'. In terms of the first appearance of floral (pin) buds, it could be as early as March (rather than the November 'average'). Flowering in some trees commenced as early as February (compared to the March 'average') or did not finish until January (compared to the November 'average'). Variations such as these were usually evident in a few trees, particularly those at Molong, suggesting a degree of 'plasticity' in populations at the centre of the north-south distribution of *E. albens*.

Unlike average bud abundance in tree stands, where a high abundance year was always followed by a year of low abundance, some individual trees budded abundantly each year over periods ranging from two to four years. Individual differences such as these suggest – contrary to our suggestion from an earlier but shorter (1995-1999) observation period at Cowra (Semple et al. 2007) – that prior rainfall in a particular season is not a general determinant of bud (flower) abundance, except perhaps in those years when all trees flower abundantly. Such variability may have positive benefits for successful reproduction in a variable climate such as Australia's.

ACKNOWLEDGEMENTS

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The Early Devonian Trilobite *Craspedarges* from the Winduck Group, Western New South Wales.

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Specimens of the lichid trilobite *Craspedarges wilcanniae* Gürich from the Early Devonian Winduck Group in 'The Meadows' area, near Cobar, in western New South Wales, enable a revised description and a neotype to be designated to replace types destroyed during World War II.

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KEYWORDS: Cobar, *Craspedarges*, Early Devonian, Lichidae, trilobites, western New South Wales, Winduck Group.

INTRODUCTION

In 'The Meadows' area (Figure 1), south–west of Cobar in western New South Wales, the Early Devonian (Lochkovian) lichid trilobite *Craspedarges wilcanniae* occurs in the Winduck Group (Glen 1987), a unit within the widely distributed Cobar Supergroup. The stratigraphy and brachiopod faunas of this area have been described elsewhere (Sherwin 1992, 1995) and on a broader scale the structural setting has been described by Glen (1990). Geological mapping in this particular area was handicapped by poor outcrop but the favoured interpretation is that the Winduck and Amphitheatre Groups have an interfingering relationship (Figure 2), with the Winduck Group sedimentation continuing for a longer period. Trilobites have not been reported previously from this area, the nearest occurrences in the Cobar Supergroup being in the vicinity of Cobar (Baker et al. 1975, Fletcher 1975), 60 kilometres north–east of "The Meadows". Ebach and Edgecombe (1999) described a new species of the proetid *Cordania* from the vicinity of "The Bluff", south of Cobar, in the Biddabirra Formation (Amphitheatre Group) which underlies the Winduck Group. Fletcher (1975) also described several other species of trilobites from the vicinity of Cobar and several localities north–east of Nymagee where Webby (1972) had noted an *Encrinurus* occurrence. From that same area, Landrum and Sherwin (1976) described a new proetid, *Warburgella (Anambon) jelli*, regarded by Yolkin (1983) as a junior synonym of the Eurasian species *Warburgella tcherkesovae* Maximova and *Warburgella waigatschensis* (Tschernyschev and Yakovlev, 1898). Strusz (1980) reviewed the species of *Encrinurus* described by Fletcher and regarded the specific attributions as doubtful because of the poor preservation. The stratigraphy of the Nymagee localities has been described by Felton (1981). The lichid trilobite *Craspedarges wilcanniae* Gürich, found at several localities within the Winduck Group, was described from erratics, believed derived from the Cobar Supergroup, in Cretaceous sediments at White Cliffs (Gürich 1901) about 230 kilometres north-west of "The Meadows" (Figure 1).

Several genera of trilobites are represented in "The Meadows" district but only the lichid species is described here. The encrinurids occur in pinkish mudstones of the Late Silurian to Early Devonian Amphitheatre Group and are generally complete, although fine details are not well preserved. In the Winduck Group probable *Gravicalymene* is associated with *Craspedarges* but is otherwise too poorly preserved to warrant description and proetids are represented by a nondescript pygidium.

AGE OF THE FAUNA

The brachiopods associated with *Craspedarges wilcanniae* indicate an Early Devonian (Lochkovian) age (Sherwin 1995). The only other recorded species of *Craspedarges*, *C. superbus*, was described from

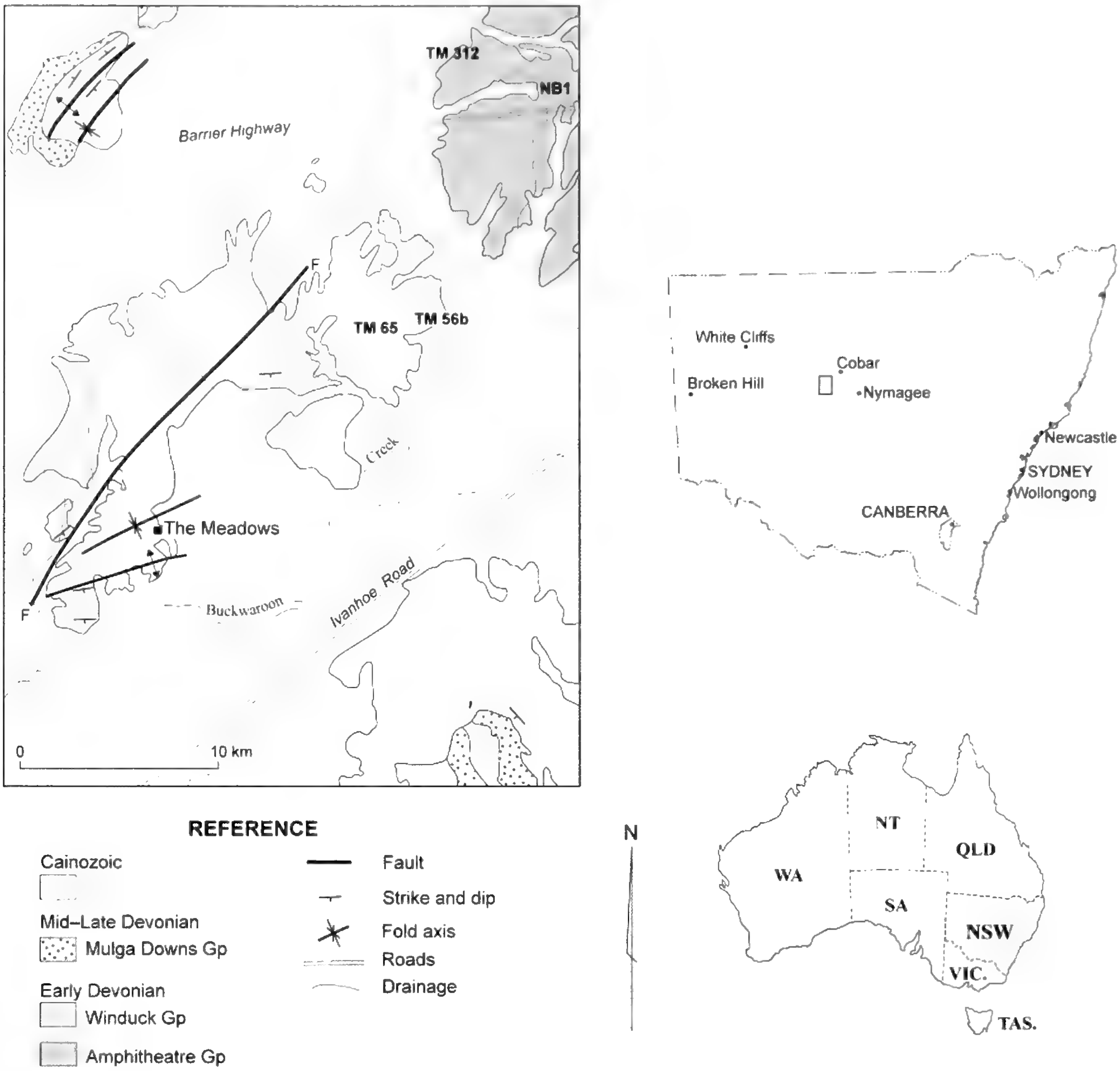

Figure 1. Locality diagram showing places mentioned in text, fossil localities and geological sketch map, modified from Rose (1965).

the 'Gedinnian to Emsian or early Eifelian' Fukuji Series in Japan by Kobayashi and Hamada (1977a, b), although the generic identification was queried by Thomas and Holloway (1988). Lichid trilobites have been described from Early Devonian (Pragian–Emsian) limestones in New South Wales (Edgell 1955; Chatterton 1971; Chatterton et al. 1979; Edgecombe and Wright 2004) and quartzose clastics in Victoria (Gill 1939; Holloway and Neil 1982) but all belong to the genus *Acanthopyge* except for one doubtful reference to *Terranovia* from New South Wales (Chatterton and Wright 1986).

SYSTEMATIC PALAEONTOLOGY

Morphological terms, unless otherwise specified, are as defined in the Treatise on Invertebrate Paleontology (Moore, ed. 1959), supplemented with lichid morphology of Thomas and Holloway (1988) except that we do not regard the occipital ring as part of the glabella.. All specimens are stored in the collections of the Geological Survey of New South Wales at Londonderry in western Sydney. External moulds were studied using latex casts and all specimens, whether casts or originals, were whitened with MgO for photography. Actual specimens were blackened with water colour before application of MgO.

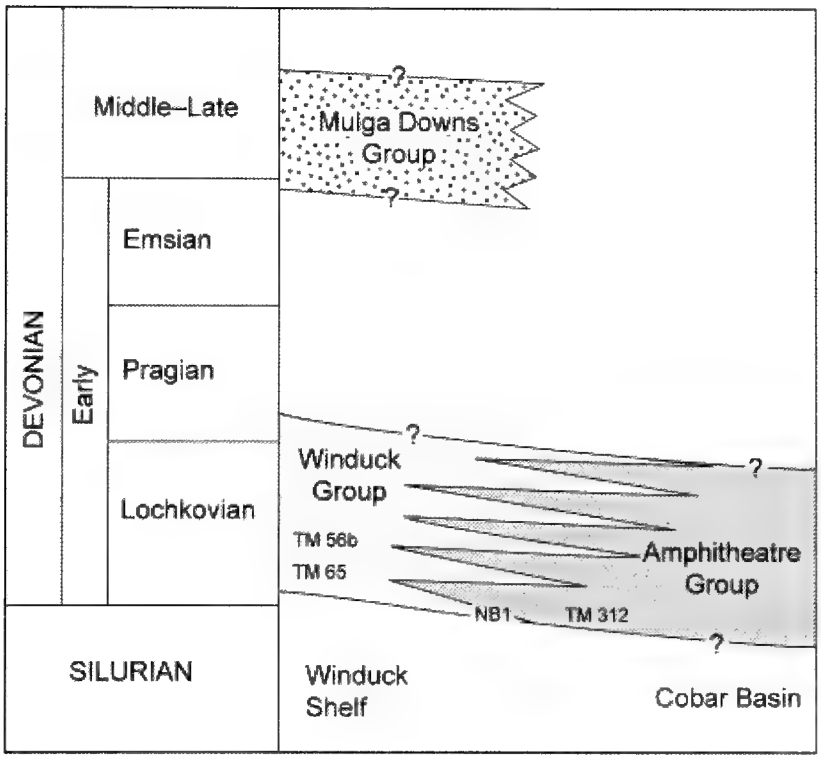

Figure 2. Stratigraphic relationships in "The Meadows" district, modified from Glen (1987), showing approximate stratigraphic position of trilobite localities. *Craspedarges wilcanniae* occurs at localities TM56b and TM65. Encrinurus occurs at localities NB1 and TM312. In this area it has not been possible to recognise formations within the Amphitheatre and Winduck Groups.

Family LICHIDAE Hawle and Corda, 1847
Subfamily TROCHURINAE Phleger, 1936
Craspedarges Gürich, 1901

Type species
Craspedarges wilcanniae Gürich, 1901

Diagnosis (revised)

Trochurine with very globose cranidium; anterior border wide and gently convex in section (sag.), becoming flatter near suture; longitudinal furrows shallow posteriorly, much deeper anteriorly including in front of S1 and subparallel for most of length from posterior edge of cranidium, diverging anteriorly to join border furrow; S1 deep behind bullar lobes, weak between longitudinal furrows; portion of L1 between longitudinal furrows much lower than occipital ring and median lobe but approximately the same width (trans.) as the occipital ring. Pygidium approximately as wide as long with narrow well developed raised border; rachis approximately one third the maximum width of the pygidium; first pair of pleurae backwardly flexed, second less so but more inclined to rachis, third subparallel to rachis; abaxial ends of pleurae continued beyond border as tapered spines with circular cross sections; rachis parallel sided for approximately one third length of pygidium, remainder tapered and continued beyond border as terminal spine flanked by a pair of border spines.

Remarks

The types of this genus are believed to have been destroyed with the remainder of Gürich's collection, housed originally in Breslau (now Wrocław), when Hamburg was bombed during World War II. Although a significant part of the collection survived the war, there is no trace of the types of *Craspedarges* or even the associated brachiopods (J. Dzik, pers. comm.).The search described by Thomas and Holloway (1988) was repeated as well as extended to the Geological Survey of New South Wales collections without any success. This redescription is based upon material found *in situ* in sandstones of the Winduck Group. Gürich's types came from erratic boulders, as noted above, but the exact source, or sources, of the erratics is unknown, there being very little pre–Quaternary outcrop between White Cliffs and 'The Meadows', although the erratics are comparable in lithology and faunal content (Dun 1898) with the Winduck Group.

Because of doubts about the source of the erratics it is necessary to establish that the lichids from the Winduck Group are truly *Craspedarges*. Gürich's material consisted of an internal mould of an incomplete cranidium and three fragmentary moulds of ventral surfaces of the pygidium. The cranidium, except for some flattening indicated by a line drawing of the profile, matches the Winduck Group material. Matching the pygidia is difficult because the one pygidium known from the Winduck Group has more or less uniformly slender marginal spines preserved whereas two (Gürich, pl. 18, figures 6 and 8) of Gürich's specimens have comparatively short and wide spines. These two particular specimens are very fragmentary and it is not at all certain that they belong to the same species, ie., *C. wilcanniae*. The remaining fragment illustrated by Gürich (pl. 18, figure 7) is of the posterior margin and is reconcilable to a greater extent with the Winduck Group specimen. Gürich's specimens are illustrated by drawings only so that there is a possibility that the figures are not necessarily an accurate representation of the original specimens, especially his diagrammatic sketch of a flattened and incomplete cranidium (pl. 20, figure 20). The illustration in the trilobite Treatise (Moore 1959, figure 396–6a) is a line drawing that does not correspond with either of Gürich's sketches but seems to be based upon a composite of the two. The cephalic profile in the Treatise (figure 396–6b) is clearly copied from Gürich (figure 1a) but the anterior border has been changed from planar to slightly concave and the figure generally flattened. In this paper (figure 3, A and B) a slightly flattened cranidium has been placed alongside the comparatively undeformed neotype to show the distorted anterior border resembles the Treatise illustration. The shading in Gürich's illustration (pl. 18, figure 1) suggests that some convexity remains in the left side of the anterior border.

Craspedarges is closely related to *Richterarges*, as noted by Thomas and Holloway (1988), the major differences being the more prominent anterior border and much deeper anterior part of the longitudinal furrows. A slight midlength expansion in the median lobe of *Richterarges* has no analogue in the corresponding part of *Craspedarges* where the sides of the median lobe are straight. The pygidium of *Richterarges* has only two distinct pleurae compared with three in *Craspedarges*. Thomas and Holloway also postulated that *Craspedarges* was derived from *Richterarges* in about Late Silurian to Early Devonian time, which accords with the age of the Winduck Group. However. the pygidial segmentation in *Craspedarges* is less effaced than *Richterarges*, suggesting that it departed earlier from the ancestral hemiargid stock.

Pollit et al. (2005) carried out a cladistic study and Bayesian analysis of the Family Lichidae but excluded *Craspedarges* from consideration because of its poorly known morphology; they did recognise that it is closely related to the group represented by *Acanthopyge*, *Akantharges*, *Ceratarges* and *Borealarges* and in other respects to the group containing *Richterarges* and *Terranovia*.

Craspedarges wilcanniae Gürich, 1901 (Figure 3)
1901 *Craspedarges wilcanniae* Gürich, p. 532–538, pl. 18, figures 1, 6–8; pl. 20, figure 20.

Neotype

MMF 31377(5) a cranidium lacking the postero–lateral extremities.

Neotype locality

TM 56b, Winduck Group, Early Devonian (Lochkovian).

Other material

MMF 31333 anterior of cranidium: MMF 31334 posterior half of cranidium; MMF 31399 and 31400 poorly preserved cranidia; MMF 31377(10) and (11) hypostomes; MMF 31398 incomplete pygidium. The numbers in brackets refer to individual specimens on slabs with numerous fossils.

Other localities

TM 65, Winduck Group (MMF 31399 only).

Diagnosis

Craspedarges with 1L undivided between longitudinal furrows.

Description

The cranidium is very strongly convex, almost globose. The border is very distinct and anteriorly convex in section (sag.), being broadest near the anterior and posterior ends of the suture. The border furrow is narrow, except at the genal angles, and well defined. The rachial furrows are indistinct on the posterior border and effaced on the postero–lateral cranidial lobe between the palpebral lobe and posterior border furrow. The occipital ring is poorly defined laterally because of the weak posterior rachial furrows, but is clearly differentiated from 1L by the occipital furrow. The longitudinal furrows are weak between the posterior margin and S1 but deep anteriorly and sub–parallel along the inner sides of the bullar lobes. The median part of 1L is well marked by the longitudinal furrows and comparative depression among otherwise inflated lobes but the lateral ends are lost in the undifferentiated postero–lateral cranidial lobes. The bullar lobes are clearly defined by the circumscribing furrows. The median lobe is the most inflated part of the cranidium and very wide anteriorly, though the antero–lateral extremities do not overlap the bullar lobes. The surface is covered with small pointed tubercles that are finer on the border. [The perforations on some tubercles are believed to be bubbles in the latex cast and are irregular in distribution.] The free cheeks are unknown.

The hypostome is wider than long although the posterior border is incomplete on both specimens. The posterior lobe is narrow (sag.) and crescentic in shape compared with the larger subquadrate anterior lobe. The surface of at least the median body is

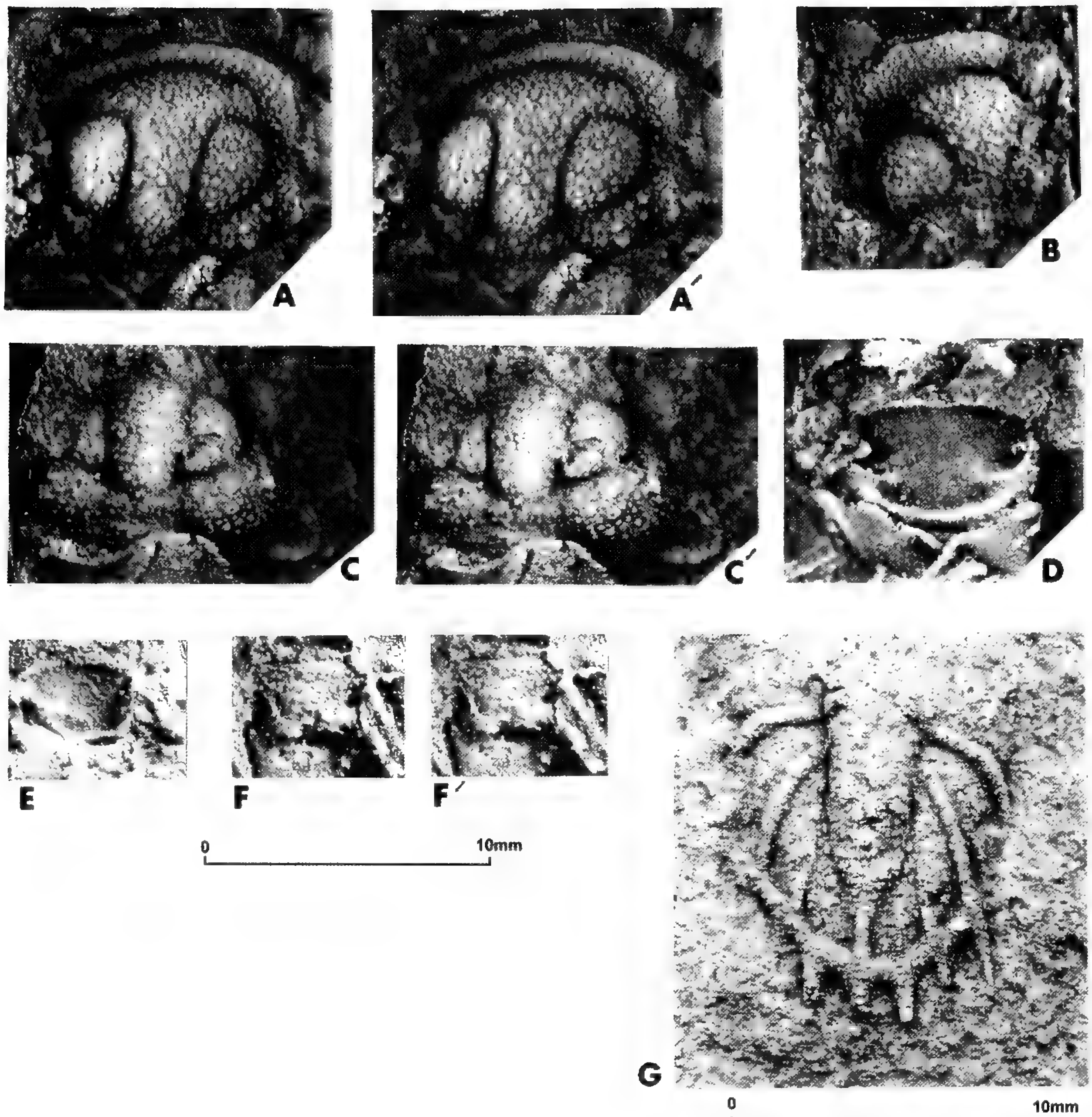

Figure 3. ***Craspedarges wilcanniae*** **Gürich; A, A' MMF 31377(5) neotype, stereo pair of latex cast of exterior of incomplete cranidium; B MMF 31399 latex cast of exterior of flattened incomplete cranidium showing impact on anterior border; C, C' MMF 31334 stereo pair of latex cast of exterior of posterior part of cranidium; D MMF 31377(11) latex cast of interior of hypostome; E–F MMF 31377(10) latex casts of interior and exterior of hypostome, E interior, F, F′ stereo pair of incomplete exterior; G MMF 31398 latex cast of incomplete pygidium.**

ornamented with tubercles finer but otherwise comparable with those on the cranidium.

No thoracic segments of this species are known.

The only pygidium is incomplete at its anterior edge and the rings are not preserved on the prominent rachis. The posterior edges of the three pleurae form well defined ribs in the pleural fields, the ribs on the second and third pleurae being continued beyond the well defined raised border as robust spines. The very poorly preserved internal mould, counterpart to the exterior in Figure 3G, shows that the first pleura is also continued beyond the border as a marginal spine of uncertain length. The internal mould also shows a short, comparatively broader spine corresponding to the anterior edge of the second pleura, making a total of five pairs of marginal spines. The pair flanking the terminal spine are in the position that would correspond to a fourth pair of pleurae. The surface is covered with irregularly distributed and widely spaced granules. The doublure is unclear in extent but is approximately as wide as the border.

Dimensions

Because of the fragmentary preservation some of the dimensions have been extrapolated by doubling measurable half widths.

	length (mm)	width (mm)
MMF 31377(5) cranidium	9.0	9.5
MMF 31334 cranidium (posterior)		12.5
MMF 31398 pygidium (ex spines)	10.5	10.0

Remarks

The reasons for assuming that these specimens are truly conspecific with Gürich's originals are discussed under the generic remarks. The only other species assigned to this genus, *Craspedarges superbus* Kobayashi and Hamada (1977a) from Japan, was questionably assigned to *Richterarges* by Thomas and Holloway (1988), although this decision was influenced by the poorly known morphology of *Craspedarges wilcanniae*. The extra pair of pleural segments and five pairs of marginal spines on the pygidium described by Kobayashi and Hamada (1977a) is in agreement with *Craspedarges wilcanniae*, the main distinction being that S1 in *Craspedarges superbus* is not discrete but instead merges medially with the occipital furrow. The age of *Craspedarges superbus* is imprecise, Kobayashi and Hamada (1977b) giving an age range from Gedinnian to early Eifelian. The earlier limit accords with the age of *Craspedarges wilcanniae* and the Winduck Group.

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APPENDIX
FOSSIL LOCALITIES

Grid references (GR) are from 'The Meadows' 1:100 000 topographic map. Other localities were sampled using the Barnato 1:250 000 grid; the original grid reference, shown in brackets, has been retained. Unless otherwise stated the fossils are in sandstone beds protruding above the surrounding scree of finer, more thinly bedded sediments or soil. All localities are within the Cobar Supergroup but in this region it has not been possible to subdivide the Amphitheatre and Winduck Groups.

NB 1 GR 559 123 (Barnato 1:250 000 GR 34601015): unnamed off white fine grained quartzose sandstone member, Amphitheatre Group.

TM 56b GR 459 008: fine grained micaceous quartz sandstone, Winduck Group.

TM 65 GR 4630 0095: fine grained orthoquartzite, Winduck Group.

TM 312 GR 505 130: pale reddish purple massive or thickly bedded siltstone exposed in gravel scrapes, Amphitheatre Group.

Sexual Dimorphism in the Adult South African (Cape) Fur Seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): Standard Body Length and Skull Morphology

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We examine differences in standard body length and skull morphology of male (n = 65) and female (n = 18) South African (Cape) fur seals, *Arctocephalus pusillus pusillus*, from the coast of southern Africa with the aim to develop an objective method for determining the sex of fur seal skulls. Males were found to be significantly larger than females in standard body length, with K-means cluster analysis successfully identifying 2 relatively homogeneous groups. Principal component analysis (covariance matrix) showed that the underlying data structure for male and female skull variables was different, and that most of this variation was expressed in overall skull size rather than shape. Males were significantly larger than females in 30 of the 31 skull variables. Breadth of brain case was significantly different for the genders. Relative to condylobasal length, males were significantly larger than females in 13 of the 31 skull variables used in the present study. These were gnathion to posterior end of nasals, breadth at preorbital processes, least interorbital constriction, breadth at supraorbital processes, greatest bicanine breadth, breadth of palate at postcanine 1 and 3, calvarial breadth, mastoid breadth, gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, height of skull at base of mastoid and height of mandible at meatus. In males, these variables were associated with the acquisition and defense of territory (e.g., large head size and mass; increased structural strength of the skull; increased bite capacity). Two skull ratio parameters, breadth of braincase/condylobasal length and length of upper postcanine row/condylobasal length were significantly higher in females compared to males. Based solely on the skull data, mature males can be reliably distinguished from immature males and females using both (a) Classification and Regression Tree (CART) and (b) Hierarchical Cluster Analysis. Both approaches had difficulty in reliably distinguishing immature males from females. The Classification and Regression Tree method was the more successful in correctly distinguishing immature males from females.

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KEYWORDS: *Arctocephalus pusillus pusillus*, identification of sex, multivariate analysis, Otariidae, polygyny, Pinnipeds, principle component and cladistic analysis, sexual dimorphism, skull morphometrics, South Africa fur seal, standard body length.

INTRODUCTION

Sexual dimorphism is a form of non-geographic variation that can be generated in a species by the process of sexual selection (Bartholomew, 1970; Alexander et al., 1979; Stirling, 1983). Highly polygynous species such as fur seals, sea lions and elephant seals, generally exhibit a high degree of sexual dimorphism (Laws, 1953; Ralls, 1977; Alexander et al., 1979; Stirling, 1983; Sirianni and Swindler, 1985; McLaren, 1993; Arnould and Warneke, 2002). Differences in reproductive success among males of these species are large, and competition for access to females is intense. Selection pressure appears to favour the development of traits that enhance male fighting ability, including intimidating body size, weaponry and skin thickness (Laws, 1953; Bartholomew, 1970; Le Boeuf, 1974; Alexander et al., 1979; McCann, 1981; Stirling, 1983).

Breeding Southern fur seals *(Arctocephalus* spp.) are among the most territorial of animals, are strongly sexually dimorphic in body size, polygynous and gregarious (Peterson, 1968; Harrison et al., 1968; Stirling, 1970; Bryden, 1972; Alexander et al., 1979; Bonner, 1981; McKenzie et al., 2007). In the southern hemisphere, breeding status male fur seals (beachmasters) generally arrive at the rookeries around November to establish territories. Pregnant females arrive soon after. Once females are present in the male's territory, males guard females until they come into oestrus post-partum. Females give birth within one week of coming ashore and then mate with the nearest male during the short breeding (pupping/ mating) season (Guinet et al., 1998). Males seldom leave the territory until the breeding season is over (Rand, 1967; Stirling, 1970; Miller 1974; Peterson, 1968; Harrison et al., 1968; Bonner, 1981). After mating, the territorial system gradually breaks down and males return to sea to replenish their physiological reserves. Males do not care for their young.

When establishing territories, male fur seals threaten each other with vocal and visual displays, emphasising their size, to intimidate competitors (Bonner, 1968; Stirling, 1970; Stirling and Warneke, 1971; Miller, 1974; Shaughnessy and Ross, 1980). Much time is spent in making visual and vocal threats to rival males and chasing them away, but fights may develop, occasionally resulting in severe injury or death (Rand, 1967; Stirling, 1970; Shaughnessy and Ross, 1980; Trillmich, 1984; Campagna and Le Boeuf, 1988).

Adult male fur seals are about 3 to 5 times heavier and about 1/4 longer than adult females (Stirling, 1983; David, 1989; Boness, 1991; Guinet et al., 1998; Arnould and Warneke, 2002; Stewardson et al., 2009). Large body size is in itself an intimidating form of display to discourage rival males from attempting an actual physical challenge and in the event of a physical challenge is advantageous in competitive interactions and enables breeding bulls to remain resident on territories for longer periods of time without feeding (Rand, 1967; Miller, 1975; Payne, 1978, 1979; Stirling, 1970, 1983). Strong fore-quarters, enlarged jaw and neck muscles, robust canines, increased structural strength of the skull, and long, thick neck hair (protective mane or wig), also appear to be potentially advantageous in the acquisition and maintenance of territory; quantitative information on these features, however, are lacking (Miller, 1991).

Here we examine morphological differences between skulls (n = 31 variables) of male (n = 65) and female (n = 18) South African (Cape) fur seals *Arctocephalus pusillus pusillus*, from the coast of southern Africa. Body length information was also included in analyses where available. Where possible, comparisons are made to the closely related Australian fur seal *Arctocephalus pusillus doriferus* (King, 1969; Brunner, 1998ab, 2000; Brunner et al., 2002; Arnould and Warneke, 2002; Brunner et al., 2004; Stewardson et al., 2008, 2009) and other otarid species for which morphological data are available such as the Steller sea lion (*Eumetopias jubatus*) (Winship et al., 2001).

For many life history, conservation and ecological studies it is important to be able to determine the sex of skull material in museum collections, skulls of animals found dead or accidentally killed in fishing operations or killed in other ways. Often only the skull is available. We show that two types of multivariate analysis [(a) Classification and Regression Tree (CART) and (b) Hierarchical Cluster Analysis] can be used to objectively distinguish mature male, immature male and female skulls of the South African fur seal (*A. pusillus pusillus*). By extension the approach could be applied to other fur seals, particularly the Australian fur seal (*A. pusillus doriferus*) and the New Zealand fur seal (*A. australis forsteri*).

MATERIALS AND METHODS

Collection of specimens

South African (Cape) fur seals (*Arctocephalus* *pusillus pusillus*) were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34° 03'S, 23° 24'E) and East London (33° 03'S 27° 54'E), from August 1978 to December 1995 (Stewardson et al., 2008, 2009), and accessioned at the Port Elizabeth Museum (PEM). Specimens were collected dead or dying from the coastline and some from accidental drowning in fishnets; none were deliberately killed (cf. Guinet et al., 1998). Routine necropsies were performed and biological parameters recorded, based on recommendations of the Committee on Marine Mammals (1967). Animals were aged from incremental lines observed in the dentine of upper canines (Stewardson et al., 2008, 2009). The sample was supplemented with measurements from 11 known-aged adult males (animals tagged as pups) from Marine and Coastal Management (MCM), Cape Town. The specimens from the MCM collection have accession numbers beginning with MCM (e.g. MCM 1809). The MCM collection also housed 5 tag-aged adult females and 3 tag-aged sub adult/juvenile females.

All animals considered adults had reached full reproductive capacity, i.e., males ≥ 8 y (Stewardson et al., 1998; Stewardson et al., 2008, 2009) and females ≥ 3 y (J.H.M. David, pers. comm.). When age was not known, males ≥ 170 cm (Stewardson et al., 2008, 2009) and females ≥ 135 cm (Guinet et al., 1998; J.H.M. David, pers. comm.) were considered fully adult males and females and included in the analysis as adults even if their dentition age was less than 8 y for males. South African fur seals ≥ 12 y cannot be aged from counts of growth layer groups (GLG) in the dentine of upper canines because of closure of the pulp cavity. Estimated longevity for male South African Fur seals is c. 20 y (Wickens, 1993; Stewardson et al., 2008, 2009). There is much less information on the longevity of female South African fur seals (despite the large numbers of animals that are shot in culling and hunting operations) but Wickens (1993) based on zoo records concluded that females could live to c. 30 y.

Australian male fur seals (*A. pusillus doriferus*) also have a similar lifespan of about 20 years but female Australian fur seals based on age tags are currently known to live to well over 20 y (Arnould and Warneke, 2002). Seal life spans in a range of seal species average about 15 to 20 y for males and in excess of 20 y for females (New Zealand fur seal (*A. australis forsteri*), McKenzie et al., 2007; Antarctic fur seal (*A. gazella*), Payne, 1978, 1979); Steller sea lion (*Eumetopias jubatus*), Winship et al., 2001).

Museum records

The data set on the males used in the present study has already been published in (Stewardson et al., 2008) and further details can be found in Stewardson (2001). The list of male specimens used in the present study is shown in Appendix 1. There were 39 adult males, 24 immature sub adult males and two juvenile males only 2 years old. No standard body length measurements were available on four (4) of the adult males (PEM 2004, PEM 2007, PEM 2013, PEM 2036) but it is unlikely that any adult male skulls would be assigned to the wrong sex because mature male skulls are much larger than females and more heavily built. However, there were no **SBL** measurements available on four (4) of the immature males (PEM 2006, PEM 2009, PEM 2010 and PEM 2014). This raises some doubts about the certainty that these specimens were correctly identified as males. Generally if the **SBL** had been determined, the genitalia would have been available for examination. The raw data set for the females (18 adults, 4 juveniles and sub adults) is shown in Appendix 2 and the means and standard deviations in Appendix 3. All the female carcasses were complete enough for reliable determination of their sex.

Skull variables

A total of 32 skull measurements were recorded (Table 1). However, one of these variables, height of sagittal crest, was not examined statistically because there were few measurements for females and also because we have found that sagittal crest measurements seem to provide little useful information in male skulls (Stewardson et al., 2008). Thus, statistical analysis was conducted on 31 of the 32 variables. Skull preparation and measurement procedures follow Stewardson et al. (2008).

Statistical analyses

Six methods of analyses were employed. Firstly, two sample t-tests (assuming equal variance) were used to test the hypothesis that the mean value of a skull variable was significantly different for males and females against an appropriate alternative hypothesis (H_0: $\mu_{males}=\mu_{females}$; H_1: $\mu_{males}>\mu_{females}$; H_1: $\mu_{females} > \mu_{males}$). Since more than 1 skull variable was being considered, the Bonferroni correction was used - the experiment-wise error rate was divided by the total number of tests performed (Cochran, 1977).

Secondly, K-means clustering, a non-hierarchical cluster analysis was used to classify observations into 1 of 2 groups based on some of the skull variables. Observations on some of the skull variables from both sexes were pooled so that initially there is a single cluster with its centre as the mean vector of the variables considered. These observations were then assigned at random to two sets. Step 1 entails calculating the mean vector of the variables considered (centroid) for each set. Step 2 entails allocating each observation to the cluster whose centroid is closest to that observation. These two steps are repeated until a stopping criterion is met (there is no further change in the assignment of the data points). Before doing this all variables were standardised. Closest neighbour (similarity) was measured using Euclidean distance (Johnson and Wichern, 1992). The groupings of skull variables we considered were dorsal, palatal, lateral and mandibular. We also used k-means clustering to classify observations into 1 of 2 groups using standard body length.

Thirdly, plots of $\log_e$ of each skull variable against $\log_e$ of standard body length **(SBL)** for the genders were examined. 'Robust' regression (Huber M-Regression) was used to fit straight lines ($\log y = \log a + b \log x$) to the transformed data (Weisberg, 1985; Myers, 1990).

Fourthly, principal component analysis (PCA) was used. One useful application of PCA is identifying the most important sources of variation in anatomical measurements for various species (Jackson, 1991; Jolliffe, 2002). When the covariance matrix is used and the data has not been standardized the first principle component (PC) usually has all positive coefficients and according to Jolliffe (2002) this reflects the overall 'size' of the individuals. The other PCs usually contrast some measurements with others and according to Jolliffe (2002) this can often be interpreted as reflecting certain aspects of 'shape', which are important to the species.

Skull measurements were recorded in the same units; therefore a covariance matrix was used to calculate PCs (however this gives greater weight to larger, and hence possibly more variable measurements because the variables are not all treated on an equal footing). Genders were examined separately because the grouped PCA was quite different, in most cases, to either the separate male PCA or female PCA.

PCA and two sample t-tests were calculated in Minitab (Minitab Inc., Slate College, 1999, 12.23). K-means cluster analyses for skull variables and **SBL** were calculated in Minitab (Minitab Inc., Slate College, 1999, 12.23) and in SPSS (SPSS Inc., Chicago, Illinois, 1989-1999, 9.0.1), respectively. This was necessary because Minitab could only perform K-means cluster analysis for 2 or more variables, therefore **SBL** (a single variable) was analysed in SPSS. The regressions were fitted in S-PLUS (MathSoft, Inc., Seattle, 1999, 5.1).

Fifthly, the data mining approach, Classification and Regression Trees (CART), a technique that generates a binary decision tree, was used to classify the observations. In this approach, the set of data is progressively sub-divided based on values of predictor variables into groups that contain higher proportions of "successes" and higher proportions of "failures". The relative importance of the predictor variables is assessed in terms of how much they contribute to successful splits into more homogeneous sub-groups. The classification is most commonly carried out using the Gini criterion, which always selects the split that maximises the proportion of "successes" in one of the groups (Petocz, 2003). Data mining techniques are attractive because no distributional assumptions are needed, data sets can have missing data and analyses are less time consuming. The training data used to create the binary decision set was the set of all animals that have already been determined to be adult males, immature males and mature females. SPSS Clementine 12.0 was used for the analysis.

Finally, Minitab was also used to perform hierarchical clustering and produce dendrograms showing the degree of similarity of the skull data for males, females and immature males. In general, the conclusions reached were similar to those from the CART analysis: it was possible to distinguish mature males from immature males and mature females but it was not possible to clearly distinguish immature males from females.

Unless otherwise stated values are means quoted ± standard errors with the number of data points in brackets.

RESULTS

Standard body length (SBL)

SBL ranged from 157-201 cm in males (n = 33, **SBL** was not recorded for 4 of the adult males) and 135-179 cm in females (n = 18). Mean lengths were 182.9 ± 2.3 (n = 33) and 149.1 ± 2.5 (n = 18), respectively. The two sample t-tests on our data indicated that adult males were significantly larger than adult females (Table 1). The ratio of mean female **SBL** to mean male **SBL** was 1:1.23.

K-means cluster analysis successfully identified 2 relatively homogeneous groups from the pooled data, i.e., cluster 1, predominantly males and cluster 2, predominantly females (Table 2). Of the 18 females, 17 (94%) were correctly classified. Of the 33 males, 28 (85%) were correctly classified.

Table 1: Summary statistics (mean, S.E, C.V. & n) for skull measurements (mm) and standard body lengths (cm) from male and female South African fur seals (*Arctocephalus pusillus pusillus*), and comparison between the mean of the two sexes (two sample t-test). Skull measurements relative to condylobasal length (CBL) are given in brackets. Refer to Stewardson et al. (2008) for a description of skull measurement procedures.

Skull variables	Male				Female				Two sample t-test			Significant Size Difference
	mean	S.E.	C.V.	n	mean	S.E.	C.V.	n	T	P	df	
Dorsal												
Dl Condylobasal length **(CBL)**	247.1	2.1	5.2	37	212.2	1.8	3.5	18	12.7	< 0.0005	50	**M > F****
D2 Gnathion to middle of occipital crest	217.7 (0.88)	2.8 (0.005)	7.6 (3.43)	35	182.9 (0.86)	1.4 (0.004)	3.2 (2.07)	18	^{T}11.5 (2.64)	< 0.0005 (0.011)	50 (49)	**M > F**** (M = F)
D3 Gnathion to posterior end of nasals	88.9 (0.36)	1.2 (0.003)	8.4 (4.72)	36	72.5 (0.34)	1.0 (0.003)	5.8 (4.26)	18	10.3 (3.96)	< 0.0005 (< 0.0005)	51 (39)	**M > F**** **(M > F**)**
D4 Greatest width of anterior nares	28.6 (0.12)	0.5 (0.001)	9.4 (6.98)	36	24.0 (0.11)	0.5 (0.002)	7.8 (6.87)	15	6.9 (0.96)	< 0.0005 (0.345)	37 (27)	**M > F**** (M = F)
D5 Greatest length of nasals	44.0 (0.18)	0.9 (0.003)	11.7 (8.70)	35	37.5 (0.18)	0.7 (0.003)	7.4 (6.29)	17	5.9 (0.03)	< 0.0005 (0.978)	49 (42)	**M > F**** (M = F)
D6 Breadth at preorbital processes	68.1 (0.28)	0.9 (0.002)	7.4 (4.61)	33	53.3 (0.25)	1.0 (0.003)	6.9 (5.15)	14	^{T}11.2 (5.95)	< 0.0005 (< 0.0005)	33 (24)	**M > F**** **(M > F**)**
D7 Least interorbital constriction	37.7 (0.15)	0.5 (0.002)	7.8 (7.12)	32	28.0 (0.13)	0.9 (0.003)	12.4 (10.45)	16	^{T}9.7 (5.52)	< 0.0005 (< 0.0005)	26 (24)	**M > F**** **(M > F**)**
D8 Breadth at supraorbital processes	56.8 (0.23)	0.9 (0.003)	9.3 (8.35)	33	43.9 (0.21)	1.0 (0.004)	8.9 (7.75)	16	9.6 (4.60)	< 0.0005 (< 0.0005)	38 (35)	M > F** **(M > F**)**
D9 Breadth of brain case	84.2 (0.34)	0.6 (0.003)	4.5 (5.63)	36	82.0 (0.39)	1.1 (0.005)	5.5 (5.09)	18	1.8 (7.87)	0.089 (< 0.0005)	29 (33)	M = F **(F > M**)**
Palatal												
P10 Palatal notch to incisors	105.0 (0.42)	1.4 (0.004)	8.1 (5.12)	37	88.0 (0.41)	1.6 (0.007)	7.9 (6.75)	18	7.9 (1.30)	< 0.0005 (0.204)	40 (27)	**M > F**** (M = F)
P11 Length of upper postcanine row	60.4 (0.24)	0.7 (0.002)	7.4 (6.08)	37	54.9 (0.26)	0.6 (0.003)	4.7 (4.58)	18	5.8 (3.87)	< 0.0005 (< 0.0005)	51 (41)	**M > F**** **(F > M**)**
P12 Greatest bicanine breadth	50.9 (0.21)	0.9 (0.002)	10.1 (6.75)	37	37.0 (0.17)	0.8 (0.003)	9.5 (6.80)	18	11.7 (8.72)	< 0.0005 (< 0.0005)	47 (39)	**M > F**** **(M > F**)**
P13 Gnathion to posterior end of maxilla	116.4 (0.47)	1.2 (0.002)	6.4 (2.82)	36	99.0 (0.47)	0.9 (0.002)	3.8 (1.71)	17	11.4 (1.83)	< 0.0005 (0.740)	50 (47)	**M > F**** (M = F)

Table 1 continued

Skull variables	Male				Female				Two sample t-test			Significant Size Difference
	mean	S.E.	C.V.	n	mean	S.E.	C.V.	n	T	P	df	
P14 Breadth of zygomatic root of maxilla	15.7 (0.06)	0.3 (0.001)	13.3 (10.19)	37	12.2 (0.06)	0.3 (0.001)	11.0 (10.27)	18	7.6 (3.49)	< 0.0005 (0.001)	48 (36)	M > F** (M = F)
P15 Breadth of palate at postcanine 1	25.7 (0.01)	0.6 (0.002)	13.4 (11.05)	33	18.7 (0.09)	0.5 (0.002)	12.3 (10.39)	18	8.7 (5.32)	< 0.0005 (< 0.0005)	46 (42)	M > F** (M > F**)
P16 Breadth of palate at postcanine 3	27.8 (0.11)	0.5 (0.002)	10.9 (8.74)	34	21.1 (0.10)	0.3 (0.002)	6.7 (6.45)	17	10.8 (5.37)	< 0.0005 (< 0.0005)	48 (45)	M > F** (M > F**)
P17 Breadth of palate at postcanine 5	33.8 (0.14)	0.5 (0.002)	9.7 (7.71)	36	26.8 (0.13)	0.5 (0.002)	8.0 (8.02)	18	9.4 (3.42)	< 0.0005 (0.002)	48 (35)	M > F** (M = F)
P18 Gnathion to hind border of postglenoid process	187.5 (0.76)	1.9 (0.002)	6.1 (1.56)	35	159.0 (0.75)	1.5 (0.003)	4.0 (1.43)	18	11.6 (2.43)	<0.0005 (0.020)	50 (37)	M > F** (M = F)
P19 Bizygomatic breath	141.4 (0.57)	1.7 (0.006)	7.4 (5.88)	37	120.1 (0.57)	1.8 (0.005)	6.5 (4.10)	18	8.5 (0.87)	<0.0005 (0.388)	44 (46)	M > F** (M = F)
P20 Basion to zygomatic root (anterior)	168.5 (0.68)	1.5 (0.002)	5.4 (1.70)	36	145.5 (0.69)	1.2 (0.003)	3.6 (1.62)	18	^{T}11.8 (1.61)	< 0.0005 (0.117)	50 (35)	M> F** (M = F)
P21 Calvarial breadth	116.7 (0.47)	1.1 (0.003)	5.5 (3.20)	35	95.2 (0.45)	1.0 (0.003)	4.5 (2.79)	18	^{T}14.4 (5.73)	< 0.0005 (< 0.0005)	50 (40)	M> F** (M > F**)
P22 Mastoid breadth	132.6 (0.54)	1.7 (0.004)	7.6 (4.26)	35	107.5 (0.51)	1.4 (0.005)	5.7 (3.80)	18	11.2 (5.13)	< 0.0005 (< 0.0005)	49 (40)	M> F** (M > F**)
P23 Basion to bend of pterygoid	79.0 (0.32)	0.6 (0.002)	4.5 (3.23)	35	69.4 (0.33)	0.7 (0.002)	4.1 (3.10)	18	10.6 (2.29)	< 0.0005 (0.028)	41 (35)	M > F** (M = F)
Lateral												
L24 Gnathion to foramen infraorbital	75.0 (0.30)	0.9 (0.001)	7.0 (3.00)	37	60.8 (0.29)	1.1 (0.004)	7.3 (5.49)	17	10.3 (4.06)	< 0.0005 (0.0006)	36 (21)	M > F** (M > F*)
L25 Gnathion to hind border of preorbital process	82.2 (0.33)	1.0 (0.002)	7.0 (2.87)	36	65.8 (0.31)	0.9 (0.003)	5.2 (3.36)	16	12.8 (6.77)	< 0.0005 (< 0.0005)	45 (26)	M > F** (M > F*)
L26 Height of skull at bottom of mastoid	108.7 (0.49)	1.8 (0.005)	10.0 (6.54)	36	88.7 (0.41)	1.5 (0.004)	5.7 (3.59)	11	8.5 (3.79)	< 0.0005 (0.0006)	37 (33)	M > F** (M > F**)
L27a Height of sagittal crest	-	-	-	-	-	-	-	-	-	-	-	-

Table 1 continued

Mandibular												
M28 Length of mandible	173.7 (0.70)	1.7 (0.002)	5.9 (2.09)	36	146.2 (0.69)	1.9 (0.005)	5.5 (2.75)	17	10.6 (2.20)	< 0.0005 (0.038)	39 (25)	**M > F**** (M = F)
M29 Length of mandibular tooth row	69.9 (0.29)	0.8 (0.002)	6.0 (4.49)	31	55.2 (0.26)	1.5 (0.007)	10.9 (11.19)	17	ᵀ 10.0 (ᵀ3.70)	< 0.0005 (< 0.001)	40 (26)	**M > F**** (M = F)
Skull variables	**Male**				**Female**				**Two sample t-test**			**Significant Size Difference**
	mean	**S.E.**	**C.V.**	**n**	**mean**	**S.E.**	**C.V.**	**n**	**T**	**P**	**df**	
M30 Length of lower postcanine row	47.1 (0.19)	0.4 (0.001)	5.7 (4.55)	35	42.5 (0.20)	0.5 (0.002)	5.0 (4.47)	16	6.6 (3.62)	< 0.0005 (< 0.001)	35 (28)	**M > F**** (M = F)
M31 Height of mandible at meatus	58.3 (0.24)	1.1 (0.003)	11.3 (7.97)	37	44.1 (0.21)	0.9 (0.003)	8.7 (6.64)	17	10.0 (6.10)	< 0.0005 (< 0.0005)	48 (41)	**M > F**** **(M > F**)**
M32 Angularis to coronoideus	58.7 (0.24)	1.0 (0.003)	10.5 (6.70)	35	47.3 (0.22)	0.9 (0.003)	7.4 (6.01)	17	8.4 (3.22)	< 0.0005 (0.0026)	48 (37)	**M > F**** (M = F)
Standard body length (SBL)	182.9	2.3	7.2	33	149.1	2.5	7.1	18	10.0	< 0.0005	41	**(M > F**)**

a Height of sagittal crest (L27) was not examined statistically because there were too few measurements for females. However, in large animals, male crest height was greater than female crest height.
Students-t normality assumption did not hold (data skewed); therefore the data was transformed using Box-Cox transformation (Myers, 1990).
* Significant at the 5% level, with Bonferroni correction.
** Significant at the 1% level, with Bonferroni correction.
df values were calculated for a two sample t-test allowing for unequal variances.
C.V. is coefficient of variation S.E./mean X 100.

Table 2: Classification of skull measurements of South African fur seals using K-means clusters analysis. n is the number of animals. All variables except standard body length (SBL) were standardised (dorsal, palatal and mandibular).

Skull variables	Sex	Cluster 1	Cluster 2	n
Dorsal	Male	22 (96%)	1 (4%)	23
	Female	0	11 (100%)	11
Palatal	Male	24 (92%)	2 (8%)	26
	Female	0	17 (100%)	17
Lateral	Male	28 (80%)	7 (20%)	35
	Female	0	10 (100%)	17
Mandibular	Male	25 (93%)	2 (7%)	27
	Female	1 (6%)	16 (94%)	17
Standard body length	Male	28 (85%)	5 (15%)	33
	Female	1 (6%)	17 (94%)	18

Skull variables

Absolute skull size: two sample t-tests

The two sample t-tests indicated that 30 of the 31 mean skull variables were significantly larger in males than in females, i.e., we reject H_0 in favour of H_1: $\mu_{male} > \mu_{female}$ (Table 1, Fig. 1). Mean value of breadth of brain case **(D9)** was not significantly different for the genders (Table 1). The coefficient of variation (C.V.) was larger in males, with the following exceptions: least interorbital constriction **(D7)**, breadth of brain case **(D9)**, gnathion to anterior of foramen infraorbital **(L24)** and length of mandibular tooth row **(M29)** (Table 1). Height of sagittal crest **(L27)** was not examined statistically because there were too many skulls with missing or damaged sagittal crests.

Relative skull size: two sample t-tests

When skull variables were analysed relative to condylobasal length **(CBL, D1)**, males were found to be significantly larger than females for 13 (43%) variables: (1) gnathion to posterior end of nasals **(D3)**, (2) breadth at preorbital processes **(D8)**, (3) least interorbital constriction **(D7)**, (4) breadth at supraorbital processes **(D8)**, (5) greatest bicanine breadth **(P12)**, (6) breadth of palate at postcanine 1

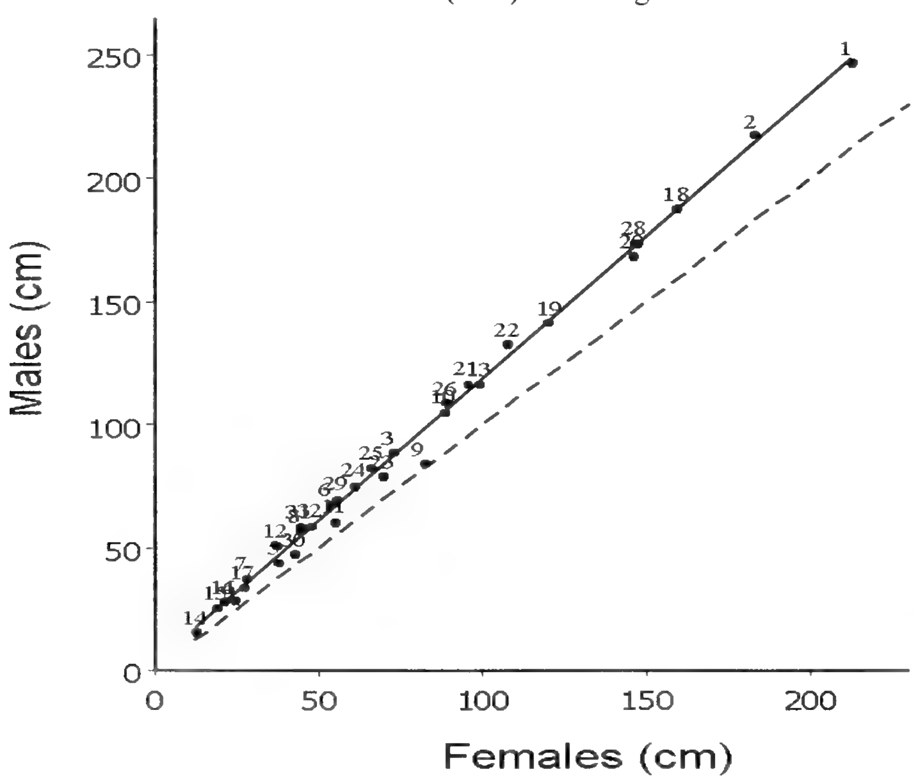


Fig. 1: Mean values of 31 skull variables for male and female South African fur seals. Numbers correspond to skull variables listed in Table 1 (numbers 1-9 correspond to parameters D1 to D9, 10-23 to P10 to P23 and 24-32 to L24 to L32). Numbers above the dashed line, males > females; numbers on the line, males = females; numbers below the line, females > males. Minitab could only perform K-means cluster analysis if there was ≥ 2 variables, therefore SBL (a single variable) was analysed in SPSS. SBL was not recorded for 4 of the 39 males (i.e., n = 35).

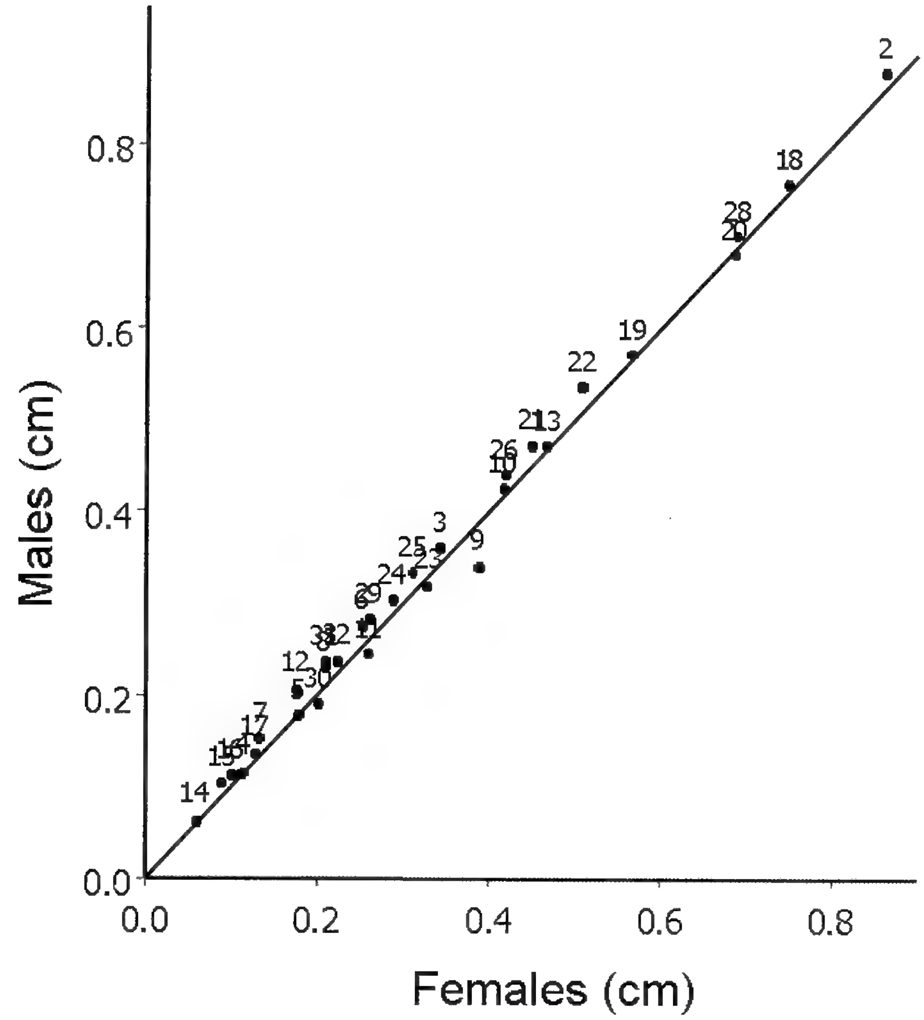


Fig. 2: Mean values of 30 skull variables, relative to condylobasal length, for male and female South African fur seals. Numbers correspond to skull variables listed in Table 1 (numbers 1-9 correspond to parameters D1 to D9, D10-23 to P10 to P23 and P24-32 to L24 to L32). Numbers above the line, males > females; numbers on the line, males = females, numbers below the line, females > males.

(P15), (7) breadth of palate at postcanine 3 **(P16)**, (8) calvarial breadth **(P21)**, (9) mastoid breadth **(P22)**, (10) gnathion to foramen infraorbital **(L24)**, (11) gnathion to hind border of preorbital process **(L25)**, (12) height of skull at bottom of mastoid **(L26)** and (13) height of mandible at meatus **(M31)** (Table 1, Fig. 2). Differences between the genders were highly significant ($P < 0.001$); apart from gnathion to foramen infraorbital **(L24)** and height of skull at bottom of mastoid **(L26)**, which were significant at the 5% level (Table 1).

Breadth of brain case **(D9)** was significantly different in 'absolute size' for males and females, but 'relative to **CBL**' parameter **D9/D1** for females was larger than males (Table 1). Length of upper postcanine row **(P11)** was larger in 'absolute size' in males, but 'relative to **CBL**' **P11/D1** in females was larger than in males (Table 1).

The remaining 15 (50%) variables were not significantly different for the genders (Table 1). Since males were larger than females in 'absolute size', this suggested that the 15 variables were proportionate to **CBL** regardless of sex, i.e., the ratio relative to **CBL (D1)** was significantly different for the genders.

The coefficient of variation for values 'relative to **CBL**' was larger in males for about 1/3 rd of all variables (Table 1). Exceptions were breadth at preorbital processes **(D6)**, least interorbital constriction **(D7)**, palatal notch to incisors **(P10)**, breadth of zygomatic root of maxilla **(P14)**, breadth of palate at postcanine 5 **(P17)**, gnathion to foramen infraorbital **(L24)**, gnathion to hind border of preorbital process **(L25)**, length of mandible **(M28)** and length of mandibular tooth row **(M29)**. The coefficients of 2 of these variables (least interorbital constriction **(D7)** and length of mandibular tooth row **(M29)**) were considerably larger in females in both 'absolute size' and size 'relative to **CBL**' **(M29/D1** and **D7/D1).**

K-means cluster analysis

K-means cluster analysis successfully identified 2 relatively homogeneous groups from the pooled data, i.e., cluster 1, predominantly males and cluster 2, predominantly females (Table 2). Classification based on dorsal, palatal and mandibular observations was highly successful in recapturing the 2 groups. Classification based on lateral observations was less successful.

Apart from 1 mandibular variable, all females were correctly classified. The majority of males were correctly classified with the following exceptions - 1 dorsal, 2 palatal, 2 mandibular and 7 lateral variables were incorrectly classified as females (Table 2). Misclassification occurred in small males only.

Fig. 3

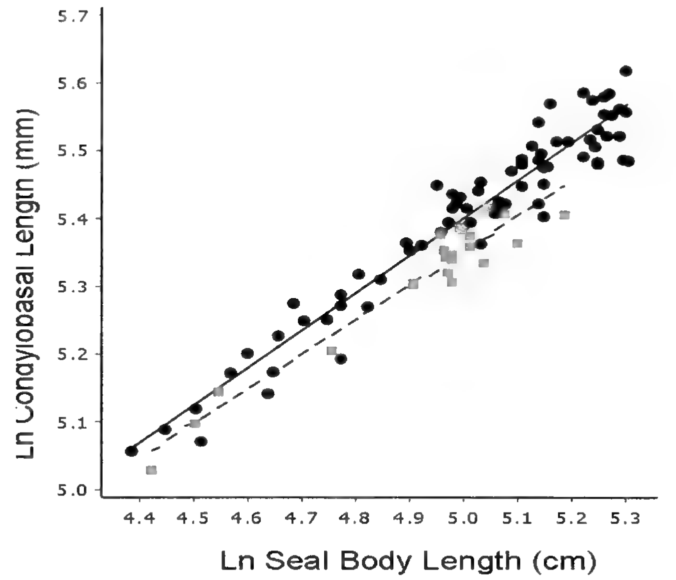


Fig. 4

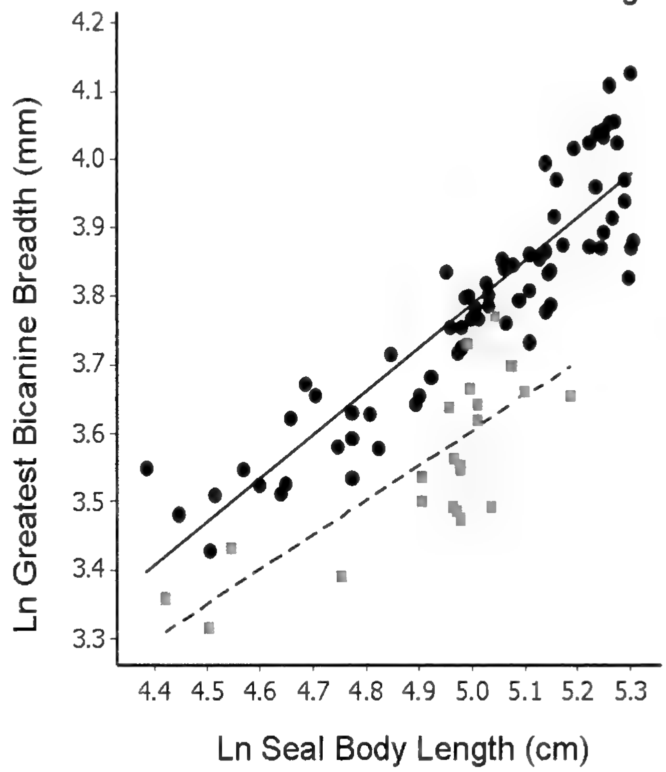
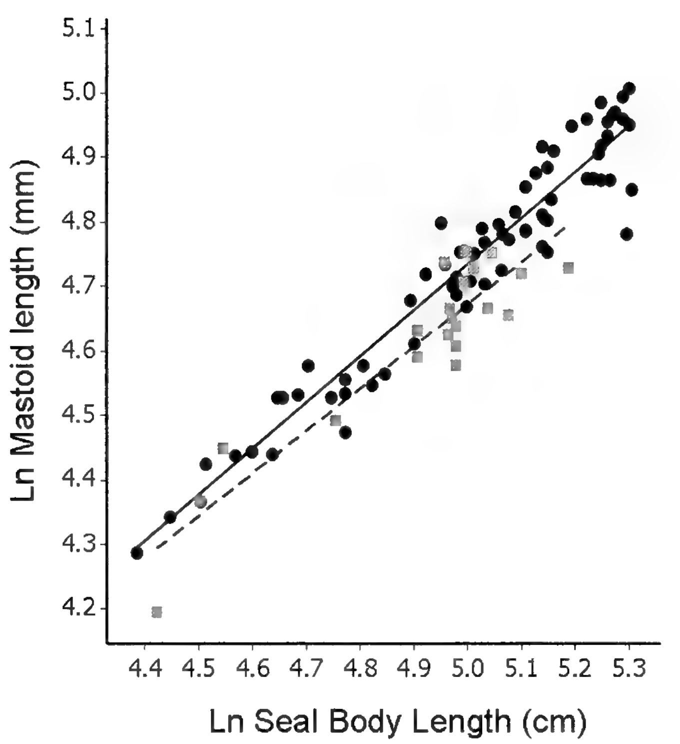


Fig. 5



Figs. 3, 4 & 5: Bivariate plot of: (3) log [CBL (D1) (mm)] on log (SBL (cm)); (4) log [greatest bicanine breadth (P12) (mm)] on log (SBL (cm)); (5) log [mastoid breadth (P22) (mm)] on log (SBL (cm). Circles, males. Squares, females.

Linear regression

All transformed variables were regressed on $\log_e$ (**SBL** in cm). Three variables that best depicted maximum discrimination between the sexes, using regression, are given in Figs. 3, 4 and 5. These were **CBL (D1)**, greatest bicanine breadth **(P12)** and mastoid breadth **(P22)**. These plots (males closed black circles, females grey squares) clearly show pronounced sexual dimorphism in adult South African fur seals, supporting findings of the two-sample t-test and K-means cluster analysis.

Principal component (PC) analysis

The first 3 PCs accounted for most of the variation. The first PC (PCI) can be interpreted as a measure of overall skull size while PC2 and PC3 define certain aspects of shape (Table 3). Interpretations for the first 3 PCs for the 2 genders are given in Table 4, together with the percentage of total variation given by each PC. The variances of corresponding PCs for the two genders do vary and interpretations are dissimilar for most pairs of PCs.

Determining the gender of an isolated skull

It is claimed that it is often possible to make a visual determination of the gender of an isolated South African fur seal skull, provided the skull is from an adult animal (Brunner, 1998ab). However, visual identification based on morphology of the skull alone can be misleading, e.g., young adult males can be mistaken for larger, older females and sex determination of a pup from examining the skull alone would be very difficult. A more objective procedure in determining sexes of skulls would be desirable. In most practical situations if the carcass was available for examination, the sex would usually be determinable, however for many museum specimens only the skull is available. The

Table 3: Principal component (PC) analysis of covariance matrix for adult male and adult female South African fur seals, showing principal components, eigenvalues, proportions and cumulative proportions of the first three principal components. Proportion gives the amount of the total variation that the PC accounted for. Cumulative tally gives the amount the first PC accounted for, then the amount that the first two PCs accounted for and finally the amount of total variation the first three PCs accounted for. Height of sagittal crest (L27) was not examined statistically because there were few measurements for females.

	PC I	PC II	PC III	PC I	PC II	PC III
Dorsal	Males (n = 23)			Females (n = 10)		
D1 Condylobasal length	-0.58	-0.35	-0.50	-0.61	0.48	0.38
D2 Gnathion to middle of occipital crest	-0.71.	-0.06	0.52	-0.28	-0.001	-0.32
D3 Gnathion to posterior end of nasals	-0.28	0.30	-0.28	-0.24	-0.49	0.09
D4 Greatest width of anterior nares	-0.10	0.16	0.03	-0.16	0.28	0.06
D5 Greatest length of nasals	-0.16	0.34	0.02	-0.08	-0.25	0.04
D6 Breadth at preorbital processes	-0.19	0.30	-0.28	-0.41	0.15	-0.17
D7 Least interorbital constriction	-0.08	0.29	0.09	-0.37	-0.15	-0.14
D8 Greatest breadth at supraorbital processes	-0.08	0.49	0.38	-0.36	-0.39	-0.43
D9 Breadth of brain case	-0.03	-0.48	0.41	-0.15	-0.44	0.71
Eigenvalue	**444.9**	**36.1**	**15.7**	**93.7**	**17.7**	**12.7**
Proportion	**0.84**	**0.07**	**0.03**	**0.68**	**0.13**	**0.09**
Cumulative	**0.84**	**0.91**	**0.94**	**0.68**	**0.81**	**0.91**
Palatal	Males (n = 26)			Females (n = 16)		
P10 Palatal notch to incisors	-0.31	-0.21.	0.82	-0.34	0.83	0.32
P11 Length of upper postcanine row	-0.13	-0.13	0.10	-0.08	-0.06	-0.02
P12 Greatest bicanine breadth	-0.19	0.03	-0.01	-0.20	-0.08	-0.19
P13 Gnathion to posterior end of maxilla	-0.30	-0.34	-0.06	-0.24	0.04	0.10
P14 Breadth of zygomatic root of maxilla	-0.07	-0.01	-0.003	-0.03	-0.04	0.04
P15 Breadth of palate at postcanine 1	-0.10	0.03	-0.14	-0.11	0.08	-0.21
P16 Breadth of palate at postcanine 3	-0.08	0.04	-0.08	-0.03	0.09	-0.24
P17 Breadth of palate at postcanine 5	-0.10	0.05	-0.14	-0.02	0.08	-0.24
P18 Gnathion to posterior border of postglenoid	-0.50	-0.18	-0.06	-0.41	-0.16	-0.21
P19 Bizygomatic breadth	-0.30	0.86	0.23	-0.53	-0.15	0.27
P20 Basion to zygomatic root	-0.41	-0.11	-0.13	-0.30	0.13	-0.66
P21 Calvarial breadth	-0.25	0.13	-0.31	-0.26	-0.15	0.19
P22 Mastoid breadth	-0.39	0.05	-0.28	-0.37	-0.42	0.17
P23 Basion to bend of pterygoid	-0.13	-0.08	-0.13	-0.13	0.14	0.26
Eigenvalue	**507.1**	**84.4**	**35.0**	**155.5**	**44.4**	**13.9**
Proportion	**0.73**	**0.12**	**0.05**	**0.62**	**0.18**	**0.06**
Cumulative	**0.73**	**0.85**	**0.90**	**0.62**	**0.79**	**0.85**
Lateral	Males (n = 35)			Females (n = 10)		
L24 Gnathion to anterior of foramen infraorbital	0.39	-0.56	0.73	0.24	-0.71	0.66
L25 Gnathion to posterior border of preorbital process	0.43	-0.59	-0.68	0.33	-0.58	-0.74
L26 Height of skull at base of mastoid	0.82	0.58	0.01	0.91	0.40	0.09
L27a Height of sagittal crest	-	-	-	-	-	-
Eigenvalue	**153.8**	**14.5**	**0.7**	**31.4**	**6.3**	**0.8**
Proportion	**0.91**	**0.09**	**0.004**	**0.82**	**0.16**	**0.02**
Cumulative	**0.91**	**0.996**	**1.00**	**0.82**	**0.98**	**1.00**
Mandibular	Males (n = 26)			Females (n = 16)		
M28 Length of mandible	-0.73	0.38	-0.41	-0.86	-0.20	-0.35
M29 Length of mandibular tooth row	-0.19	0.45	0.57	-0.13	0.96	-0.23
M30 Length of lower postcanine row	-0.12	0.47	0.13	-0.15	-0.09	-0.37
M31 Height of mandible at meatus	-0.49	-0.48	0.63	-0.37	0.05	0.50
M32 Angularis to coronoideus	-0.42	-0.46	-0.31	-0.30	0.14	0.66
Eigenvalue	**145.2**	**13.9**	**8.0**	**88.5**	**27.2**	**9.1**
Proportion	**0.84**	**0.08**	**0.05**	**0.70**	**0.21**	**0.07**
Cumulative	**0.84**	**0.92**	**0.97**	**0.70**	**0.91**	**0.98**

Table 4: Interpretations for the first 3 principal components for the skulls parameters for adult male and adult female South African fur seals. Variables that contributed predominantly to size and/or shapes, i.e. variables with loadings ≥ 0.36 (absolute value) were used in the covariance matrix. Only 2 principal components were considered for the analysis of lateral components because component 3 was 2% or less of total variation.

Male	Female
Dorsal Component 1 (male 84%, female 68%)	
CBL **(D1)** and gnathion to middle of occipital crest **(D2)** measure overall size.	CBL **(D1)**, breadth at preorbital processes **(D6)**, least interorbital constriction **(D7)** and greatest breadth at supraorbital processes **(D8)** measures overall size.
Component 2 (male 7%, female 13%)	
Contrasts greatest breadth at supraorbital processes **(D8)** with CBL **(D1)** and breadth of brain case **(D9)**.	Contrasts CBL **(D1)** with gnathion to posterior end of nasals **(D3)**, greatest breadth at supraorbital processes **(D8)** and breadth of brain case **(D9)**.
Component 3 (male 3%, female 9%)	
Contrasts CBL **(D1)** with gnathion to middle of occipital crest **(D2)**, greatest breath at supraorbital processes **(D8)** and breath of brain case **(D9)**.	Contrasts greatest breadth at supraorbital processes **(D8)** with CBL **(D1)** and breadth of brain case **(D9)**.
Palatal Component 1 (male 73%, female 62%)	
Gnathion to posterior border of postglenoid process **(P18)**, basion to zygomatic root **(P20)** and mastoid breadth **(P22)** measure overall size.	Gnathion to posterior border of postglenoid process **(P18)**, bizygomatic breath **(P19)** and mastoid breadth **(P22)** measure overall size.
Component 2 (male 12%, female 18%)	
Bizygomatic breadth **(P19)** dominates.	Contrasts palatal notch to incisors **(P10)** with mastoid breadth **(P22)**.
Component 3 (male 5%, female 6%)	
Palatal notch to incisors **(P10)** dominates	Bastion to zygomatic root **(P20)** dominates.
Lateral (only 2 PCs considered) Component 1 (male 91%, female 82%)	
Height of skull at base of mastoid **(L26)**, gnathion to posterior border of preorbital process **(L25)** and gnathion to anterior of foramen infraorbital **(L24)** measure overall size.	Height of skull at base of mastoid process **(L26)** measures overall size.
Component 2 (male 9%, female 16%)	
Contrasts height of skull at base of mastoid **(L26)** with gnathion to anterior of foramen infraorbital **(L24)** and gnathion to posterior border of preorbital process **(L25)**.	Contrasts height of skull at base of mastoid **(L26)** with gnathion to anterior of foramen infraorbital **(L24)** and gnathion to posterior border of preorbital process **(L25)**.
Mandibular Component 1 (male 84%, female 70%)	
Length of mandible **(M28)**, height of mandible at meatus **(M31)** and angularis to coronoideus **(M32)** measure overall size.	Length of mandible **(M28)** and height of mandible at meatus **(M31)** measure overall size.
Component 2 (male 8%, female 21%)	
Contrasts height of mandible at meatus **(M31)** and angularis to coronoideus **(M32)** with others [length of mandible **(M28)**, length of mandibular tooth row **(M29)**, length of lower postcanine row **(M30)**].	Length of mandibular tooth row **(M29)** dominates.
Component 3 (male 5%, female 7%)	
Contrasts length of mandible **(M28)** with length of mandibular tooth row **(M29)** and height of mandible at meatus **(M31)**.	Contrasts length of mandible **(M28)** and length of lower postcanine row **(M30)** with height of mandible at meatus **(M31)** and angularis to coronoideus **(M30)**.

sex of tagged individuals would nearly always be known, as it would have been recorded when they were tagged.

We have focused on trying to develop a method for making an objective determination of sex based on only skull material. Aging untagged specimens from dentition (counting the growth layer groups in the upper canine) is an important component of making an objective sex determination.

The skull of an adult male ≥ 10 y is larger (**CBL** ≥248 mm; mastoid breadth ≥ 134 mm) and more robust than the skull of a similar aged female. In adult males, bony deposits occur throughout the parietal region of the skull, which become more prominent with increasing age (Rand, 1949ab; Stewardson et al., 2008; present study). Mean size of male sexually dimorphic traits, according to age (y), have been summarised elsewhere (Stewardson et al., 2008, 2009).

Classification and Regression Tree using 3 levels (58 animals)

Fig. 6 shows an animal is classified as being an immature male if **I25**<=73.7, **P12**<=35.85 and **P16**<=17.24 or if **I25**<=73.7, **P12**>35.85 and **M32**<=50.5 or if **I25**>73.7, **P12**<=45.1 and **D5**<=41.65. An animal is classified as being a mature female if **I25**<73.7, **P12**<=35.85 and **P16**>17.25 or if **I24**<=73.7, **P12**>35.85 and **M32**>50.5. An animal is classified as being a mature male if **I25**>73.7 and **P12**>45.1 or if **I25**>73.7, **P12**<=45.1 and **D5**>41.65. This rule correctly classifies 94.82% of the animals. Three immature males are misclassified as being a mature female (15% of all immature males). All mature females are correctly classified as being mature females, and all mature males are correctly classified as being mature females. Fig. 6 includes a prediction matrix to summarise the classification of the animals.

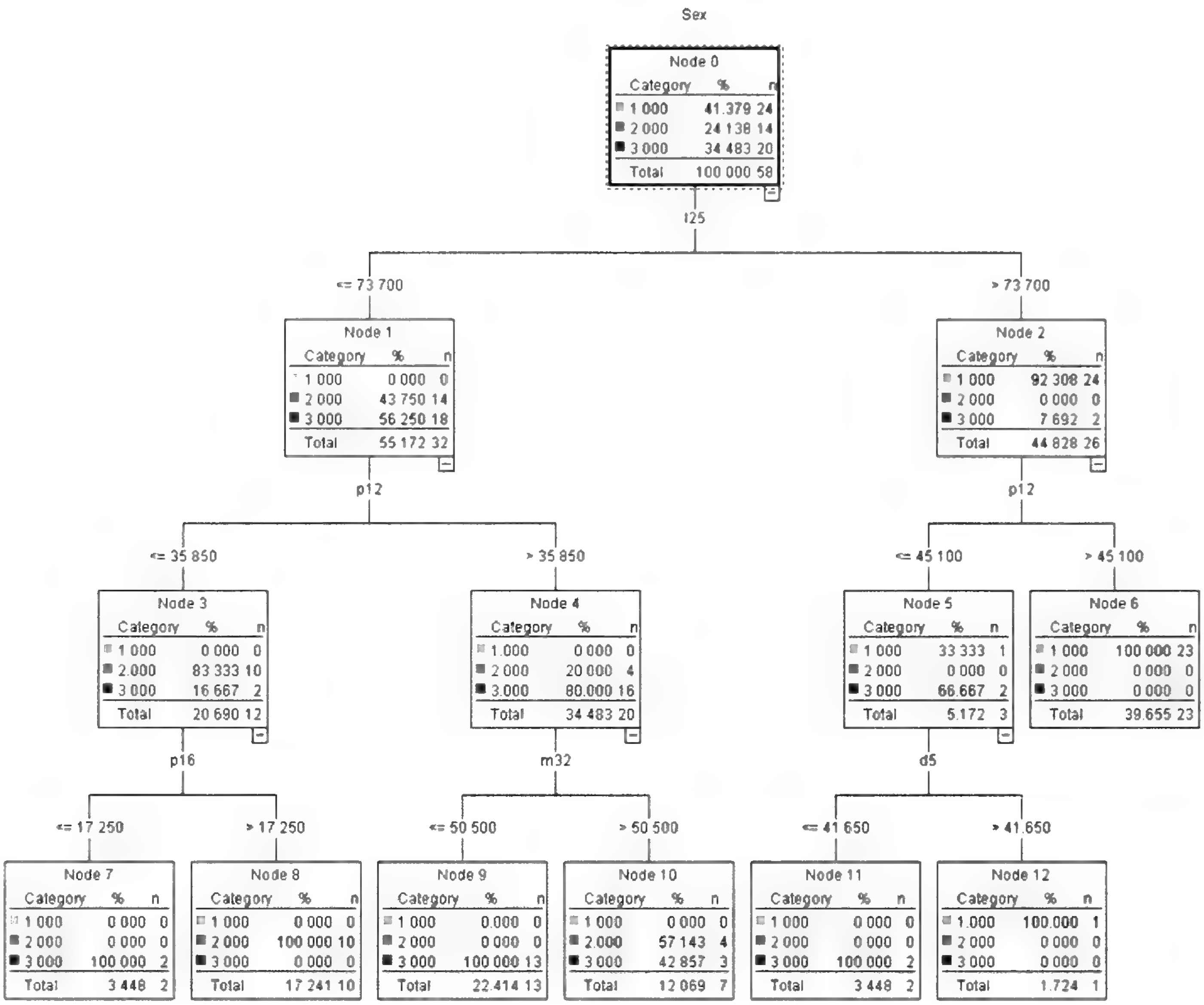
Hierarchical Cluster Analysis of skull parameters to produce a dendrogram (30 animals)

Cluster analysis was performed on thirty individuals where data on all variables were available, not counting **SBL** and sagittal crest height (**L27**). The observations were clustered using complete linkage (furthest neighbour) and Euclidean distance on all variables excluding **SBL** and **L27**. The four immature males lacking **SBL** data and hence for which there was some doubt about their actual sex (PEM 2006, 2009, 2010 & 2014) were excluded from the analysis. Cutting the dendrogram (Fig. 7) at a similarity level of 66.67 (or distance of 90) produces four clusters. The first cluster contains 2 males, 6 immature males and 2 females: PEM 975-M, PEM 2048-M, PEM 1014-F, PEM 1138-F, PEM 2046-IM, MCM 4577-IM, MCM 5133-IM, PEM 2050-IM, PEM 2052-IM, and PEM 2081-IM. The second cluster contains all males (10/10): PEM 1453-M, PEM 1892-M, PEM 2049-M, PEM 2051-M, PEM 2054-M, PEM 2087-M, PEM 2140-M, PEM 2141-M, PEM 2143-M, and PEM 2151-M. The third cluster contains 4 immature males and 3 females: PEM 2084-F, MCM 4578-F, MCM 5154-F, MCM 4595-IM, MCM 4996-IM, MCM 5002-IM, and MCM 5135-IM. The fourth cluster contains one female and 2 immature males: MCM 4994-F, MCM 4989-IM and MCM 5145-IM. Inclusion in the dendrogram of **SBL** data did not improve the ability to distinguish between immature males and females. Thus using cluster analysis it is easily possible to distinguish mature males from immature males and females but it is not possible to separate immature males from females.

DISCUSSION

Possible bias

Several factors must be taken into consideration when interpreting the data. Firstly, the sample size is small; in particular only 6 of the 14 females were aged. Secondly, there may be an over representation of either larger or smaller individuals in the data set which may possibly bias the results. Thirdly, although identical variables were taken from PEM and MCM animals, PEM variables were recorded by the first author, whereas MCM variables were recorded by the third author, introducing possible inter-observer error. However, the most likely source of bias is that some of the museum specimens identified as immature males may have been incorrectly sexed, especially if only the skull had been collected and the carcass had not been inspected properly, was badly decayed or was not available for examination. The results of the Classification and Regression Tree (Fig. 6) and the Cluster Analysis dendrogram (Fig. 7) emphasize that caution should be taken about the common claim that male and female skulls can be distinguished by visual inspection (Brunner 1998ab). The Classification and Regression Tree analysis was the more successful in correctly identifying the sex of the skulls. The cladistic dendrogram method had no difficulty in recognising mature male skulls but female and immature male skulls cannot be objectively separated from one another.



Prediction Matrix for 3-level Classification (n and %)			
Sex	Predicted Adult Male (1)	Predicted Female (2)	Predicted Immature Male (3)
Adult Male (1)	24 (100%)	0 (0%)	0 (0%)
Female (2)	0 (0%)	14 (100%)	0 (0%)
Immature Male (3)	0 (0%)	3 (15%)	17 (85%)

Fig. 6: Classification and Regressions Tree (CART) using three levels of skull data sets of adult male (M), immature male (IM) and female (F) South African fur seals (Total n = 58). A table is included to indicate successful and unsuccessful determinations of sex (M/F) and male reproductive status (IM/M). All the adult males (n = 24) were successfully identified as adult males. Three (3) immature males or 15% of the total (n = 20) were incorrectly classified as females but all the known females (n = 14) were correctly identified as females.

Principal component analysis: skull size and shape

For both genders, **CBL**, mastoid breadth, height of skull at base of mastoid, gnathion to posterior border of postglenoid process and length of mandible contributed the most to overall skull size (in multidimensional space). Gnathion to middle of occipital crest and basion to zygomatic root were predominant in males but not in females. Bizygomatic breadth was predominant in females but not in males.

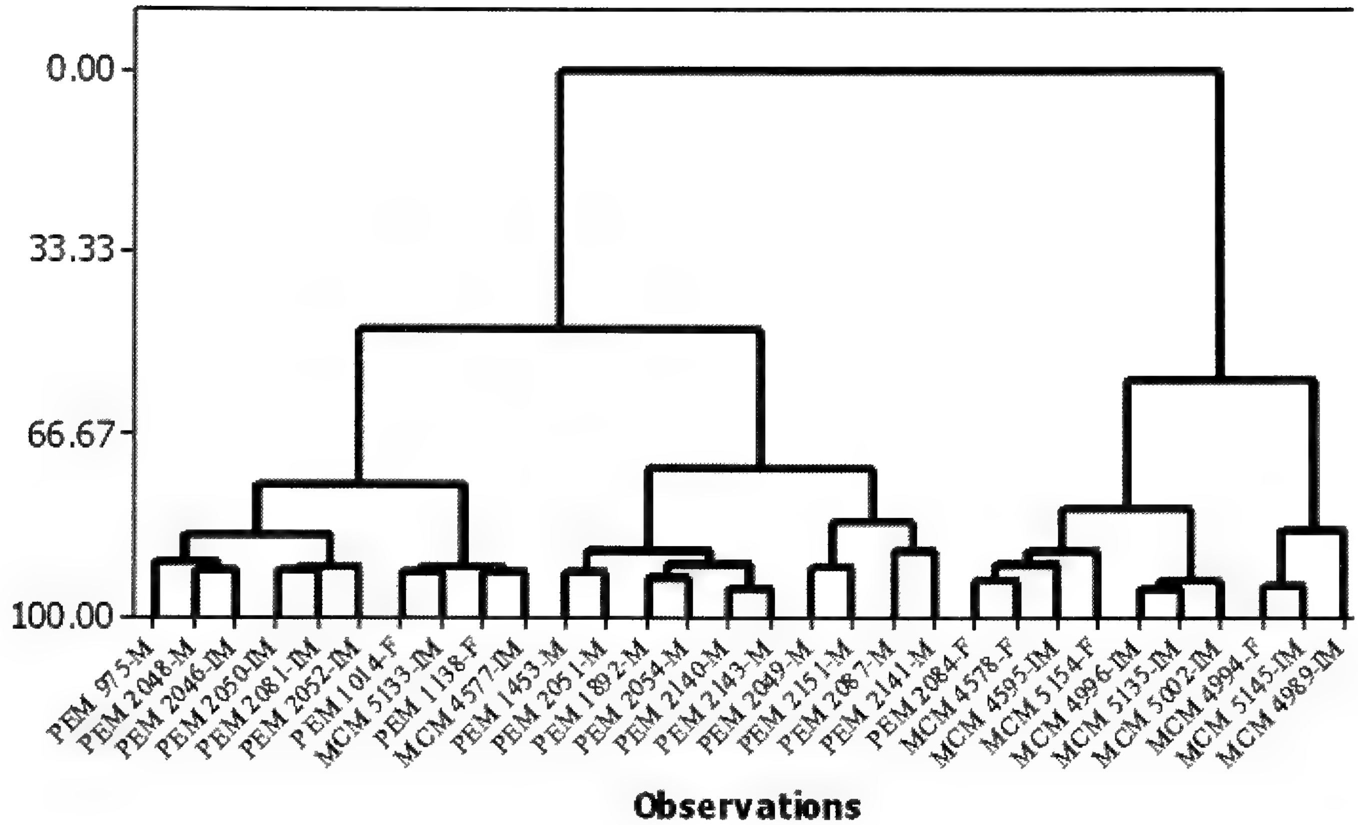


Fig. 7: Cladistic dendrogram based on complete sets of skull data for adult male (M), immature male (IM) and female (F) South African fur seals (Total n = 30). At the 66.67% similarity level the dendrogram divides into four groups or clades. One clade (#2) at the centre consists entirely of mature males (10/10) but the other three groups consist of two mature males (M), and a mixture of immature males (IM) and females (F). Clade (#1) consists of 2 females, 2 males and 6 immature males, clade (#3) consists of 3 females and 4 immature males and clade (#4) consists of 1 female and 2 immature males.

Predominant variables contributing to shape in both genders were **CBL**, breadth at supraorbital processes, breadth of brain case, palatal notch to incisors, gnathion to anterior of foramen infraorbital, gnathion to posterior border of preorbital process, height of skull at base of mastoid, length of mandible, length of mandibular tooth row, length of lower postcanine row, height of mandible at meatus and angularis to coronoideus (see figures of South African fur seal skulls in Stewardson et al., 2008).

Bizygomatic breadth contributed predominantly to skull shape in males but not in females. Gnathion to posterior end of nasals, basion to zygomatic root and mastoid breadth contributed predominantly to skull shape in females but not in males.

These findings indicate that the underlying data structure for males and females was different. Differences occurred in the combination of predominant variables, and in their magnitude and sign.

General pattern of growth

Although male South African fur seals are slightly heavier than females (4.5 *vs.* 6.4 kg) at birth, growth patterns for the genders are reportedly similar up until puberty (Warneke and Shaughnessy, 1985). Males attain puberty between 3 and 4 y (Rand 1949b; Warneke and Shaughnessy, 1985; Stewardson et al., 1998) and females between 3 and 5 y (Rand 1949a; Warneke and Shaughnessy, 1985; Guinet et al., 1998, J.H.M David, pers. comm.).

Although males are sexually mature at an early age, they are physically unable to hold a harem until much later. Full reproductive status (social maturity) is deferred until full size and competitive vigour are developed. Males normally do not reach breeding or "beachmaster" status until about 10 y (Rand, 1949b; Stewardson et al., 1998). Some never attain breeding status. Females approximate adult size at about 5 y of age, while males attain adult size between 8 and 10 y (Rand, 1949a; Stewardson 2001; Stewardson et al., 2008, 2009). Adult males may weigh up to 353 kg (mean, 250 kg), while females may weigh up to 122 kg (mean, 58 kg) (David 1987; Guinet et al., 1998; J.H.M David, pers. comm.).

Redigitising the Australian fur seal data from Arnould and Warneke (2002), as described previously in our study of body size in male Australian and South African fur seals (Stewardson et al., 2009), it was possible to estimate the **SBL** of adult (>135 cm) female Australian fur seals to be 157 ± 0.758 (n = 144) cm. A two-sample t-test shows that Australian female fur seals were significantly larger than South African female fur seals ($p < 0.001$) but the overall difference is small (7.9 ± 2.6 cm). Guinet et al. (1998) based on adult females shot at a breeding colony in Namibia found the mean **SBL** of female South African fur seals to be 147 ± 0.56 cm (n = 157), which is not significantly different to that calculated in the present study (Appendix 3: 149 ± 2.49 cm, n = 18) . A two-sample t-test using their data, with its much larger sample size, leads to the same conclusion that female South African fur seals are slightly smaller than their Australian counterparts. These results are similar to the finding in male South African vs. Australian fur seals that the South African form of *Arctocephalus pusillus* is slightly smaller than the Australian variety (Stewardson et al., 2009). Overall then, both male and female South African fur seals are smaller than in the case of the Australian fur seal.

Studies of increase in **SBL** vs. age consistently show monophasic post-weaning growth patterns with different growth kinetics for each sex in the South African fur seal (Stewardson et al., 1998, 2008, 2009), Australian fur seal (Arnould and Warneke, 2002; Brunner et al., 2004; Stewardson et al., 2008, 2009) and other polygynous breeding pinnipeds which exhibit pronounced size dimorphism, e.g., Antarctic fur seal (*A. gazella*) and Southern fur seal (*A. tropicalis*) (Daneri et al., 2005), New Zealand fur seal (*A. australis forsteri*) (Brunner, 1998b; Brunner et al., 2004; McKenzie et al., 2007), Northern fur seals (*Callorhinus ursinus*) (McLaren, 1993) and the Steller sea lion (*Eumetopias jubatus*), based on several hundred individuals (Winship et al., 2001).

Development of the skull in male South African fur seals exhibits monophasic growth in some variables and biphasic growth in others (Stewardson et al., 2008, 2009). In males, biphasic growth in skull parameters is associated with reaching an age of about 8 to 10 y when some males attain full-breeding status (Stewardson et al., 2008). Similar growth patterns have been reported in the skulls of male New Zealand fur seals (Brunner, 1998ab; Brunner et al., 2004). There does not appear to be sufficient size/age data available to make statements about the growth dynamics of the female skull of any of the fur seal species.

Variation among adult males

The coefficient of variation for most skull variables was larger in males than in females (Stewardson et al., 2008; present study). Variability in adult males at least partly reflects differences in social status. Differences in physical appearance will be most noticeable before and during the breeding season when breeding bulls build up their body reserves. The specimens used in the present series of studies of South African fur seals (*A. pusillus pusillus*) (Stewardson et al., 2008, 2009) were based on fur seals collected from feeding areas on the eastern coast of South Africa rather than from breeding colonies and so would consist of a mixture of breeding and non-breeding animals. Data available on Australian fur seal (*A. pusillus doriferus*) are based on animals collected from breeding colonies (Arnould and Warneke, 2002; Brunner et al., 2004).

Loci of sexual dimorphism

Dorsal

Males were significantly larger than females 'relative to **CBL**' in four of the nine dorsal variables (gnathion to posterior end of nasals **(D3)**, breadth at preorbital processes **(D6)**, least interorbital constriction **(D7)**, breadth at supraorbital processes **(D8)**). In both genders, these variables form part of the splanchnocranium (gnathion to posterior end of nasals **(D3)**) and the frontal region (least interorbital constriction **(D7)** and breadth at supraorbital processes **(D8)**), and are associated with respiration/vocalisation (gnathion to posterior end of nasals **(D3)**) and feeding (breadth at supraorbital processes **(D8)**).

In males, at least two of these variables have obvious functional significance with respect to territorial acquisition and defence. Least interorbital constriction **(D7)** and breadth at supraorbital processes **(D8)** contribute to the structural strength of the skull, and shield the animal against blows to the head (especially the eyes) during combat with rival males. They also increase the width of the face of the seal, making it appear more intimidating to its rivals.

Palatal

Males were significantly larger than females 'relative to **CBL**' in five of the 14 palatal variables (greatest bicanine breadth **(P12)**, breadth of palate at postcanine 1 **(P15)** and postcanine 3 **(P16)**, calvarial breadth **(P21)** and mastoid breadth **(P22)**). In both genders, greatest bicanine breadth **(P12)**, breadth of palate at postcanine 1 **(P15)** and postcanine 3 **(P16)**, form part of the palatal region and are like other parameters from that part of the skull (greatest bicanine breadth **(P12)**, breadth of palate at postcanine 1 **(P15)** and postcanine 3 **(P15)**) are associated with feeding and respiration / vocalisation (greatest bicanine breadth). Calvarial breadth **(P21)** and mastoid breadth **(P22)** form part of the basicranium and are associated primarily with auditory function (calvarial breadth **(P21)**, mastoid breadth **(P22)**).

Enlargement of the canines (greatest bicanine breadth **(P12)**) enables males to inflict a potentially lethal bite during combat. The rostrum is broad (palatal breadth at postcanine 1 **(P15)** and postcanine 3 **(P16)**), accommodating the large canines. Enlargement of calvarial breadth **(P21)** and mastoid breadth **(P22)** increases intimidating size of the face and increases the structural strength of the skull (large head size/ mass).

Lateral

Males were significantly larger than females 'relative to **CBL**' in all lateral variables; that is, gnathion to anterior of foramen infraorbital **(L24)**, gnathion to hind border of preorbital process **(L25)** and height of skull at bottom of mastoid **(L26)**. In both genders, gnathion to foramen infraorbital **(L25)** and gnathion to hind border of preorbital process **(L25)** form part of the splanchnocranium and are associated with respiration/ vocalisation. Enlargement of skull height and facial length in males increases the overall head size.

Mandible

Males were significantly larger than females 'relative to **CBL**' in only one mandibular variable (height of mandible at meatus, **M31**). This variable is associated with auditory function and feeding in both genders (Stewardson et al., 2008). Enlargement of this variable in males increases gape and provides a larger surface area for muscle (masseter and temporalis) attachment. Large jaws and jaw muscles are advantageous in territorial combat.

Significance of the dimorphism

In male South African fur seals, there appears to be strong selection pressure for the development of certain morphological traits associated with fighting ability and body size and mass. It is important to note that beachmasters spend much of their time vocalising and intimidating rivals by displays which emphasise their size and the likely consequences of a rival attempting to challenge them rather than actual fighting (Rand, 1967; Stirling and Warneke, 1971; Miller, 1991). In male South African fur seals, selection pressure appears to favour large body mass. Stewardson et al. (2008, 2009) showed that males (mean, 183 cm) were significantly larger in standard body length than females (mean, 149 cm). Thus, on the mass/length cubed rule one would expect a male to weigh about 2 times that of an average female. Relative differences in body mass are much higher: large males in breeding condition may be 4-5 times heavier (average about 250 kg) than adult females, which average about 58 kg (David, 1989; Guinet et al., 1998; J.H.M David, pers. comm.). Large males have an advantage over their smaller rivals in gaining high social rank through vocalisation, intimidating display and fighting (Stirling and Warneke, 1971; Miller, 1991). Furthermore, large males in breeding condition have a well developed fat store. This thick blubber layer enables males to remain resident on territory for long periods (up to 40 days) without feeding and provides protection as well (Peterson, 1968; Alexander et al., 1979; McCann, 1981; Campagna and Le Boeuf, 1988; Boness, 1991). As in most seals, if for any reason a male abandons his territory, it will quickly be occupied by a rival male and the usurper will most likely have to be removed by actual combat (Rand, 1967; Le Boeuf, 1974; Miller, 1974; McCann, 1981; Campagna and Le Boeuf, 1988). There is a high risk of injury and/or failure in attempting to regain breeding territory.

Selection pressure also appears to favour the development of certain skull traits that appear to be associated with potential and actual fighting ability. In the present study, traits which are significantly larger in males appear to be associated with bite force (e.g., broad canines, increased surface area for muscle attachment, large gape), large head size/ mass (e.g., increased mastoid and calvarial breadth) and/or structural strength of the skull (protection against damage from direct blows to the head during combat).

Sexual dimorphism of the skull in southern fur seals has also been reported for the Australian and New Zealand fur seals (Australian fur seal, *A. pusillus doriferus* and New Zealand fur seal, *A. australis forsteri)* (Brunner, 1998ab). As with the South African fur seal, sexually dimorphic traits are mainly those characteristics that increase the ability of males to acquire and defend territory in the short breeding season whether by simply visually and vocally intimidating potential opponents or by actual combat (Bartholomew, 1970; Stewardson et al., 1998).

CONCLUSIONS

Information presented in the study demonstrates that there is pronounced sexual dimorphism in adult South African fur seals with respect to body length, body mass, skull size and skull shape. Male South African fur seals were significantly larger than females in **SBL**, and 43% of skull variables were found to be significantly larger in males relative to **CBL**. These variables were associated with fighting ability, e.g., large head size/mass, increased structural strength of the skull and/or increased bite capacity. Principal component analysis showed that the underlying data structure for males and females was different, and that most variation between the sexes was expressed in overall skull size rather than shape. This makes it generally easy to distinguish mature male and female skulls but problematic to distinguish skulls from sub-adult males from adult females. Condylobasal length **(CBL or D1)**, height of skull at bottom of mastoid **(L26)** and length of mandible **(M28)** contributed considerably to overall size, with gnathion to middle of occipital crest **(D2)** predominating in males only. Classification and Regression Tree analysis and cluster analysis dendrograms were both very successful for distinguishing mature male skulls from immature male and female skulls but Classification and Regression Tree was better than cluster analysis in distinguishing immature male from female skulls. The material used in the present study was from a feeding, not breeding area: it would be interesting to attempt to determine whether breeding bulls constitute an identifiable subset of the total adult male population some of which never breed.

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APPENDIX 1

Museum ascension numbers of male South African Fur seal specimens used in the present study. The data set of skull and body measurements on these specimens has been published previously in Stewardson et al. (2008). PEM stands for Post Elizabeth Museum (Port Elizabeth, South Africa), MCM stands for Marine and Coastal Management (Cape Town, South Africa).

The ascension numbers of the 39 adult male animals used in the present study were:
MCM 1809, MCM 4597, MCM 4992, PEM 898, PEM 951, PEM 958, PEM 975, PEM 1453, PEM 1507, PEM 1560, PEM 1587, PEM 1698, PEM 1868, PEM 1877, PEM 1879, PEM 1882, PEM 1890, PEM 1892, PEM 1895, PEM 2004, PEM 2007, PEM 2013, PEM 2036, PEM 2048, PEM 2049, PEM 2051, PEM 2052, PEM 2054, PEM 2082, PEM 2081, PEM 2087, PEM 2132, PEM 2140, PEM 2141, PEM 2143, PEM 2151, PEM 2248, PEM 2252, PEM 2258.

The skulls classed as immature (subadult) males (n = 24) were:
MCM 2763, MCM 2795, MCM 3582, MCM 3586, MCM 3587, MCM 3636, MCM 4365, MCM 4388, MCM 4577, MCM 4595, , MCM 4996, MCM 5002, MCM 5133, MCM 5135, MCM 5136, PEM 1704, PEM 1891, PEM 2006, PEM 2009, PEM 2010, PEM 2014, PEM 2046, PEM 2050, PEM 2053.

There were two (2) juvenile males only 2 years old:
MCM 4989, MCM 5145.

APPENDIX 2

Skull measurements and body measurements of female South African fur seals. SBL is standard body length (cm), all other parameters are coded as for Table 1 and are in mm.

Adults

Museum number	Age y	SBL cm	D1 mm	D2 mm	D3 mm	D4 mm	D5 mm	D6 mm	D7 mm	D8 mm	D9 mm	P10 mm	P11 mm	P12 mm	P13 mm	P14 mm	P15 mm
PEM 918	-	144.0	204.5	172.3	72.8	-	40.1	52.4	28.3	40.0	80.0	78.6	55.1	33.1	93.4	11.0	18.8
PEM 929	-	160.0	222.8	190.7	75.4	-		52.3	28.0	44.3	96.3	94.0	55.8	41.0	100.2	14.0	22.4
PEM 931	-	150.0	212.6	184.9	71.4	-	34.8		29.0	44.8	79.0	72.9	59.6	38.7	99.0	12.0	17.4
PEM 957	-	150.0	215.9	184.3	74.0	23.6	39.2	58.4	29.6	42.9	81.8	90.9	56.1	37.8	102.6	14.0	20.5
PEM 1014	-	147.0	218.2	183.9	69.9	26.5	36.0	53.5	28.5	40.4	82.5	93.0	53.0	42.3	102.6	14.0	20.6
PEM 1133	-	155.0	225.0	190.7	79.6	24.8	42.4	-	31.9	46.5	82.1	94.8	55.8	44.0	105.6	13.0	20.5
PEM 1136	-	164.0	213.6	186.4	76.5	23.3	40.0	-	31.3	49.7	81.8	87.4	50.9	39.4	97.0	13.0	18.1
PEM 1138	-	142.0	216.3	190.1	78.5	23.3	41.4	56.3	31.6	47.1	83.8	85.5	58.4	38.5	102.7	12.0	19.2
PEM 1861	-	179.0	222.6	186.5	75.7	26.6	37.2	60.5	31.4	48.8	84.8	96.0	54.0	39.2	103.5	9.4	22.4
PEM 2084	-	145.0	208.3	181.2	71.3	21.0	36.4	50.3	28.8	44.1	79.3	89.1	56.6	35.2	98.0	12.0	17.4
MCM 101	-	148.0	217.6	187.2	73.5	26.9	38.9	57.6	31.9	50.3	82.3	92.4	57.5	39.6	100.8	13.1	19.9
MCM 1496	11.0	154.0	207.4	181.7	66.4	24.2	36.6	49.2	21.8	36.2	79.4	83.2	52.8	33.3	93.6	11.7	12.8
MCM 1551	12.0	145.0	201.5	178.3	69.3	25.0	33.9	52.0	24.2	-	82.9	83.4	53.9	35.4	93.6	10.4	19.4
MCM 1552	12.0	135.0	201.3	168.7	62.1	23.9	31.2	-	-	-	81.2	92.4	52.0	33.6	86.5	10.9	17.6
MCM 1556	12.0	143.5	209.2	179.9	71.2	24.8	37.6	50.7	21.5	43.2	79.8	91.2	55.5	35.8	98.9	11.3	18.8
MCM 4394	9.0	143.0	211.3	185.0	70.7	23.3	36.2	54.6	24.4	42.0	72.7	97.6	57.0	32.9	98.8	11.0	16.7
MCM 4578	-	145.0	210.2	179.1	74.8	21.1	38.6	49.3	22.8	39.3	84.4	85.7	55.0	32.3	98.1	13.0	16.9
MCM 5154	-	135.0	200.8	181.3	71.4	21.4	37.5	49.1	23.9	42.7	82.3	76.5	49.9	34.4	94.8	13.4	17.1

Museum number	P16 mm	P17 mm	P18 mm	P19 mm	P20 mm	P21 mm	P22 mm	P23 mm	L24 mm	L25 mm	L26 mm	L27 mm	M28 mm	M29 mm	M30 mm	M31 mm	M32 mm
PEM 918	21.2	29.1	152.0	108.1	140.0	93.3	104.7	68.9	57.4	64.5	85.9	-	141.3	56.1	40.5	41.6	48.0
PEM 929	24.1	30.4	163.0	118.4	154.0	95.3	105.2	73.7	61.1	66.1	93.7	-	155.0	60.6	42.8	49.0	51.0
PEM 931	19.0	26.0	164.0	118.6	144.0	97.6	113.2	66.3	60.0	66.6	92.2	-	156.1	48.6	47.6	47.8	48.0
PEM 957	20.6	26.3	162.0	127.4	146.0	104.0	113.3	70.0	-	-		-	-	-	-	-	-
PEM 1014	20.7	25.5	164.0	123.6	147.0	99.3	110.7	68.4	63.5	68.3	91.6	-	154.0	62.5	44.0	48.5	52.0
PEM 1133	-	27.6	170.0	132.8	156.0	102.0	115.8	73.3	64.0	69.4	92.2	-	160.7	64.3	44.5	49.8	53.0
PEM 1136	20.1	26.5	163.0	122.8	144.0	96.7	112.2	68.9	63.7	70.8	91.2	-	150.0	42.5	26.3	46.1	49.0
PEM 1138	22.8	27.7	163.0	131.9	149.0	98.6	114.1	73.1	63.5	69.6	92.6	-	148.0	53.0	40.7	47.6	51.0
PEM 1861	22.4	24.4	166.0	126.0	153.0	95.3	113.2	73.6	62.5		91.7	-	150.7	43.3	43.7	41.0	44.0
PEM 2084	19.6	24.6	156.0	119.0	140.0	92.9	103.3	66.3	61.3	67.7	82.3	-	147.1	60.3	44.1	42.7	44.0
MCM 101	21.2	29.1	165.3	132.1	149.7	98.3	116.2	70.9	71.1	69.6	-	5.1	151.2	53.0	42.3	49.4	51.3
MCM 1496	21.4	27.0	155.8	116.4	144.8	92.9	106.4	70.5	57.2	62.7	-	0.3	141.9	57.7	43.2	39.1	44.9
MCM 1551	23.1	29.3	151.9	113.6	143.3	90.4	97.3	67.3	57.2	60.8	-	-	135.3	55.3	41.2	41.3	43.5
MCM 1552	20.0	24.0	148.4	110.2	140.4	89.5	98.6	68.2	50.5	58.9	-	0.0	135.8	53.7	39.2	42.0	48.3
MCM 1556	22.6	29.0	157.9	117.5	143.0	94.4	106.3	64.9	56.7	63.3	-	-	143.7	57.8	42.4	42.0	47.1
MCM 4394	20.2	27.8	153.8	114.0	141.6	93.4	102.0	72.3	62.0	66.2	-	0.0	141.2	59.0	43.0	40.7	43.2
MCM 4578	20.6	24.7	157.9	119.4	146.9	91.8	100.2	66.6	62.6	65.2	80.8	0.1	141.5	54.4	39.9	39.7	42.7
MCM 5154	19.6	22.9	148.7	109.1	136.9	87.4	102.6	66.4	58.5	63.2	81.3	0.0	132.5	55.8	40.3	40.7	43.5

Juveniles/Subadults

Museum number	Age y	SBL cm	D1 mm	D2 mm	D3 mm	D4 mm	D5 mm	D6 mm	D7 mm	D8 mm	D9 mm	P10 mm	P11 mm	P12 mm	P13 mm	P14 mm	P15 mm
MCM 1802	2.9	116.0	182.0	154.9	58.4	20.8	28.5	48.2	24.8	37.5	81.1	74.8	46.9	29.7	84.6	11.9	15.4
MCM 4990	1.8	83.0	152.7	132.3	51.7	18.1	24.5	40.2	20.4	36.2	77.4	61.4	41.0	28.8	69.7	10.0	12.9
MCM 4994	1.8	90.0	163.7	144.7	47.3	16.9	21.1	42.4	20.2	34.9	76.2	71.4	42.4	27.6	72.3	10.6	12.0

Museum number	P16 mm	P17 mm	P18 mm	P19 mm	P20 mm	P21 mm	P22 mm	P23 mm	L24 mm	L25 mm	L26 mm	L27 mm	M28 mm	M29 mm	M30 mm	M31 mm	M32 mm
MCM 1802	18.0	21.4	132.2	103.7	125.4	82.0	89.3	64.5	50.0	57.0		0.0	120.3	50.7	38.2	32.2	33.9
MCM 4990	17.5	20.7	108.9	85.5	107.5	71.2	66.3	54.6	39.6	45.7		0.0	98.3	44.0	31.7	25.3	29.3
MCM 4994	18.3	20.7	116.6	87.4	115.2	75.3	78.8	60.5	41.8	47.1	69.2	0.0	103.7	45.1	33.2	22.1	30.0

APPENDIX 3.

Numbers of Individuals, Means, Standard deviations, Standard Errors and ranges of Standard Body length (SBL) and Skull Measurements in Female South African fur seals.

	SBL	D1	D2	D3	D4	D5	D6	D7	D8	D9	P10	P11	P12	P13	P14	P15
Units	cm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
Count (n)	18.00	18.00	18.00	18.00	15.00	17.00	14.00	17.00	16.00	18.00	18.00	18.00	18.00	18.00	18.00	18.00
Mean	149.14	212.17	182.90	72.47	23.98	37.53	53.30	26.99	43.89	82.02	88.03	54.94	37.03	98.32	12.18	18.69
SD	10.55	7.50	5.91	4.21	1.88	2.79	3.69	5.21	3.92	4.48	6.97	2.56	3.51	4.66	1.34	2.29
SE	2.49	1.77	1.39	0.99	0.49	0.68	0.99	1.26	0.98	1.06	1.64	0.60	0.83	1.10	0.32	0.54
Maximum	179.00	225.00	190.70	79.60	26.90	42.40	60.50	31.90	50.30	96.30	97.60	59.60	44.00	105.60	14.00	22.40
Minimum	135.00	200.80	168.70	62.10	21.00	31.20	49.10	11.50	36.20	72.70	72.90	49.90	32.30	86.50	9.40	12.80

	P16	P17	P18	P19	P20	P21	P22	P23	L24	L25	L26	L27	M28	M29	M30	M31	M32
Units	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
Count	17.00	18.00	18.00	18.00	18.00	18.00	18.00	18.00	17.00	16.00	11.00	6.00	17.00	17.00	17.00	17.00	17.00
Mean	21.13	26.77	159.04	120.05	145.53	95.17	107.52	69.42	60.75	65.81	88.68	0.92	146.24	55.17	41.51	44.06	47.32
SD	1.43	2.14	6.34	7.75	5.23	4.31	6.15	2.88	4.43	3.41	5.04	2.05	7.99	6.02	4.43	3.84	3.51
SE	0.35	0.50	1.49	1.83	1.23	1.02	1.45	0.68	1.07	0.85	1.52	0.84	1.94	1.46	1.08	0.93	0.85
Maximum	24.10	30.40	170.00	132.80	156.00	104.00	116.20	73.70	71.10	70.80	93.70	5.10	160.70	64.30	47.60	49.80	53.00
Minimum	19.00	22.90	148.40	108.10	136.90	87.40	97.30	64.90	50.50	58.90	80.80	0.00	132.50	42.50	26.30	39.10	42.70

Bacular Measurements for Age Determination and Growth in the Male South African Fur Seal, *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae)

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Morphology, relative size and growth of the baculum in 103 South African fur seals, *Arctocephalus pusillus pusillus,* from the Eastern Cape coast of South Africa are described. Bacular measurements (n = 8 linear variables and mass) were examined in relation to standard body length (**SBL**), bacular length (**BL**) and chronological age (y) using linear regression. Animals ranged from < 1 month to ≥ 12 y. Bacular shape was most similar to *Callorhinus ursinus (*Northern fur seal) and *Zalophus californianus* (California sea lion). For the range of ages represented in this study, the baculum continued to increase in size until at least 10 y; with growth slowing between 8-10 y, when social maturity (full reproductive capacity) is attained. Growth in bacular length (**BL**), distal height and bacular mass peaked at 8 y; middle shaft height and distal shaft height peaked at 9 y; proximal height, proximal width, distal width and proximal shaft height peaked at 10 y. In the largest animal (age ≥ 12 y), maximum bacular length was 139 mm and mass 12.5 g. Relative to **SBL**, bacular length (**BL**) increased rapidly in young animals, peaked at 9 y (6.9%), and then declined. Bacular mass and distal height expressed greatest overall growth, followed by proximal height, proximal shaft height and bacular length. At 9 y, mean bacular length and mass was 117 ± 2.7 (± SE, n = 4) mm and 7 ± 0.7 (4) g; growth rates in bacular length and mass were 311% and 7125% (relative to age zero), and 5% and 27% (between years); and bacular length (**BL**) was about 6.9% of **SBL**. For all males ≥12 months, most bacular variables grew at a faster rate than **SBL** and **BL**. Exceptions included proximal width which was isometric to **SBL**; distal width and distal shaft height which were isometric to bacular length; and proximal width which was negatively allometric relative to **BL**. Bacular length (**BL**) was found to be a useful predictor of **SBL** and seal age group (pup, yearling, subadult, adult), but only a 'rough indicator' of absolute age.

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KEYWORDS: age classification, age determination, *Arctocephalus pusillus pusillus*, baculum morphometrics, Otariidae, Pinnipeds, South African fur seal, standard body length.

INTRODUCTION

The mammalian baculum (*os penis*) is found in all carnivores, except the hyena (Ewer, 1973). This morphologically diverse bone has received considerable scientific attention in the field of mammalian systematics (McLaren, 1960; Sutton and Nadler, 1974; Kim et al., 1975; Morejohn, 1975; Lee and Schmidly, 1977; Patterson and Thaeler, 1982; Patterson, 1983), and has been used as an index of age, puberty and social maturity for several species of mammals, including pinnipeds (Hamilton, 1939; Elder, 1951; Laws, 1956; Hewer, 1964; Bester, 1990). The function of the baculum in carnivorous mammals remains controversial. It may lack specific function (Burt, 1939; Mayr, 1963) or may be adaptive in various interactions of males and females during copulation, with function differing considerably between species (Scheffer and Kenyon, 1963; Long and Frank, 1968; Ewer, 1973; Miller, 1974; Morejohn, 1975; Patterson and Thaeler, 1982; Eberhard, 1985, 1996; Dixson, 1995; Miller et al., 1996, 1998, 1999; Miller and Burton 2001). The baculum bone of carnivores is classified as a heterotopic bone because it forms from ossification of connective tissue (Miller, 2009). The proximal end of the baculum is attached to the fibrous *corpora cavenosa penis*.

Within the Otariidae, information on the morphology of the baculum is available for *Arctocephalus pusillus pusillus* (South African fur seal), *Arctocephalus pusillus doriferus* (Australian fur seal); *Arctocephalus gazella* (Antarctic fur seal); *Arctocephalus tropicalis (*Sub Antarctic fur seal); *Callorhinus ursinus (*Northern fur seal); *Eumetopias jubatus* (Stellers sea lion); *Neophoca cinerea*, *(*Australian sea lion); *Otaria byroni* (South American fur seal); *Phocarctos hookeri* (New Zealand or Hookers sea lion) and *Zalophus californianus* (California sea lion) (Chaine, 1925; Hamilton, 1939; Rand, 1949,1956; Scheffer, 1950; Mohr, 1963; Scheffer and Kenyon, 1963; Kim et al., 1975; Morejohn, 1975; Bester, 1990; Laws and Sinha, 1993). Of these, the northern fur seal has been studied in most detail (Scheffer, 1950; Scheffer and Kenyon, 1963; Kim et al., 1975; Morejohn, 1975).

Information on bacular growth based on bulls reliably aged from tooth structure, or on bulls of known age (i.e. bulls tagged or branded as pups), is only available for *Callorhinus ursinus* (northern fur seal) (Scheffer, 1950), *Arctocephalus tropicalis* (Sub Antarctic fur seal) (Bester, 1990) and *Arctocephalus pusillus pusillus,* South African fur seal (Oosthuizen and Miller, 2000). A large data set of reliably aged material is also available on the baculum of the phocid harp seal (*Pagophilus greonlandicus*) (Miller et al., 1998; 1999; Miller and Burton 2001). These studies indicate that: (i) the baculum increases in length and mass with increasing age; (ii) bacular growth may be fairly constant, as in the northern fur seal, harp seal and subantarctic fur seal, or there may be an increase in the rate of growth at puberty, as has been suggested in the South African fur seal; (iii) there may be a sudden increase in the rate of bacular growth when individuals attain social maturity (full reproductive capacity); and (iv) there is a decline in the rate of bacular growth in socially mature bulls.

Seal baculum and testicles are used in oriental aphrodisiac medicine and gastronomy and so there is a legal and illicit trade in seal genitalia (Miller, 2009). Demand outstrips supply and the origin of material sold is often in doubt. Bacula from South African fur seals are part of the legal trade in seal body parts. Other southern fur seals are not legally hunted for body parts. It would be naïve to imagine that there is not some illicit trade in body parts from other southern hemisphere seals and sea lions. The other major legal source of seal body parts is from the Harp seal (*Pagophilis greonlandicus*) where illustrations, information on morphometrics, growth and development of the baculum are available (Miller and Burton, 2001; Miller 2009). Museums and zoologists can be asked to identify seal body parts by customs authorities to determine whether they are from legally hunted species or not: morphometric knowledge of the seal baculum is important for conservation reasons.

Here we examine the bacula of 103 male South African fur seals from the Eastern Cape coast of South Africa. We provide illustrations of bacula from the species to aid in identification. Specific objectives were to: (i) describe the general morphology of the baculum; (ii) quantify growth of bacular measurements (n = 8 linear variables and mass) relative to standard body length **(SBL)** (n = 89 bulls), bacular length (**BL**) (n = 103 bulls), and chronological age (n = 50 bulls); (iii) determine if the baculum is a useful indicator of social maturity; and (iv) determine if bacular length (**BL**) is a useful indicator of age and/or standard body length (**SBL**). Currently there are only two reliable means of determining the age of South African fur seals (Stewardson, 2001; Stewardson et al., 2008). The first is based on tagging as pups, the other is based on dentition but the dentition method is only valid for bulls less than about 12 y. Unfortunately, age assignment based upon skull suture closure criteria are known to be inaccurate and of value only for seals ≥ 12y in South African fur seals (Stewardson, 2001) which invalidates some early work on baculum statistics vs. age (Rand, 1956; Mohr, 1963).

MATERIALS AND METHODS

Collection of specimens

South African fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34° 03'S, 23° 24'E) and East London (33° 03'S, 27° 54'E), from August 1978 to December 1995, and accessioned at the Port Elizabeth Museum (PEM), Port Elizabeth, South Africa. One animal (PEM2238) was collected NE of the study area, at Durban. From this collection, bacula from 103 males were selected for examination. The list of specimens used in the present study, along with their

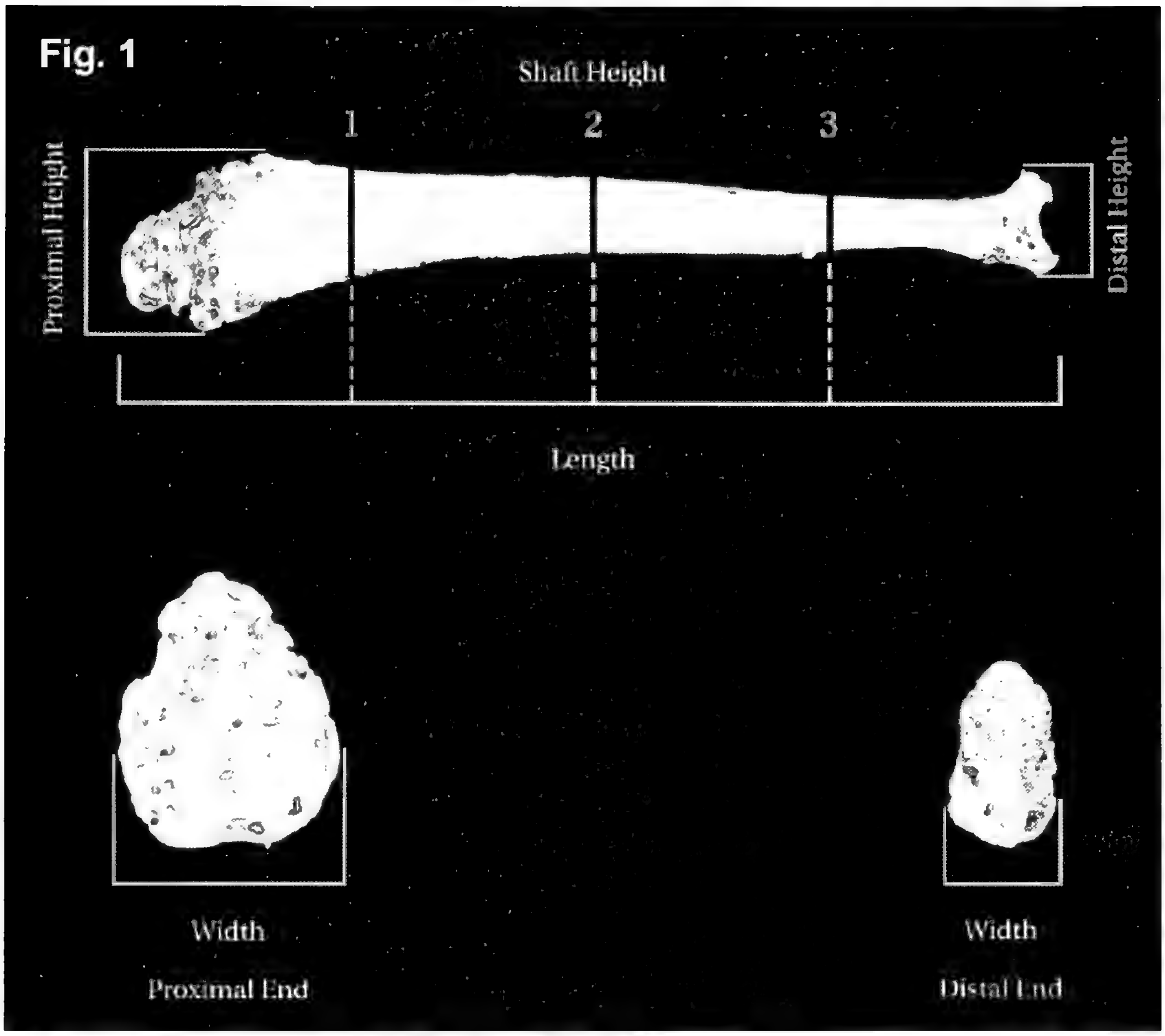

Fig. 1 Diagram of a South African fur seal baculum indicating the variables measured (Var 1-8): Bacular length (Var 1 or BL); Proximal height (Var 2); Proximal width (Var 3); Distal height (Var 4); Distal width (Var 5); Three cross sectional parameters of the shaft: (1) Proximal shaft height (Var 6); (2) Middle shaft height (Var 7) and (3) distal shaft height (Var 8). Specimen provided by P Shaughnessy.

museum ascension numbers and location and dates of collection, are listed in Stewardson et al. (2008). Apart from specimens collected before May 1992 (n = 29), all specimens were collected by the first author and were found dead, dying or had drowned in fishnets.

Preparation and measurement of bacula

Bacula were defleshed and macerated in water for 1-2 months. Water was changed regularly. Bacula were then washed in mild detergent and air dried at room temperature. Dry specimens were weighed using an electronic balance and measurements (n = 8 linear variables) were taken using a vernier calliper (to 0.1 g and 0.1 mm) following Morejohn (1975) (Fig. 1). All bacular measurements were recorded by the first author.

Age determination

Of the 103 bulls in the study: (i) 40 were aged from counts of incremental lines observed in the dentine of upper canines (growth layer groups, GLG) as described in Stewardson et al. (2008). Dentition-based ages fell into 3 categories: (i) age range 1-10 y; (ii) 10 were identified as adults > 12 y (i.e., pulp cavity of the upper canine was closed); and (iii) 53 for a variety of reasons could not be aged. None were tagged individuals. South African fur seals older than 12 y cannot be aged from counts of growth layer groups (GLG) in the dentine of upper canines because the pulp cavity closes (Stewardson et al., 2008).

In studies of South African fur seals, 1st November is taken as the birthdate of all seals based upon estimates of the average birthdate of pups in breeding

Table 1. The age distribution of male South African fur seals used in the present study. Estimated age from counts of incremental lines observed in the dentine of upper canine (n = 40). An additional 10 males were ≥ 12 y, i.e., pulp cavity closed. Pups were greater than one month of age.

Age group	Age (y)	Frequency	Percentage
Pups	< 1	3	6
Yearling	1	5	10
Subadult	2	0	0
	3	0	0
	4	1	2
	5	3	6
	6	2	4
	7	11	22
Adult	8	8	16
	9	4	8
	10	3	6
	≥ 12	10	20
Total		50	100

colonies (Rand, 1949; Oosthuizen and Miller, 2000). For this study, the following age groups were used: pup (< 1 months to 6 months); yearling (7 months to 1 y 6 months); subadult (1 y 7 months to 7 y 6 months); and adult (> 7 y 7 months) (rounded to whole years in Table 1) (see Stewardson et al., 2008, 2009). No individuals of 2 y to 3 y were available. Data on very old bulls that had been tagged as pups were not available. The estimated longevity of bull South African fur seals is about 20 y based primarily on zoo animals (Wickens, 1993). Currently, examination of tooth structure is the most precise method of age determination in untagged pinnipeds; however, counts are not without error. For information of the reliability of this method see Oosthuizen (1997) and Stewardson et al. (2008).

The limitations of age determinations based upon dentition become apparent if one realises that it would be reasonable to assume that the longevity of South African fur seal bulls in the wild would be at least 15 y (based upon documentation on the Australian fur seal, *A. pusillus doriferus*; Arnould and Warneke, 2002), which implies that dentition can only age male South African fur seals up to only about 2/3 of their total potential lifespan.

Statistical analysis

Bacular measurement error

Duplicate measurements of bacular length were taken from 50 randomly selected bacula to assess measurement error. The Wilcoxon sign-rank test was used on the differences to test H_0: median = 0, versus H_1: median ≠ 0.

Bacular length (BL) expressed in relation to standard body length (SBL)

Standard body length **(SBL)** is defined as the length from the nose to the tail in a straight line with the animal on its back (Committee on Marine mammals, 1967). Growth in **BL**, relative to standard body length (**SBL**), was calculated as follows, using paired samples only:

BL (mm) /SBL (mm) x 100%

As the approximate variance of the ratio estimate is difficult to calculate, percentages must be interpreted with caution (Cochran, 1977, p. 153).

Bacular growth relative to age zero, RGR Y_0

Percent change in bacular measurement at age t, relative to value at age zero, was calculated as follows:

$$[(Y_t - Y_0)/Y_0] \times 100\%$$

where, Y_0 = mean bacular measurement from pups < 1 months of age (age zero), and Y_t = mean bacular measurement for age t (age class in y).

Bacular growth relative to the previous year (annual bacular growth), RGR Y_{t-1}

The percent change in value at age t, relative to the value at age t-1, was calculated as follows:

$$[(Y_t - Y_{t-1})/Y_{t-1}] \times 100\%$$

where, Y_t = mean bacular measurement for age (t), and Y_{t-1} = mean bacular measurement for age t-1 (between years). RGRs were calculated for bulls that were 7-10 y.

Bacular length (BL) as an indicator of SBL and age

The degree of linear relationship between Log_e **(BL)**, Log_e **(SBL)** and Age (y) was calculated using the Spearman rank-order correlation coefficient. Linear discriminant function analysis (Mahalanobis squared distance) was used to predict the likelihood that an individual seal will belong to a particular age group (pup, yearling, subadult, adult) using one independent variable, bacular length (see Stewardson et al., 2008, 2009 for further details).

Bivariate allometric regression

The relationship between each bacular measurement (**Var 1** to **9**) and: (i) **SBL**, (ii) **BL**, and (iii) age (y), was investigated using linear regression, semi-log plots (Log_e y = mx + b) or the log/log logarithmic transformation of the allometric equation, $y = ax^b$, which may equivalently be written as $Log_e y = Log_e a + b.Log_e x$. For most analyses the three one month-old pups were not included (hence n = 37). 'Robust' regression (Huber M-Regression) was used to fit straight lines to the untransformed or transformed data. The degree of linear relationship between the transformed variables was calculated using the Spearman rank-order correlation coefficient, r (Gibbons and Chakraborti, 1992). Testing of model assumptions, and hypotheses about the slope of the line, followed methods described by Stewardson et al. (2008).

Statistical analysis and graphics were implemented in Minitab (Minitab Inc., State College, 1999, 12.23); Microsoft ® Excel 97 (Microsoft Corp., Seattle, 1997) and SPLUS 7.0 (MathSoft, Inc., Seattle, 2005, version 7.0).

RESULTS

Bacular measurement error

Of the 50 bacula that were measured twice, measurements were reproducible at the 5% significance level (p-value = 0.052).

Bacular morphology

Bacular length (**BL**) and mass ranged from 26.6 to 139.3 mm and 0.1 to 12.5 g, respectively (Table 2).

The youngest animals in the sample were < 1 month of age. In these individuals, the baculum was short, thin and rod-like, with no obvious distinction between the proximal and distal ends (Fig. 2a and 2b). The shaft was slightly curved anteriorly (variable).

In yearlings, the baculum increased substantially in length and mass (Table 3). The distal end was slightly rounded but, there was no sign of bifurcation (Fig. 2c).

In subadults, most bacula curved upwards at the distal end (i.e., superiorly, see Fig. 2d). At the distal end of the baculum, there were two narrow projections (knobs): a well-developed ventral knob and a less prominent dorsal knob (Fig. 2d). In older subadults, the ventral knob extended upwards and outwards forming a double knob (variable). The proximal end of the bacula was bulbous in all bulls ≥ 4 y.

In adults (> 8 to 9 y) the baculum was well developed, with pronounced thickening of the proximal end. Contrast Fig. 2d which is a 7 year old subadult with Fig. 2e which is a 10 year old (Fig. 2). At the bifurcated distal end, the ventral knob usually extended further than the dorsal knob. In older males, the baculum was more robust, but not necessarily longer. Small osseous growths were commonly found on the proximal end of the baculum (n = 18 subadult and adult bacula) creating a rough surface where the fibrous tissue of the *corpus cavernosum penis* attached. In some older specimens (n = 16 bacula), small knob-like growths (usually 1 or 2) were observed along the edge of the urethral groove, at the proximal ventral surface of the baculum.

Bacular length expressed in relation to SBL

Relative to **SBL**, **BL** increased rapidly in young animals, peaks at about 9 y (6.9%), and then declines in old bulls ≥ 12 y, i.e., adults 8 to 10 y, mean 6.6 ± 0.122% (n = 13) vs. adults ≥ 12y, 6.09 ± 0.32% (n = 9); t-test p< 0.01. More detailed relative growth patterns for subadults, adults and old bulls could not be established because the sample size is too small and **SBL** was not available for all specimens (**SBL**s for 12 animals drowned in fishnets were not recorded because rough conditions at sea precluded measurement of **SBL**).

Bacular growth relative to age zero, RGR Y_0

Percent change in value of bacular measurement at age *t*, relative to value at age zero, is presented in Table 4. In yearlings, bacular mass was the most rapidly growing variable, followed by bacular length, proximal height, distal height, proximal shaft height, proximal width and distal shaft height/middle shaft height. Distal width showed little sign of growth.

Growth of bacular variables continued to increase until at least 10 y, with bacular mass, middle shaft height and distal shaft height expressing continued growth in bulls ≥ 12 y. Bacular mass and distal height expressed greatest overall growth, followed by proximal height, proximal shaft height and bacular length (Table 4).

Bacular growth relative to the previous year, RGR Y_{t-1}

Percent change in value of bacular measurement at age *t,* relative to value at age *t*-1, for bulls 7-10 y, is presented in Table 4. Percent increment in bacular length, distal height and bacular mass peaked at 8 y; middle shaft height and distal shaft height peaked at 9 y; proximal height, proximal width distal width and proximal shaft height peaked at 10y.

Age group	Age (y)	n	Var 1 (BL)	Var 2	Var 3	Var 4	Var 5	Var 6	Var 7	Var 8	Var 9
Pup	< 1	3	28.5 ± 1.6	2.6 ± 0.5	3.5 ± 0.3	2.2 ± 0.3	1.7 ± 0.2	2.4 ± 0.2	2.2 ± 0.2	1.9 ± 0.1	0.1 ± 0.0
			(9.6)-	(31.5) 9.0%	(12.5) 12.3%	(24.7) 7.8%	(18.3) 5.9%	(13.6) 8.3%	(15.7) 7.7%	(7.9) 6.8%	(0) 0.4%
Yearling	1	5	47.8 ± 1.7	3.5 ± 0.1	4.2 ± 0.1	2.9 ± 0.2	1.7 ± 0.04	3.0 ± 0.1	2.5 ± 0.1	2.2 ± 0.2	0.3 ± 0.03
			(8.0) -	(7.7) 7.3%	(6.6) 8.8%	(15.8) 6.1%	(5.9) 3.6%	(5.0) 6.2%	(12.2) 5.2%	(18.2) 4.6%	(23.6) 0.6%
Subadult	4	1	86.6	5.3	6.6	7.3	2.8	5.9	5.5	4.4	2.4
	5	3	97.1 ± 4.6	9.4 ± 2.5	7.7 ± 0.9	9.4 ± 0.6	4.2 ± 0.8	7.0 ± 0.6	5.8 ± 0.2	5.0 ± 0.2	3.4 ± 0.4
			(8.2)-	(45.3) 9.7%	(20.9) 7.9%	(10.5) 9.7%	(31.0) 4.3%	(13.6) 7.2%	(4.6) 6.0%	(8.4) 5.1%	(21.2) 3.5%
	6	2	99.5 ± 2.8	8.2 ± 0.1	6.7 ± 1.5	10.9 ± 0.1	3.9 ± 0.6	7.1 ± 0.9	5.4 ± 0.2	4.5 ± 0.1	3.1 ± 0.1
			(3.9)-	(0.9) 8.2%	(31.7) 6.7%	(0.7) 10.9%	(20.2) 3.9%	(17.9) 7.1%	(5.2) 5.4%	(3.1) 4.5%	(2.3) 3.1%
	7	11	101.4 ± 2.7	9.8 ± 1.0	7.6 ± 0.4	10.7 ± 0.6	4.0 ± 0.2	7.2 ± 0.3	6.3 ± 0.3	5.3 ± 0.2	4.1 ± 0.4
			(9.0) -	(33.4) 9.7%	(16.3) 7.5%	(17.8) 10.5%	(17.5) 4.0%	(14.8) 7.1%	(13.3) 6.2%	(14.3) 5.3%	(34.0) 4.0%
	4-7	**1 7**	**99.5 ± 2.1**	**9.3 ± 0.8**	**7.5 ± 0.3**	**10.3 ± 0.4**	**4.0 ± 0.2**	**7.1 ± 0.2**	**6.1 ± 0.2**	**5.1 ± 0.2**	**3.7 ± 0.3**
			(8.7) -	(34.6) 9.3%	(17.5) 7.5%	(17.5) 10.3%	(20.5) 4.0%	(14.4) 7.1%	(12.5) 6.1%	(13.9) 5.1%	(33.1) 3.7%
Adult	8	8	111.4 ± 3.1	11.3 ± 0.8	9.4 ± 0.6	12.2 ± 0.5	4.3 ± 0.1	8.0 ± 0.3	6.9 ± 0.2	5.6 ± 0.2	5.7 ± 0.5
			(7.8) -	(19.0) 10.8%	(18.5) 8.4%	(12.3) 11.0%	(9.5) 3.9%	(11.1) 7.2%	(8.7) 6.1%	(8.4) 5.0%	(23.9) 5.1%
	9	4	116.9 ± 2.7	10.4 ± 1.8	10.8 ± 1.6	12.4 ± 0.9	4.9 ± 0.7	8.1 ± 0.5	7.6 ± 0.3	6.3 ± 0.2	7.2 ± 0.7
			(4.6) -	(35.5) 8.9%	(29.3) 9.2%	(14.5) 10.6%	(29.2) 4.2%	(12.8) 7.0%	(7.9) 6.5%	(7.8) 5.4%	(18.4) 6.2%
	10	3	117.8 ± 2.9	14.0 ± 0.8	13.5 ± 1.9	13.2 ± 0.5	6.1 ± 0.4	10.6 ± 0.3	8.1 ± 0.4	6.5 ± 0.2	7.6 ± 0.6
			(4.3) -	(9.7) 11.9%	(24.5) 11.4%	(6.2) 11.2%	(12.5) 5.2%	(4.8) 9.0%	(8.1) 6.9%	(4.7) 5.5%	(14.1) 6.5%
	8-10	**15**	**114.2 ± 2.0**	**11.6 ± 0.7**	**10.6 ± 0.7**	**12.5 ± 0.4**	**4.8 ± 0.3**	**8.6 ± 0.3**	**7.3 ± 0.2**	**6.0 ± 0.1**	**6.5 ± 0.4**
			(6.6) -	(23.1) 10.2%	(26.4) 9.3%	(11.5) 10.9%	(22.0) 4.2%	(15.4) 7.5%	(10.6) 6.4%	(9.6) 5.2%	(23.2) 6.7%
	≥ 12	10	113.1 ± 3.8	11.4 ± 0.8	10.1 ± 0.7	13.3 ± 0.7	4.9 ± 0.5	10.0 ± 0.5 [8]	8.6 ± 0.6	6.6 ± 0.3	8.3 ± 0.9
			(10.7)-	(22.6) 10.1%	(20.9) 8.9%	(17.3) 11.7%	(28.4) 4.5%	(17.2) 8.8%	(23.6) 7.6%	(12.5) 5.8%	(34.2) 7.3%
Total		**50**	**50**	**50**	**50**	**50**	**50**	**48**	**50**	**50**	**50**
Mean for males ≥ 200 cm (n = 7)			127.7 ± 2.8	13.1 ± 0.3	9.9 ± 1.0	14.4 ± 0.4	5.0 ± 0.3	10.5 ± 0.5	9.2 ± 0.3	7.1 ± 0.3	10.9 ± 0.5
[Maximum value in brackets]			[139.3]	[14.0]	[13.7]	[15.7]	[5.8]	[12.2]	[10.2]	[8.1]	[12.5]

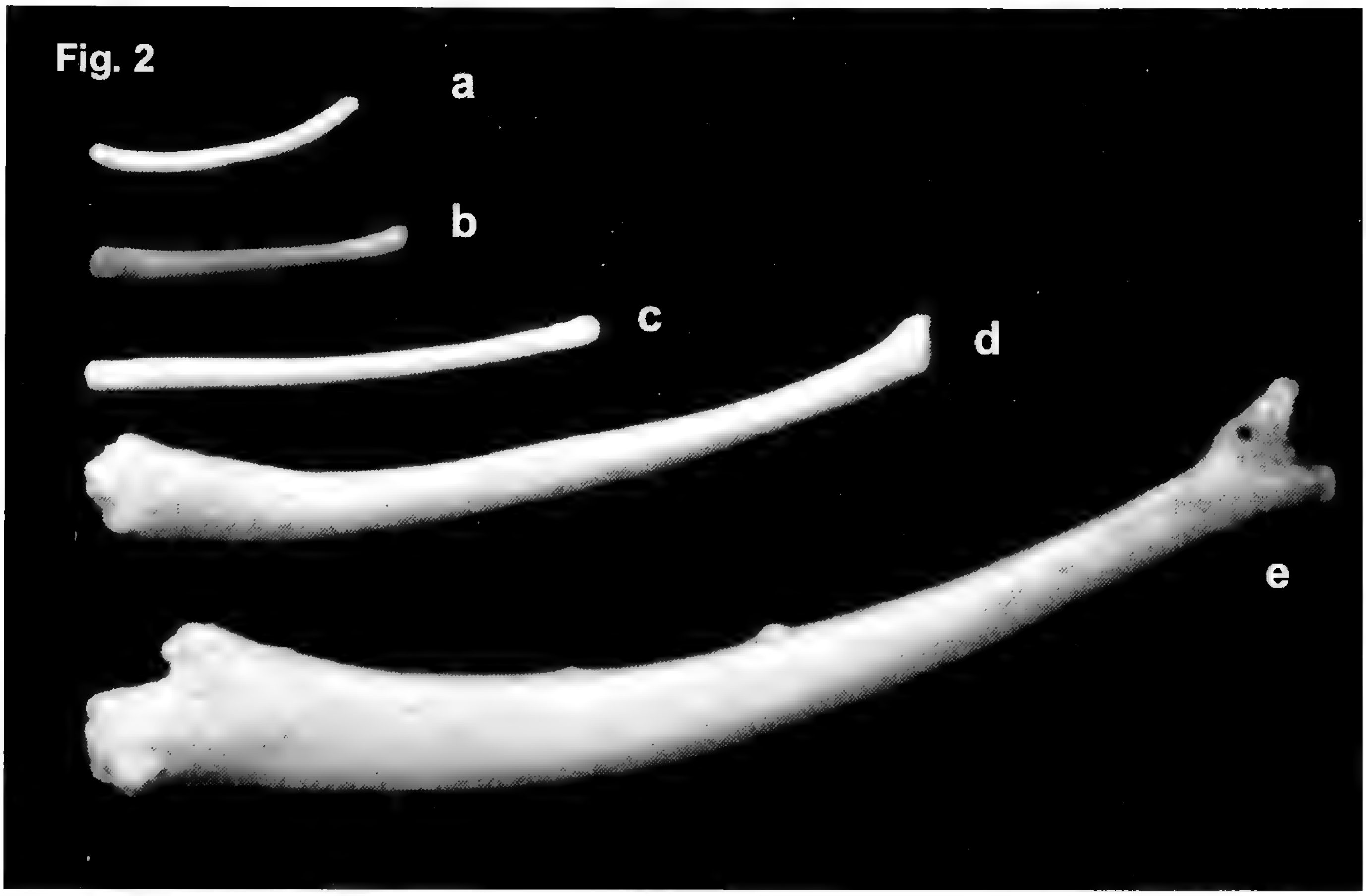

Fig. 2 Size and shape of the South African fur seal baculum in relation to age group: a. pup (PEM2020, 26.6 mm); b. pup (PEM2024, 31.6 mm); c. yearling (PEM2191, 50.7 mm); d. sub-adult, 7-y-old (PEM2053, 93.3 mm) and e. adult, 10-y-old (PEM2087, 123.3 mm).

Bacular length as an indicator of age

The plot of Bacular length (**BL**) vs. Age (y) is shown in Fig. 3. For animals 1-10 y, bacular length was highly, positively correlated with age (y) (r = 0.825, n = 38; Fig. 3). However, after fitting the straight line model, the plot of the residuals versus fitted values was examined, and the straight line model was found to be inadequate (the residuals were not scattered randomly about zero, see Weisberg, 1985, p. 23). Thus, strictly speaking bacular length could not be used as a reliable indicator of absolute age based on a simple linear model but could be used as a rough indicator of age.

For the range of ages available in this study (Table 2), the coefficient of variation in bacular length for young males 1-5 y (36.8%) was considerably higher than in older males (8-10 y, 6.6%; > 12 y, 10.7%).

Although bacular length was not a good indicator of absolute age, it was more accurately a 'rough indicator' of age group. When bacular length is known, the following linear discriminant functions can be used to categorise each observation into one of

Table 2 (LEFT). Summary statistics for bacular variables (1 - 9), according to age (y) and age group. Data presented as the mean ± SE, followed by coefficient of variation in round brackets, and bacular variable expressed as a percentage of bacular length. Maximum value of each variable (males of unknown-age) is also presented. All measurements are in mm, apart from bacular mass (g).

Variables: 1. Bacular length (BL); 2. Proximal height; 3. Proximal width; 4. Distal height; 5. Distal width; 6. Proximal shaft height; 7. Middle shaft height; 8. Distal shaft height; 9. Bacular mass. Number (n) is the number of bacula from individuals where their age had been determined based on dentition. Sample size given in square brackets where this does not equal total sample size. Mean value of variable ± SE for the 7 largest males (≥ 200 cm, SBL) of unknown-age; maximum value in brackets.

Table 3. Growth in mean bacular length (BL) relative to mean standard body length (SBL). Number (n) shows the number of canine aged animals where both BL and SBL were recorded. Of the 50 canine aged animals, SBL was not recorded for 12 animals, i.e. n = 38. Sample size is given in square brackets where this does not equal total sample size. Bacular length (BL) values are mean ± SE in mm. SBL is expressed as mean ± SE in cm. Relative bacular length (RBL) is defined as 100% x BL (mm)/SBL (mm).

Age group	Age (y)	n	Mean bacular length (BL) (mm)	Mean SBL (cm)	Relative Bacular Length (RBL) (RBL = 100xBL/SBL)
Pup	< 1	3	28.5 ± 1.6 [3]	69.0 ± 2.5 [3]	4.1% [3]
Yearling	1	5	47.8 ± 1.7 [5]	90.6 ± 2.7 [5]	5.3% [5]
Subadult	4	1	86.6	137.0	6.3%
	5	3	-	-	-
	6	2	102.2 (1 measured)	145.0 (1 measured)	7.0% [1]
	7	11	106.5 ± 3.0 [6]	159.8 ± 4.5 [6]	6.7% [6]
	4-7	**17**	**103.5 ± 3.3 [8]**	**155.1 ± 4.6 [8]**	**6.7% [8]**
Adult	8	8	110.0 ± 3.2 [7]	167.1 ± 7.1 [7]	6.6% [7]
	9	4	117.3 ± 3.8 [3]	171.0 ± 3.2 [3]	6.9% [3]
	10	3	117.8 ± 2.9	187.0 ± 1.7	6.3% [3]
	8-10	**15**	**113.5 ± 2.2[13]**	**172.6 ± 4.4 [13]**	**6.6% [13]**
	≥ 12	10	113.2 ± 4.3 [9]	185.9 ± 7.7 [9]	6.1% [9]
Total		**50**	**38**	**38**	**38**

four age groups (pups, yearlings, subadult, adults):

Pup = -5.50 + 0.39 x **BL**
Yearling = -15.53 + 0.65 x **BL**
Subadult = -67.25 + 1.35 x **BL**
Adult = -87.77 + 1.54 x **BL**

where, **BL** = bacular length (mm); Age Classes: pup, yearling, subadult and adult. The seal is classified into the age group associated with the linear discriminant function which results in the **minimum** value (see Stewardson et al., 2008, 2009). Of the 50 animals in this study, 86% were correctly classified using this method (Table 5).

Bacular length as an indicator of SBL

The plot of Log_e (**BL**) vs. Log_e (**SBL**) is shown in Fig. 4. Log_e Bacular length (**BL**) was highly positively linearly correlated with **SBL** (r = 0.877, n = 86; Fig. 4) on a plot of **SBL** (cm) vs. **BL** (mm) using robust Huber M Regression. When bacular length is known, the following equation (linear least squares fit; Log_e transformed data) can be used to predict Log_e (**BL**);

Log_e (**BL**) = -2.062 (± 0.247) + (1.3142 ± 0.0493) x Log_e (**SBL**)

where, the Spearman rank-order correlation was 0.877. M-estimate was not significant for bias (p = 0.0945) but LS-estimates for bias were significant (p = 0.00048).

Bivariate allometric regression

Spearman rank-order correlations show that bacular variables were significantly ($p \leq 0.01$) with

Table 4. Growth in bacular variables (1-9) relative to the mean value of bacular measurement (i) at age zero, RGR Y0 and (ii) from the previous year, RGR Yt-1. Growth in SBL is also given. All measurements are in mm, apart from the SBL (cm) and the bacular mass (g).

Variables: 1. Bacular length (BL), 2. Proximal height, 3. Proximal width, 4. Distal height, 5. Distal width, 6. Proximal shaft height, 7. Middle shaft height, 8. Distal shaft height, 9. Bacular mass. n is the number of canine-aged animals. SBLs of 12 animals were not recorded. Values for growth relative to age zero are presented on the left side of the relevant columns, i.e. [(Yt-Y0)/Y0] x 100 where Yt is the mean value at time t and Y0 is the value at time zero. Values for growth relative to the previous year are presented on the right hand side of the relevant columns. For animals 7 to 10 y of age, i.e. [(Yt-Yt-1)/Yt-1] x 100 where Yt-1 is the mean value for the previous year class and Yt is the mean value at time t. Sample sizes are given in brackets where this does not equal the total sample size. Instances where growth could not the calculated are marked (*) and there are two cases where the calculated growth is negative (adult age 7y; Var 4 and adult age 9y; Var 2).

Age Class	Age (y)	n	SBL	Var1 (BL)	Var 2	Var 3	Var 4	Var 5	Var 6	Var 7	Var 8	Var 9
Pup	< 1	3	-	-	-	-	-	-	-	-	-	-
Yearling	1	5	31	68	36	21	31	2	26	13	14	200
Subadult	4	1	99	204	106	89	227	68	149	150	128	2300
	5	3	*[0]	241	266	120	322	152	196	164	157	3300
	6	2	110 [1]	249	218	91	386	131	200	145	133	2950
	7	11	132; * [6]	256; 2.0	282; 20.4	118; 13.7	379; -1.5	143; 5.1	206; 2.0	186; 16.5	176; 18.8	3964; 33.2
Adult	8	8	142; 4.6 [7]	391; 9.9	341; 15.3	169; 23.4	448; 14.5	158; 6.3	239; 10.8	211; 8.9	191; 5.2	5600; 40.3
	9	4	148; 2.3 [3]	311; 4.9	304; -8.3	209; 14.9	453; 0.9	193; 13.4	243; 1.2	245; 10.9	225; 11.6	7125; 26.8
	10	3	171; 9.4	313; 0.8	447; 35.3	285; 24.7	491; 6.9	268; 25.8	346; 30.1	268; 6.6	234; 3.1	7533; 5.7
	≥ 12	10	169 [9]	297	343	189	495	196 [8]	320	290	241	8150
Total		**50**	**38**	**50**	**50**	**50**	**50**	**48**	**50**	**50**	**50**	**50**

each other (Table 6). Distal width (**Var 5**) with proximal width (**Var 3**) had the lowest correlation (r = 0.67) but most equal or exceed r = 0.80. Plots of all the data used for the bivariate allometric regressions can be found in Stewardson (2001). In the present study, the slope and intercept values and correlation coefficients (**r**) are shown in Tables 7, 8 and 9.

Regression of bacular measurement on SBL

Of the 103 seals in the study, 86 were used in regression analysis for the natural log of baculum measurement on Log_e (**SBL**). All pups (n = 3) were excluded from the regression analysis, and **SBL**s for 12 animals had not been recorded (see above).

There was little difference between the ordinary least square straight lines fitted to the data, and the 'robust' least squares straight lines fitted to the same data. The 'robust' straight line equations for regressing log of baculum measurement on log of seal length are given in Table 7. All bacular variables were highly, positively correlated with **SBL**, r ≥ 0.68. Relative to **SBL**, growth in distal height, distal width, proximal shaft height, distal shaft height and bacular mass was positively allometric; and proximal width was

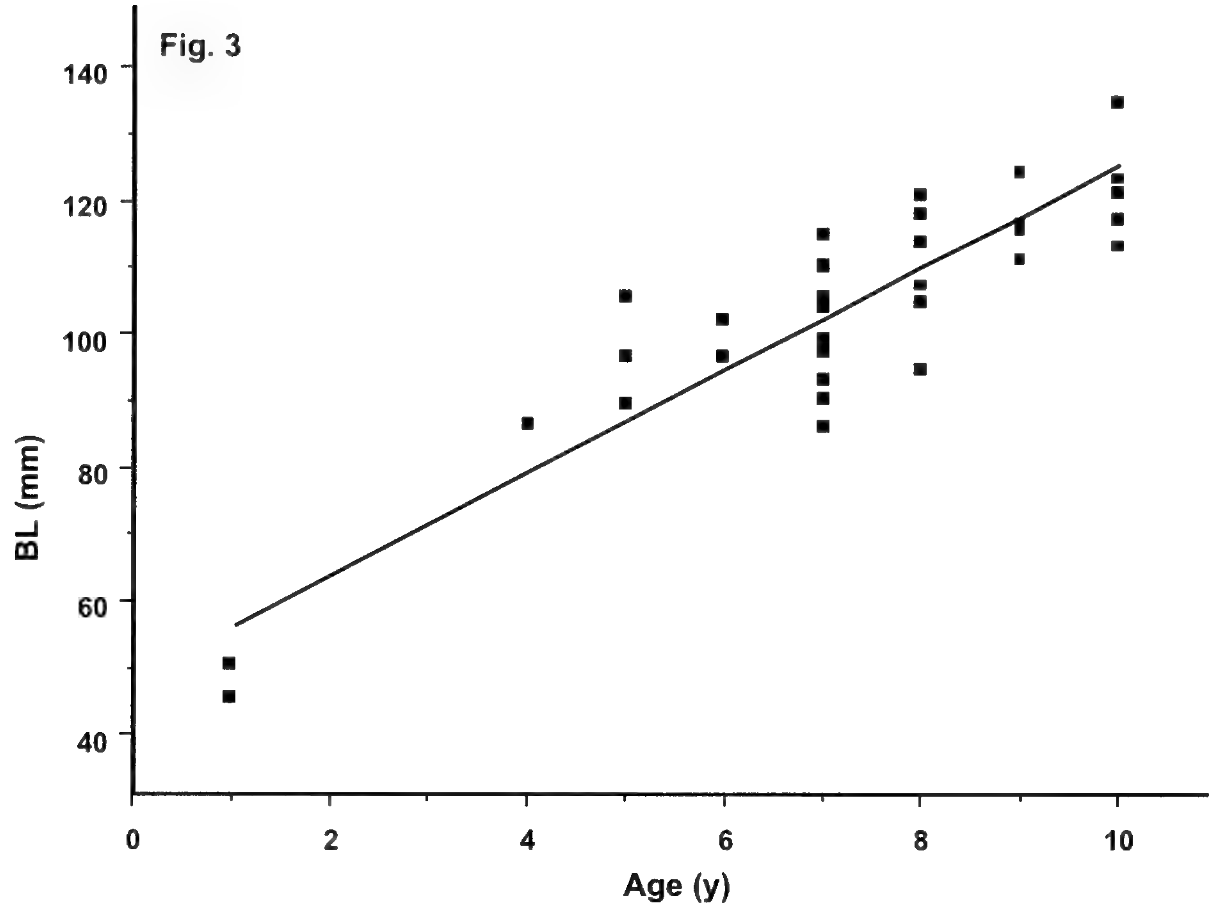

Fig. 3 Bivariate plot of Baculum Length (BL) (mm) vs. age (y) using Robust MM Linear regression. The fitted line was BL = 48.63 (± 10.39) + (7.678 ±1.346) x Age with a Spearman rank-order correlation of 0.825. The M-estimate and LS-estimate for bias were not significant. Robust MM Linear regression could also be run to predict Age (y) from BL. The fitted line was Age = -4.016 (± 1.166) + 0.108 (± 0.0111) x BL.

isometric (Table 7). Regression slopes for bacular length, proximal height and middle shaft height all had significant positive slopes > 1 (Table 7).

Value of bacular measurement on bacular length

Of the 103 seals in the study, 100 were used in regression analysis for natural log of baculum measurement on bacular length. All pups (n = 3) were excluded from the regression analysis.

All bacular variables were highly, positively correlated with bacular length, $r \geq 0.7$ (Table 8). Relative to bacular length, growth in distal height, proximal shaft height and proximal height was positively allometric relative to bacular length; distal width and distal shaft height was isometric; and proximal width was negatively allometric (Table 8). Regression slopes for middle shaft height and bacular mass scaled with positive slope (Table 8). The slope for bacular mass was considerably steeper than for other variables.

Value of bacular measurement on age

Of the 40 seals aged from upper canines, 37 were used in regression analysis for the natural log of a baculum measurement versus age. As above, all pups (n = 3) were excluded from the regression analysis.

Overall, the plots of log bacular measurements versus log **SBL** were better described by linear relationships than the plots of $\log_e$ bacular measurements versus age (see Griffiths et al., 1998, p. 126). Fig. 3 shows a plot of **BL** vs. Age (y); data for this and other fits are shown in Table 9. Proximal height vs. Log_e (**SBL**) was the only variable that roughly resembled a straight line.

DISCUSSION

Bacular size

In South African fur seals (*Arctocephalus pusillus pusillus)* from the Eastern Cape coast, maximum

Table 5. Discriminant analysis for male seal age group (pup, yearling, subadult and adult) inferred from bacular length. Number (n) is the number of animals aged from counts of incremental lines observed in the dentine of upper canines, n = 50. Percentage of animals correctly classified into age group is given in brackets. Animal classified as adults includes animals ≥ 12 y.

Known Age Group	Classification into age group				
	n	Pup	Yearling	Subadult	Adult
		(age < 7 month)	(7 month < age < 18 month)	(18 month < age < 7 y 6 month)	(age ≥ 7y 6 month)
Pup	3	**3** (100%)	0	0	0
Yearling	5	0	5 (100%)	0	0
Subadult	17	0	0	14 (82%)	4 (18%)
Adult	25	0	0	3 (16%)	21 (84%)
Total	**50**	**3**	**5**	**17**	**25**

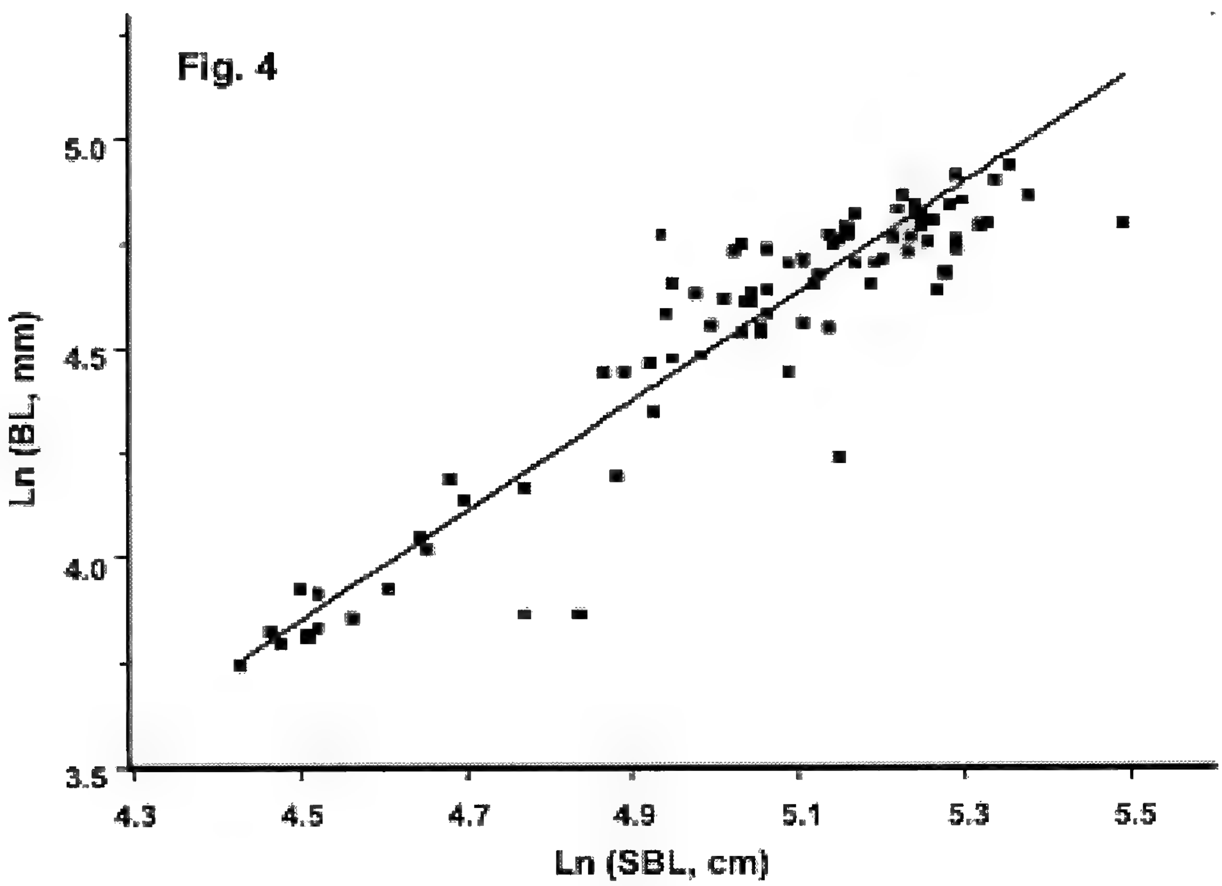

Fig. 4 Bivariate plot of Loge (BL) vs. Loge (SBL) using Robust MM Linear regression. The fitted line was Loge (BL) = -2.062 (± 0.247) + (1.3142 ± 0.0493) x Loge (SBL) with a Spearman rank-order correlation of 0.877. The M-estimate was not significant for bias (p = 0.0945) but the LS-estimate for bias was significant (p = 0.00048).

Table 6. Spearman rank-order correlation coefficients for log bacular variables. Variables: 1. bacular length (BL); 2. Proximal height; 3. Proximal width; 4. Distal height; 5. Distal width; 6. Proximal shaft height; 7. Middle shaft height; 8. Distal shaft height; 9, bacular mass. Two distal width measurements were not recorded because specimens PEM2049 and PEM2134 were damaged hence Var 5 has only 101 records. All correlations are significant at the 1% level (2-tailed), i.e. $p < 0.01$.

	Var 1 (BL)	Var 2	Var 3	Var 4	Var 5	Var 6	Var 7	Var 8	Var 9
Var 1 (BL)	1.00	0.82	0.71	0.90	0.80	0.88	0.92	0.90	0.95
Var 2	0.82	1.00	0.80	0.76	0.75	0.85	0.84	0.80	0.85
Var 3	0.71	0.80	1.00	0.69	0.67	0.76	0.75	0.70	0.77
Var 4	0.90	0.76	0.69	1.00	0.80	0.86	0.89	0.88	0.92
Var 5	0.80	0.75	0.67	0.80	1.00	0.79	0.80	0.80	0.83
Var 6	0.88	0.85	0.76	0.86	0.79	1.00	0.94	0.89	0.94
Var 7	0.92	0.84	0.75	0.89	0.79	0.94	1.00	0.96	0.97
Var 8	0.90	0.80	0.70	0.88	0.80	0.89	0.96	1.00	0.95
Var 9	0.95	0.85	0.77	0.92	0.83	0.94	0.97	0.95	1.00
Total	**103**	**103**	**103**	**103**	**101***	**103**	**103**	**103**	**103**

bacular length we found in the present study was 139.3 mm and mass was 12.5 g; however bacula up to 141 mm (Oosthuizen and Miller, 2000) and 16.8 g (Rand, 1949) have been reported for South African fur seals from other areas. Baculum length was similar to that of the Northern fur seal (*Callorhinus ursinus*) (Scheffer, 1950) and the harp seal (*Pagophilus greonlandicus*) (Miller and Burton, 2001; Miller 2009), which is a phocid seal. As with other Otariidae, bacular length of the South African fur seal is considerably smaller (proportionately to standard body length, **SBL**) than that of most Phocidae and the Odobenidae (Scheffer and Kenyon, 1963; Miller and Burton, 2001).

No systematic quantitative study seems to have been made of the growth with age of the baculum of the Australian fur seal (*Arctocephalus pusillus doriferus*) or the New Zealand fur seal (*Arctocephalus forsteri*). Basic morphometric data on the bacula of Australian and New Zealand fur seals do not appear to be readily available (Scheffer and Kenyon, 1963). At present it would be very easy to pass off illegally obtained bacula from Australian and New Zealand seals as legal South African material.

Bacular shape

Although detailed information on the morphology of the otariid bacula is sparse, bacular shape was most similar to the Northern fur seal and California seal lion (Kim *etal.*, 1975; Morejohn, 1975; King, 1983). For example, in *Arctocephalus* fur seal species, Northern fur seal and California seal lion, the adult bacular apex consists of a dorsal and a ventral knob. When viewed anteriorly, the knobs are parallel sided (*Arctocephalus* species and the California sea lion), or resemble a figure-of-eight in the California sea lion. Apical keels (lateral expansion of the apex) are present on the baculum of some California sea lion individuals, yet absent in both *Arctocephalus* species and the Northern fur seal (Kim *et al.*, 1975; Morejohn, 1975).

Bacular length (BL) as an indicator of Standard Body Length (SBL) and age

As with other species of pinnipeds, there is considerable variation in **BL** with age, especially in younger animals (Rand, 1949; Scheffer, 1950; Bester, 1990; Oosthuizen and Miller, 2000).

In male South African fur seals, **BL** was found to be a 'rough indicator' of **SBL** and age group, but not of absolute age. The classification criteria for age group, and **SBL**, developed in this study will be particularly useful when teeth are not available for age determination; a seal is decomposed/scavenged (total **SBL** cannot be measured) or because the skull is incomplete/absent (total **SBL** cannot be extrapolated from skull length); or museum records have been misplaced or destroyed. As more specimens become

Table 7 `Robust' least squares straight line equations (y = mx + b), Spearman rank-order correlation coefficients and allometry for log bacular measurement (mm) on log seal body length (cm). The number (n) is for the total number of bacula from canine-aged animals and for animals of unknown-age (the 3 pups were excluded from analysis, and SBLs from 14 males were not recorded, i.e., n = 86 bacula). r is Spearman rank-order correlation coefficient. All correlations were significant at the 1% level (2-tailed), m is the determined slope of the fitted line. NA, tests not applicable because the model assumptions required to test hypotheses about the slope of the line (m) were not met. Not significant (ns) since the p-value was > 0.05, we cannot reject Ho, in favour of H1 at the 5% significance level; therefore growth is isometric. * For distal width (Var 5) n = 84 because distal width measurements could not be measured on two specimens (see Table 6).

Dependent variable	Linear regression					Allometry		
	n	Intercept (b) ± SE	Slope (m) ± SE	r	(p-values)	Alternative Hypothesis	df	p-value
1. Length of baculum (BL)	86	-1.67 ± 0.22	1.23 ± 0.04	0.88	(< 0.01)	NA	NA	NA
2. Proximal height	86	-5.58 ± 0.45	1.54 ± 0.09	0.78	(< 0.01)	NA	NA	NA
3. Proximal width	86	-3.12 ± 0.48	1.03 ± 0.09	0.68	(< 0.01)	H_1: m ≠ 1	84	0.78 ns
4. Distal height	86	-7.88 ± 0.46	2.00 ± 0.09	0.84	(< 0.01)	H_1: m > 1	84	< 0.01
5. Distal width	84*	-5.64 ± 0.04	1.38 ± 0.09	0.80	(< 0.01)	H_1: m > 1	82	< 0.01
6. Proximal shaft height	86	-5.59 ± 0.29	1.50 ± 0.06	0.87	(< 0.01)	H_1: m > 1	84	< 0.01
7. Middle shaft height	86	-5.92 ± 0.28	1.53 ± 0.06	0.90	(< 0.01)	NA	NA	NA
8. Distal shaft height	86	-5.24 ± 0.29	1.36 ± 0.06	0.87	(< 0.01)	H_1: m > 1	84	< 0.01
9. Mass of baculum	86	-21.51 ± 0.68	4.51 ± 0.13	0.91	(< 0.01)	H_1: m > 1	84	< 0.01

Table 8. 'Robust' least squares straight line equations (y = mx + b), Spearman rank-order correlation coefficients and allometry for loge (bacular measurement) on loge (bacular length). Number (n) is the total number of bacula for canine-aged animals and animals of unknown-age (the 3 pups were excluded from analysis, i.e., n = 100 bacula). * For distal width (Var 5) n = 98 because two specimens were damaged (see Table 6). r is the Spearman rank-order correlation coefficient. All correlations are significant at the 1% level (2-tailed). Test not applicable (NA) because model assumptions required to test hypotheses about the slope of the line (m) were not met. Not significant (ns) since the p-value was > 0.05, we cannot reject H_0 in favour of H_i at the 5% significance level; therefore growth is isometric.

D.pendent variable	Linear regression					Allometry		
	n	Intercept (b) ± SE	Slope (m) ± SE	r	(p-values)	Alternative Hypothesis	df	p-value
2. Proximal height	100	-3.11 ± 0.26	1.21 ± 0.06	0.80	(< 0.01)	H_i: m > 1	98	< 0.01
3. Proximal width	100	-1.52 ± 0.29	0.79 ± 0.06	0.69	(< 0.01)	H_i: m < 1	98	0.15 ns
4. Distal height	100	-5.07 ± 0.18	1.60 ± 0.04	0.89	(< 0.01)	H_i: m >1	98	< 0.01
5. Distal width	98*	-3.61 ± 0.26	1.08 ± 0.06	0.79	(< 0.01)	H_i: m ≠ 1	96	0.15 ns
6. Proximal shaft height	100	-3.30 ± 0.17	1.16 ± 0.04	0.87	(< 0.01)	H_i: m > 1	98	< 0.01
7. Middle shaft height	100	-3.52 ± 0.15	1.17 ± 0.03	0.91	(< 0.01)	NA	NA	NA
8. Distal shaft height	100	-3.18 ± 0.29	1.05 ± 0.04	0.89	(< 0.01)	H_i: m ≠ 1	98	0.15 ns
9. Mass of baculum	100	-14.66 ± 0.29	3.49 ± 0.06	0.94	(< 0.01)	NA	NA	NA

Table 9. 'Robust' least squares straight line equations and Spearman rank-order correlation coefficients for log (bacular measurement) vs. age (y) and for log (weight) vs. age (y). n is the total number of bacula for canine-aged animals (only animals 1 to 10 y were included in the analysis, hence n = 37). SBLs for 11 aged males were not recorded. r is the Spearman rank-order coefficient. All correlations were found to be significant at the p < 0.01 level (2 tailed).

Dependent variable	'Robust' Log-Linear regression			
	n	Intercept (b) ± SE	Slope (m) ± SE	r (p-values)
1. Length of baculum (**BL**)	37	3.88 ± 0.05	0.10 ± 0.01	0.83 (< 0.01)
2. Proximal height	37	1.13 ± 0.08	0.15 ± 0.01	0.67 (< 0.01)
3. Proximal width	37	1.31 ± 0.09	0.11 ± 0.01	0.78 (< 0.01)
4. Distal height	37	1.10 ± 0.10	0.17 ± 0.01	0.76 (< 0.01)
5. Distal width	37	0.45 ± 0.07	0.13 ± 0.01	0.68 (< 0.01)
6. Proximal shaft height	37	1.05 ± 0.06	0.13 ± 0.01	0.74 (< 0.01)
7. Middle shaft height	37	0.89 ± 0.13	0.13 ± 0.01	0.85 (< 0.01)
8. Distal shaft height	37	0.82 ± 0.06	0.11 ± 0.01	0.79 (< 0.01)
9. Mass of baculum	37	-1.28 ± 0.15	0.37 ± 0.02	0.87 (< 0.01)
Standard body length (**SBL**)	26	4.46 ± 0.04	0.08 ± 0.01	0.83 (< 0.01)

available, the classification criteria would be expected to become more precise. Statistics on age vs. bacular length show that bacular length can be used as a rough indicator of age (Fig. 3) and show that it is a better indicator of age than Standard Body Length (**SBL**) in terms of correlation coefficient (r) and error of the predicted age (Stewardson et al., 2009). More determinations of bacular length in tagged bulls of known age could prove it to be a very useful method.

Bacular growth

In male South African fur seals, growth of the baculum is a differential process with most variables growing rapidly relative to **SBL** and bacular length (**BL**). Two variables were isometric and one was negatively allometric, relative to bacular length, indicating that the adult baculum was not simply an enlarged version of the juvenile baculum (see Fig. 2).

Growth changes in **BL** and mass described in this study generally support findings reported by Oosthuizen and Miller (2000) and are also similar to those reported for the harp seal (Miller and Burton, 2001) which is a phocid seal. In this study, based primarily on animals collected from the south and south-west coast of southern Africa, growth in **BL** took place rapidly up until 5 y; peaked at 9-10 y; and then slowed. Our findings could not be compared to those of Rand (1956) because, in the latter, age was estimated from cranial suture closure which has subsequently been shown to be an unreliable indicator of absolute age in this species, particularly for animals ≥ 12 y (Stewardson et al., 2008).

The biological significance of bacular growth patterns

In male South African fur seals, a growth spurt in **BL** occurs at 2-3 y (Rand, 1949; Oosthuizen and Miller, 2000), when males attain puberty (Stewardson et al., 1998). Unfortunately, we have very scanty details on the life history of South African fur seals during the dispersive juvenile stages of their life. After puberty, the baculum continues to increase in length with increasing age, approximating full length at about 9 y (Oosthuizen and Miller, 2000; present study). Bacular dimensions, other than length, approximate full size between 8-10 y (present study), when most males have attained full reproductive capacity (Stewardson et al., 1998). Although males can sire offspring at a young age (e.g., at 4 y in captivity; Linda Clokie-Van Zyl, pers. comm.), bacular growth is geared to coincide with the attainment of social maturity, presumably to enhance the effectiveness of copulation.

Socially mature male South African fur seals: (i) may achieve a high level of polygyny at large colonies (David, 1987); (ii) usually copulate once with each harem female, 5-7 days postpartum during a brief breeding season (November to late December) (David and Rand, 1986); and (iii) usually exhibit brief intromission duration (Stewardson, pers. obs.). In such males, the baculum is therefore large enough to provide sufficient mechanical support for insertion and repeated copulations (with potentially numerous females within a short period of time), and may assist in deeper penetration. The ornate apex presumably serves to stimulate the vagina of the female (Eberhard, 1985, 1996). However, the function of the apex in this species remains unclear considering that: (i) female South African fur seals are not 'induced ovulaters' like cats; (ii) copulation occurs when the female is sexually receptive and (iii) sperm competition is weak (Stewardson et al., 1998).

CONCLUSION

Data presented in this study provide more detailed information on the morphology of the South African fur seal bacula than earlier descriptions given by Rand (1956) and Mohr (1963), based on smaller data sets and more dubious age estimates. Oosthuizen and Miller (2000) used a larger data set than the present study but did not attempt a detailed analysis of bacular morphometrics. Our study provides new information on the patterns of bacular growth in relation to age and **SBL** (Oosthuizen and Miller, 2000), and demonstrate that bacular length is a 'rough indicator' of **SBL** and age group. Similar overall conclusions have been drawn from analysis of larger data sets available for the harp seal (Miller et al., 1998, 1999; Miller and Burton, 2001) which is a member of the phocidae (or true seals). The seal baculum is a heterotopic bone and so it is likely that it shows at least some growth throughout life. We have found that the size of the baculum relative to SBL does decrease in old bulls but perhaps growth layer groups (GLG) can be determined by histological sectioning of bacula. It might provide a means to estimate age in very old individuals where dentition no longer gives useful estimates of age. Bacular measurements on very old bulls where the age is known from tagging or from zoo animals are needed.

Further studies examining the morphology and growth patterns of the pinniped bacula from known age animals are required to establish species affinities and develop identification protocols for seal bacula.

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BOOK REVIEW

A Guide To The Beetles Of Australia

George Hangay and Paul Zborowski
CSIRO Publishing
130 Oxford Street (PO Box 1139)
Collingwood VIC. 3066
RRP :$ 44.95 (Au.)

At last a compact, affordable and beautifully illustrated beetle book with coloured photos and easily understood descriptions has been published. The authors have gone to great lengths to produce a very comprehensive guide to all the families of Beetles that occur in Australia and it will be of great use both by amateur as well as members of the scientific community. This will enable one to quickly identify beetles to the family level using the photos of live beetles and the concise but very clear descriptions in this new book. The coloured photos are so superb of the complete adult beetles posing in their natural habitat, it is like having the live beetle in ones hand. The photos are often larger in size than the actual beetle in real life so the identification is often successful without even the use of a microscope.

The book begins with an **Introduction** that explains what makes a beetle and what " use " beetles are, using both photos of world class (almost all of the photos, over 400, of the beetles are of live insects in a natural setting. So this will be so useful for scientific field or laboratory work, amateur naturalists or even suburban gardeners wanting identifications.

The next section is on **Anatomy** and has very clear descriptions of anatomy, various types of antennae (the photos of the antennae are clear and are almost self explanatory to explain the taxonomic term normally used in the written identification keys). The thorax, legs and the wings of the beetles have very clearly drawn illustrations, once again, making this book more user friendly than so many massive scientific taxonomic texts of the past.

The next section contains a detailed description of the **Reproduction and Development** of the larvae and adults of Beetles with numerous photos and clear and very detailed easily understood descriptions.

Food and Survival section next containing the type of food that they consume and the defences they use against their many predators.

Then, the next section is on the **Higher level of taxonomy of the Beetles,** listing suborders, and all superfamilies. This is a brief outline of four suborders and a number of superfamilies into which the families are placed. This also contains both general and specific details of the superfamilies of their taxonomic features, feeding habits, ecological data and information on those superfamilies with specimens that are known to be pests.

The next section is the Main section of the book it is the **Family Descriptions,** this covers all families that occur in Australia (177 pages). The Family Descriptions are written in a very clear, concise and easy to follow with straight forward characters listed first then photos of world class accuracy of live beetles, and where no photos they have obtained permission of illustrations from CSIRO publications. So all families have at least one form of illustration be it photo or drawn illustration however some of the more diverse families have over 20 photos that cover many of the different genera, within the family.

The **Families Descriptions** of each Family covers the following:

1. The known distributions throughout Australia
2. The beetle (larvae and adult) feeding habits
3. The ecology of both the larvae and the adults
4. The numbers of species and genera known in Australia
5. The photos are a mixture of beetles species from all states of Australia
6. Common names

After the family descriptions is a list of **Endnotes** listing over 53 references, covering taxonomic and general habits and personal communications from Australian and overseas scientists who are specialists studying Beetles.

Next is a very detailed **Glossary** (over 250 terms detailed) which explains all the taxonomic or scientific terms used any where throughout the book.

Next is a very useful Index of " **Common Names** " of many of the species of Beetles photographed or described in the book , this is often very useful for both general and scientific information reporting.

The authors in the process of producing this book have had direct support by working with over 20 of Australia and the world's leading Beetle's experts on taxonomic, biology and ecological areas of all the beetle families of Australia. They have also accessed other resources such as websites and even photos of some specimens from the Australian Museum collections.

As the book is in paperback form and the price is only $44.95, this allows it to be available to amateur young insect collectors, naturalists, scientific laboratories that study insects in details and most important this makes it a great value for money buy for University students of Biological and Agriculture courses. As Beetles are the most commonly found insects and they are the most prolific insect group as far as families and species go the lack of a book covering them has been wanting for many decades. As Beetles are often the main insect group used in many environmental impact assessment reports for the effects over time from suburban or country areas affected by pollution from such things as mining, harvesting native forests, pollution from factories etc, this will be of great benefit in quickly identifying the beetles for these reports.

I have been assisting to teach Taxonomic Entomology courses at the University of Sydney for eleven years now and there has been a desperate need for a text such as this to give the students the chance to actually enjoy the learning and studying of insect identifications. There has been a great need for a book on the taxonomy and details about Beetles of Australia of this standard for the scientific taxonomic, biological and ecological University courses for many years as the only other texts of Beetles prior to this one has been large scientific volumes covering all insect groups often costing hundreds of dollars. As the book is so reasonably priced at $44.95 and is a compact paperback, the students can take it out on their collecting field trips to guide them to where and what beetles they may find as they forage for their university course collections. The authors have also added many unusual biological and behaviour notes that the students will find enjoyable to learn about beetles as they are the most commonly collected insect by students. The general public who may be interested in beetles, will find this a reasonably priced text, interesting, enjoyable and informative book. The scientific community will make great use of this new beetle book as it has the most up to date taxonomic data, the photos are so clear, concise and so large. The photos are of beetles from all the different states of Australia so it will be of great general use throughout Australia. The easily followed description keys, the life histories, the food habits, the natural habitat in the wild, the listing of total species numbers, information of introduced species, behaviour data, the size range of the beetles and plant associations all in one book, make it an absolute must have for all scientific biological laboratories and institutions working on any insect research of beetles in Australia.

Elizabeth Jefferys
Sydney
25th May 2010

INSTRUCTIONS FOR AUTHORS

(*this is an abbreviated form – the full instructions can be obtained from our web site or from the Secretary*)

1. The *Proceedings of the Linnean Society of New South Wales* publishes original research papers dealing with any topic of natural science, particularly biological and earth sciences.

2. Manuscripts should be submitted to the Editor (M.L. Augee, PO Box 82, Kingsford NSW 2032). All manuscripts are sent to at least two referees and in the first instance three hard copies, including all figures and tables, must be supplied. Text must be set at one and a half or double spacing.

3. References are cited in the text by the authors' last name and year of publication (Smith 1987, Smith and Jones 2000). For three of more authors the citation is (Smith et al. 1988). Notice that commas are not used between the authors' names and the year, 'and' is spelled out (not &), and et al. is not in italics.

The format for the reference list is:

Journal articles:

Smith, B.S. (1987). A tale of extinction. *Journal of Paleontological Fiction* **23**, 35-78.

Smith, B.S., Wesson, R.I. and Luger, W.K. (1988). Levels of oxygen in the blood of dead Ringtail Possums. *Australian Journal of Sleep* **230**, 23-53.

Chapters or papers within an edited work:

Ralph, P.H. (2001). The use of ethanol in field studies. In 'Field techniques' (Eds. K. Thurstle and P.J. Green) pp. 34-41. (Northwood Press, Sydney).

Books:

Young, V.H. (1998). 'The story of the wombat'. (Wallaby Press, Brisbane).

4. An abstract of no more than 200 words is required. Sections in the body of the paper usually include: INTRODUCTION, MATERIALS AND METHODS, RESULTS, DISCUSSION, ACKNOWLEDGEMENTS and REFERENCES. Some topics, especially taxonomic, may require variation.

5. Subheadings within the above sections should be in the form:

Bold heading set against left margin

This is the form for the first level headings and the first line of text underneath is indented

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This is the next level, and again the first line of text underneath is indented.

Further subheadings should be avoided.

Italics are not to be used for headings but are reserved for genus and species names.

6. Up to 10 KEYWORDS are required. These are often used in computer search engines, so the more specific the terms the better. 'Australian' for example is useless. Please put in alphabetical order.

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