Chapter 3

Diversity of Early Cretaceous Mammals from Victoria, Australia

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ABSTRACT

At least six different taxa are represented among the 21 specimens of mammals found at the Early Cretaceous Flat Rocks site in southeastern Australia. Analysis of these fossils reveals that, although the yield of mammalian specimens per person-year of effort at this locality is remarkably low, it is reasonable to expect that with further effort this assemblage will ultimately prove to be as diverse as any Early Cretaceous mammal assemblage known. By contrast, the two mammalian specimens collected thus far from the Early Cretaceous Dinosaur Cove locality in southeastern Australia are all that are likely to ever be recovered there.

INTRODUCTION

Twenty-three specimens of Early Cretaceous mammals from Victoria, Australia, are now known. Most are mandibles, many having one or more teeth in place. In addition, there are two skull fragments, two postcranial elements, and one isolated tooth. To date, eight of these specimens have been illustrated and seven described. Three different genera of mammals have been formally named based on this material (Rich et al., 1997, 1999, 2001a). Fragmentary remains indicate that at least three, and perhaps as many as five, additional mammalian genera occur there.

All but two of these mammalian specimens were found at a single early Aptian locality, Flat Rocks. The Flat Rocks site is located at 38° 39′ 40±02″S, 145° 40′ 52±03″E (World Geodetic Standard, 1984) on the shore platform of the Bunarong Marine Park, Victoria, Australia. These fossils occur in the Wonthaggi Formation of the Strzelecki Group, a nonmarine, volcaniclastic sandstone and mudstone unit approximately 3000 m thick (Rich et al., 1997, 1999). The exceptions are an isolated monotreme humerus (NMV P208094) and a tooth fragment (NMV P208383) from the early Albian site of The Pillar, Slippery Rock Site, Dinosaur Cove, Victoria, Australia, located at 38° 46′ 53±1″S, 143° 24′ 15±02″E (World Geodetic Standard, 1984; Rich and Vickers-Rich, 1999). The fossils from Dinosaur Cove

occur in the Eumerella Formation of the Otway Group.

The only other place in Australia that has yielded Mesozoic mammals is the opal field of Lightning Ridge in northern New South Wales. The mammalian fossils from there have been found in widely scattered mines as a byproduct of commercial opal mining. Two mammalian jaws, each the type of a new genus and species and regarded as monotremes, have been described to date, Steropodon galmani Archer et al. (1985) and Kollikodon ritchei Flannery et al. (1995). Kielan-Jaworowski et al. (1987) interpreted the dentition of S. galmani differently than did Archer et al. (1985). In addition, one other specimen, an edentulous mammalian maxilla fragment, has been described from Lightning Ridge (Rich et al., 1989).

ABBREVIATION: NMV P Museum Victoria, Melbourne, Australia, Palaeontological Collection.

SYSTEMATICS

CLASS MAMMALIA LINNAEUS, 1758

SUBCLASS MONOTREMATA BONAPARTE, 1838

FAMILY? STEROPODONTIDAE FLANNERY, ARCHER, RICH & JONES 1995

Teinolophos trusleri Rich et al., 1999

NMV P208231, holotype, a significantly crushed left mandibular fragment containing the

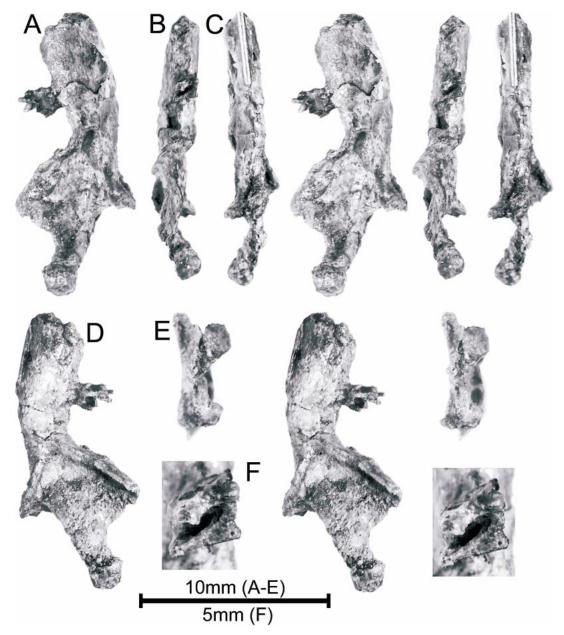


Fig. 3.1. *Teinolophos trusleri*, NMV P208231, left mandibular fragment with the most posterior molar. **A**, lingual view; **B**, dorsal view; **C**, ventral view; **D**, labial view; **E**, posterior view; **F**, most posterior molar, occlusal view. This specimen also figured in Rich et al. (1999: figs. 16, 17b–c, 18) and Rich et al. (2001c: figs. 1, 2b).

most posterior lower molar plus four alveoli anterior to it. Figure 3.1.

NMV P208526, a significantly crushed left mandibular fragment containing the four most posterior alveoli. NMV P210030, fragment of a right mandible with the four posteriormost alveoli. Figure 3.2.

The holotype was originally regarded as a "eupantothere" (Rich et al., 1999), but prep-

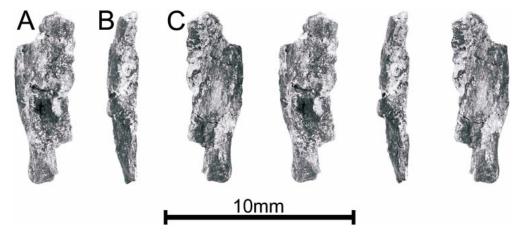


Fig. 3.2. *Teinolophos trusleri*, NMV P210030, fragment of right mandible with four posteriormost alveoli. **A**, lingual view; **B**, dorsal view; **C**, labial view.

aration of the single molar preserved on the holotype provided clear evidence that it was a monotreme (Rich et al., 2001c). The two edentulous jaw fragments are referred to *Teinolophos trusleri* on the basis of the enlarged, anteriorly placed mandibular foramen, which they share with the holotype of *T. trusleri*, in contrast to the condition found in the ausktribosphenids.

MONOTREMATA?

Unnamed Genus and Species

NMV P208094, a partial right humerus, from the early Albian site of The Pillar, Slippery Rock Site, Dinosaur Cove, Victoria, Australia. Figure 3.3.

This specimen is currently being described by Peter A. Pridmore, Thomas H. Rich, P. Vickers-Rich, and Petr P. Gambaryan. It belonged to an individual intermediate in size between a modern platypus and echidna. It was thus about the size to be expected for the humerus of the penecontemporaneous monotreme from Lightning Ridge, *Steropodon galmani*.

Among the humeri of marsupials and placentals, those of fossorial forms bear the closest resemblance to the humeri of monotremes. Despite this, there is a pattern common to monotreme humeri that readily distinguishes them from those of placentals and marsupials. With one notable exception,

NMV P208094 shares the characteristic monotreme humerus pattern. Where it differs is in the possession of an olecranon fossa, a feature unknown in other monotremes, while all but ubiquitous in placentals and marsupials. Assessing what the functional significance of that difference from other monotremes may have been is a primary objective of the ongoing study.

NMV P208185, the frontal region of a skull crushed somewhat laterally. Figure 3.4. NMV P210005, the frontal region of a skull. Figure 3.5.

NMV P 208185 and NMV P210005 are significantly larger than any other mammalian fossils from the Flat Rocks site. They would presumably belong to an individual the size of Steropodon galmani or Didelphis marsupialis. For an Early Cretaceous mammal, these two specimens are larger than most. Solely on that basis and the fact that S. galmani also occurs in Australia, these specimens are tentatively allocated to the Monotremata. Although the two specimens appear to represent the same region of the skull and are of similar size, the fact that the bone of NMV P 208185 has a well-developed external frontal crest bordering the insertion area for the temporalis muscle, as occurs in *Didelphis marsupialis* but not in any known monotreme and is approximately twice as thick as that of NMV P210005, which lacks an external frontal crest, suggests that they might not belong to the same species.

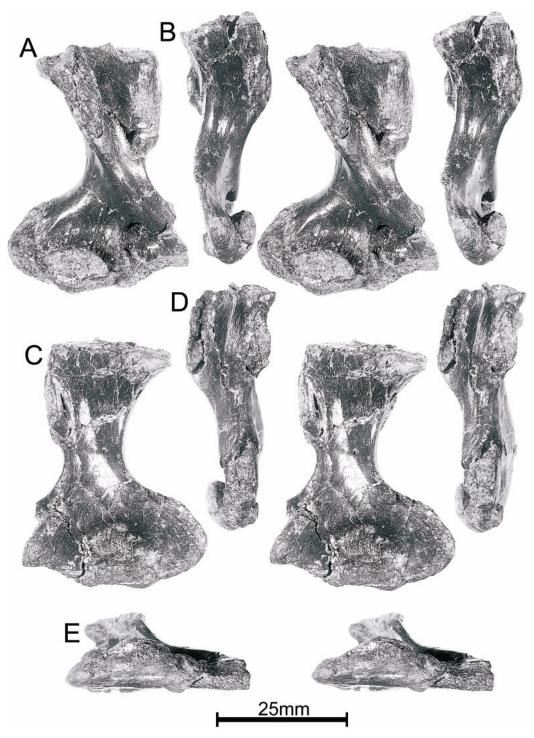


Fig. 3.3. NMV P208094, partial right humerus, from the early Albian site of The Pillar, Slippery Rock Site, Dinosaur Cove, Victoria, Australia. **A**, anterior view; **B**, lateral view; **C**, posterior view; **D**, medial view; **E**, ventral view.

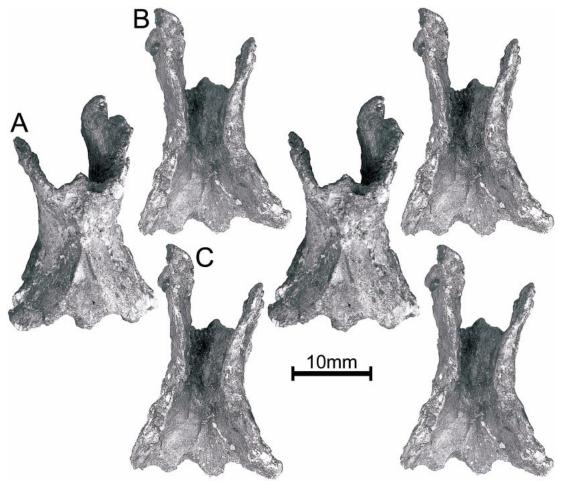


Fig. 3.4. NMV P208185, frontal region of skull crushed somewhat laterally. **A,** dorsal view; **B,** ventral view; **C,** ventral view (stereo reversed in order to provide reader with "endocast" of the dorsal surface of the brain).

SUBCLASS THERIA PARKER AND HASWELL, \$1897\$

INFRACLASS PLACENTALIA OWEN, 1837 ORDER AUSKTRIBOSPHENIDA RICH ET AL., 1997 FAMILY AUSKTRIBOSPHENIDAE RICH ET AL., 1997

Ausktribosphenos nyktos Rich et al., 1997

NMV P208090, holotype, a right mandibular fragment only slightly crushed with p6 and m1–3. Figure 3.6.

NMV P208228, a moderately crushed right mandibular fragment with p5–6 and m1–2. Figure 3.7.

NMV P208482, a heavily crushed right mandibular fragment with m2–3. Figure 3.8.

The holotype of *Ausktribosphenos nyktos* was originally identified as a tribosphenic mammal and quite possibly a placental. The interpretation of *A. tribosphenos* as a placental was challenged by Kielan-Jaworowska et al. (1998), Archer et al. (1999), and Luo et al. (2001, 2002). These arguments were countered in Rich et al. (1998), Rich et al. (2001b), and Rich et al. (2002) respectively. Rich et al. (1999) suggested that within the Placentalia, *A. nyktos* may be allied with the erinaceoids.

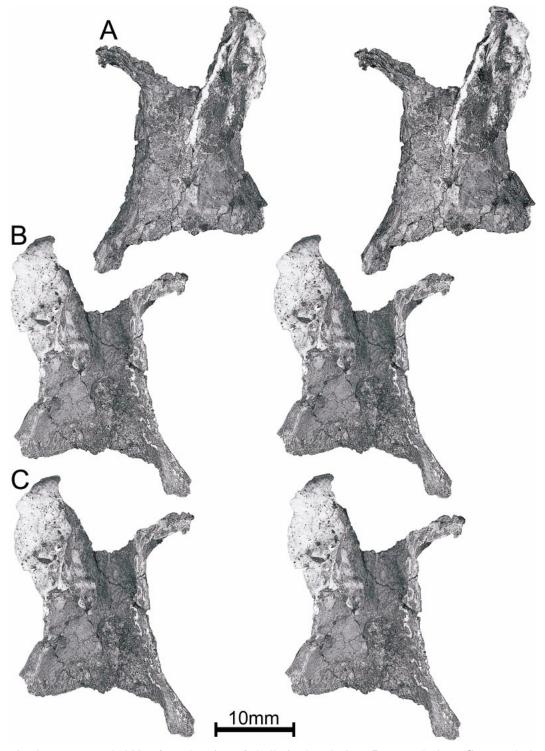
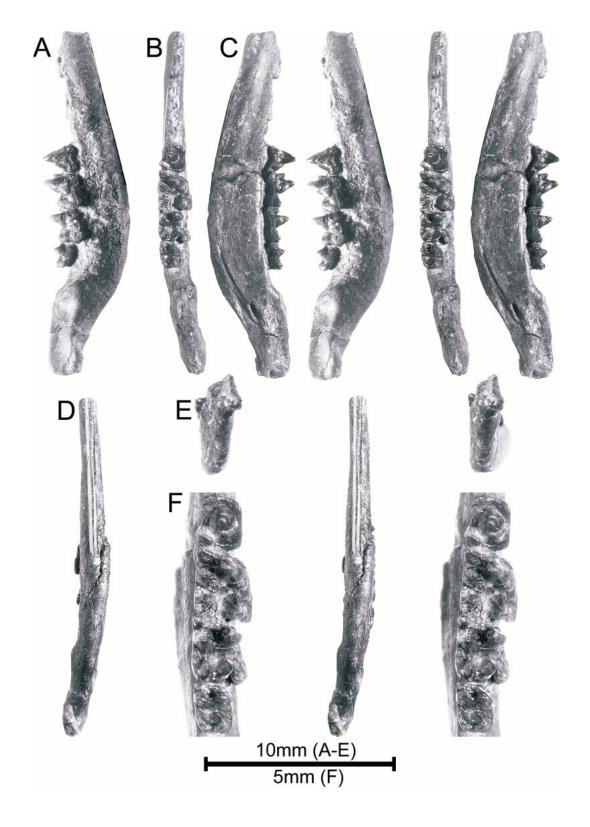


Fig. 3.5. NMV P210005, frontal region of skull. **A,** dorsal view; **B,** ventral view; **C,** ventral view (stereo reversed in order to provide reader with "endocast" of the dorsal surface of the brain).



NMV P208228 is referred to Ausktribosphenos nyktos rather than to Bishops whitmorei (see below) because the m1 is larger rather than smaller than the m2 and the degree of exaenodonty (base of the crown significantly lower on labial than lingual side of the tooth) of the lower molars is not as great (contrast in particular with figure 3.11). Only enough of NMV P208482 is preserved to distinguish it from B. whitmorei by the latter feature.

?Ausktribosphenos nyktos

NMV P210086, a right mandibular fragment with alveoli for p5–6 and m2, extremely damaged crown of m1 together with a mold of the labial side of that tooth, and partial crown of m2 embedded in matrix.

Bishops whitmorei Rich et al., 2001

NMV P210075, holotype, a left mandible originally with a single alveolus anterior to the premolars, p1–6, m1–3. p1 subsequently lost. Figures 3.9–3.10.

NMV P208484, a right mandibular fragment with m2 and alveolus for m3. Figure 3.11.

NMV P209975, a right mandibular fragment with heavily worn posterior root of p6, m1–2, and worn m3. Figure 3.12.

NMV P210070, a right mandible with p1–6, m1–3. P6–m3 damaged. Figure 3.13.

The following features exhibited in *Bishops whitmorei* contrast with those of *Ausktribospehos nyktos* and are more typical of primitive placental mammals (Rich et al., 2001a): (1) the lack of a coronoid facet on the dentary; (2) a much weaker internal mandibular groove that is not readily differentiated into a Meckelian groove and a surangular facet; (3) much weaker unnamed cristids on some lower molar talonids; and (4) location of the hypoconulid of m1 of one specimen, NMV P210070, near the midline

of the tooth and well separated from the entoconid.

NMV P208484, P209975, and P210070 are all referred to *Bishops whitmoreii* rather than to *Ausktribosphenos nkytos* because of the greater degree of exaenodonty of their lower molars. NMV P209975 and P210070 are known to be further allied with *B. whitmorei* as opposed to *A. nyktos* because m2 is larger than m1.

Unnamed Genus and Species

NMV P208582, a right mandibular fragment with a worn m3. While retaining the general molar pattern of an ausktribosphenid, the m3 of this specimen is significantly larger than that of either *Ausktribosphenos nyktos* or *Bishops whitmorei*. Figure 3.14.

TRIBOSPHENIDA

Unnamed Genus and Species

NMV P208483, a left mandibular fragment with two alveoli for a premolar, a premolar, two alveoli for posteriormost premolar or anteriormost molar, and trigonid of a molar. The premolar differs from the p4–6 of *Bishops whitmorei* and the p5–6 of *Ausktribosphenos nyktos* in lacking a postcingulum. The molar trigonid differs from *Teinolophos trusleri* in being much lower, having a prominent precingulid, and greater angle between prevallid and postvallid. Figure 3.15.

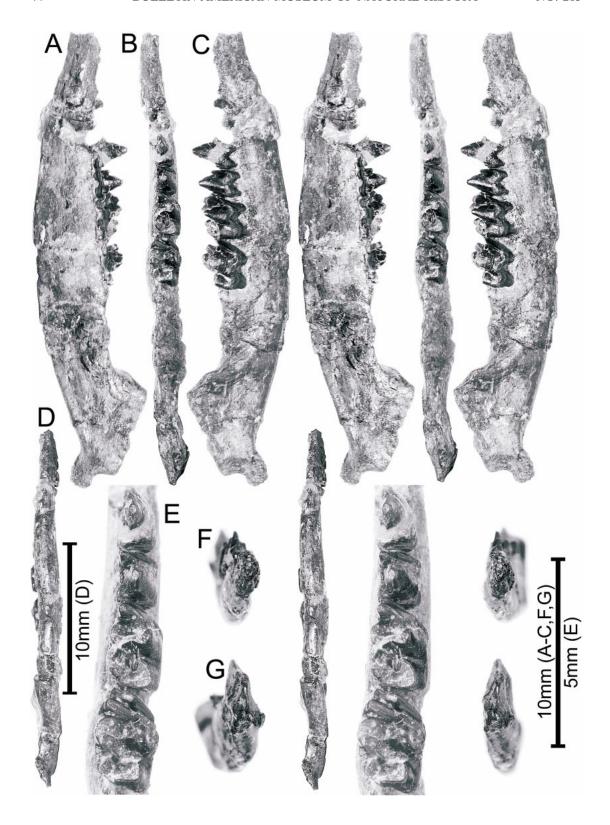
Mammalia, incertae sedis

NMV P208229, an edentulous jaw fragment with four posteriormost alveoli [stereopair in dorsal view in Rich et al. (1999: fig. 17a)].

NMV P208383, an isolated tooth fragment (premolar?) that had at least two roots. The principal cusp, flattened by a prominent wear surface, is surrounded by a low cingulum on the three sides where the crown is intact and

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Fig. 3.6. NMV P208090, holotype of *Ausktribosphenos nyktos*, right mandibular fragment only slightly crushed with p6 and m1–3. **A**, labial view; **B**, dorsal view; **C**, lingual view; **D**, ventral view; **E**, posterior view; **F**, occlusal view of p6 and m1–3. Specimen also figured in Kielan-Jaworowska et al. (1998: fig. 1c), Rich et al. (1998: fig. 1d), Rich et al. (1997: figs. 2a–f, 3; 1999: figs. 7–10), and Rich et al. (2001b: figs. 2, 4b).



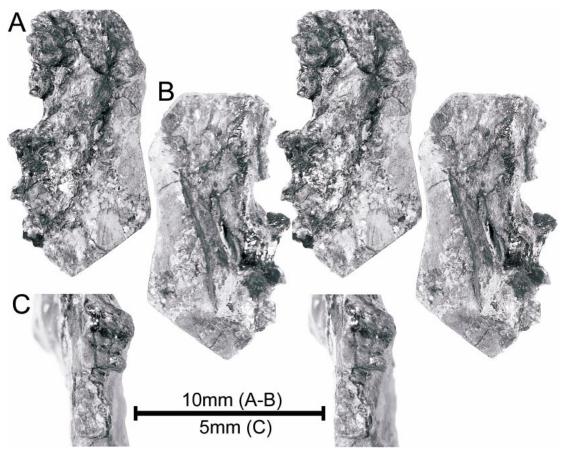


Fig. 3.8. NMV P208482, referred specimen of *Ausktribosphenos nyktos*, heavily crushed right mandibular fragment with m2–3. **A**, labial view; **B**, lingual view; **C**, occlusal view m2–3.

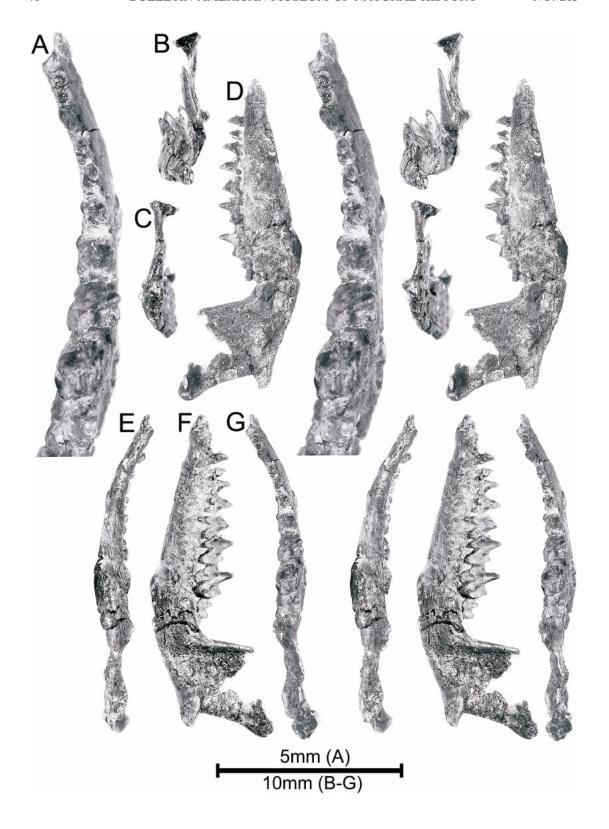
has a small segment of a crest joined to it that is parallel to the long axis of the tooth (if it is a premolar). The width of the preserved root is 2.9 mm. This tooth is much larger than any teeth of the ausktribosphenids or the monotreme known from Flat Rocks. It is also larger than the premolars of *Steropodon galmani* and *Kollikodon ritchei*, which are thus far known primarily from alveoli. The alveolus of the posterior root of the ul-

timate premolar of *S. galmani* is 2.1 mm wide (Archer et al., 1985: fig. 2b), while based on measurements of a photograph of the holotype, the three posteriormost alveoli of the premolars of *K. ritchei* are approximately 1.3 mm in width. Found at the early Albian site, The Pillar, Slippery Rock Site, Dinosaur Cove, Victoria, Australia. Figure 3.16.

NMV P212785, an edentulous left jaw

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Fig. 3.7. NMV P208228, referred specimen of *Ausktribosphenos nyktos*, moderately crushed right mandibular fragment with p5–6 and m1–2. **A**, labial view; **B**, dorsal view; **C**, lingual view; **D**, ventral view; **E**, occlusal view of p5–6 and m1–2. **F**, anterior view; **G**, posterior view. Specimen also figured in Rich et al. (1999: figs. 11–13), and Rich et al. (2001b: fig. 4c).



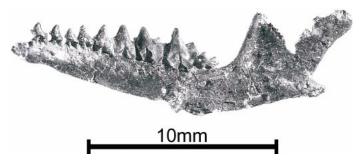


Fig. 3.10. Photograph of NMV P210075, holotype of *Bishops whitmorei*, made prior to the loss of p1. Labial view of mandible.

fragment with rear alveolus of most posterior molar.

DISCUSSION

The fossiliferous rock at both Flat Rocks and Dinosaur Cove is primarily an interdigitating mixture of conglomeratic sandstone, clay interclast conglomerates, sandstone, and claystone lenses. The sandstone is quite immature, being arkosic. It is cemented with the mineral laumonite. The conglomeratic clasts are for the most part clay galls with an occasional rock fragment, far less than 1% of the clasts.

The Dinosaur Cove monotreme humerus (NMV P208094) and Mammalia incertae sedis premolar? (NMV P208383) are thus far the only mammalian fossils ever recovered from that site. Work ceased there in 1994. At that stage, the only known remaining fossiliferous unit practical to work there was exposed at a depth of 5 m at the bottom of an excavation on the shore platform, i.e., 5 m below sea level. At that point the fossiliferous unit dipped downward into the center of Dinosaur Cove at an angle of 15°. When the site was last worked, it was necessary both to build a sandbag wall to keep out the surface sea water and to utilize three pumps continuously to remove the water that flowed through the joints in the shore platform. Although the fossiliferous unit did not terminate at that point, it was yielding no more per unit area than what approximately 75 m² of fossiliferous rock had produced at Dinosaur Cove during the previous decade, and there was no indication that taxa of any kind not known before from the site would be recovered. Hence, the site was closed down. A small quantity of fossiliferous rock from Dinosaur Cove remains to be processed. It is possible that there are additional fossil mammal remains in it, but given that only two such fossils have been recovered from several times that volume of fossiliferous rock from that locality, further mammal finds are unlikely.

The present procedure used to recover fossils from Flat Rocks is to manually break apart the fossiliferous rock with hammers and chisels to the size of sugar cubes, each surface being carefully examined as it is exposed. About six person- months of field-work are required to recover each mammalian fossil found in this manner. Experimentation with a variety of other techniques to recover fossil vertebrates from this site has thus far failed to provide a workable alternative to the current method. About two person- years of effort by dedicated volunteers each field season results in the processing of approximately 5 tons of fossiliferous rock.

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Fig. 3.9. NMV P210075, holotype of *Bishops whitmorei*, left mandible originally with a single alveolus anterior to the premolars, p1–6, m1–3. p1 subsequently lost (see fig. 3.10). **A,** occlusal view of p2–m3; **B,** anterior view; **C,** posterior view; **D,** lingual view; **E,** ventral view; **F,** labial view; **G,** dorsal view. Specimen also figured in Rich et al. (2001a: fig. 1).

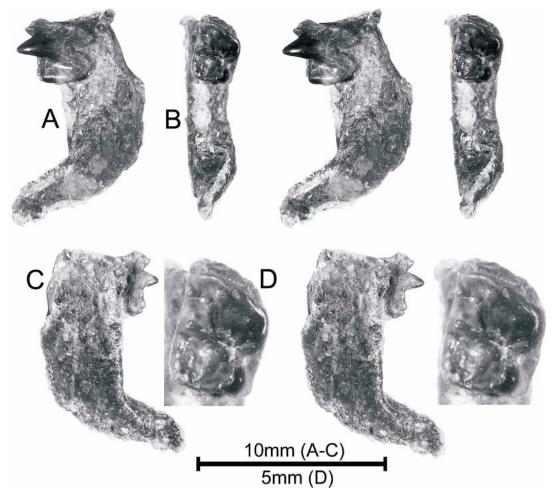
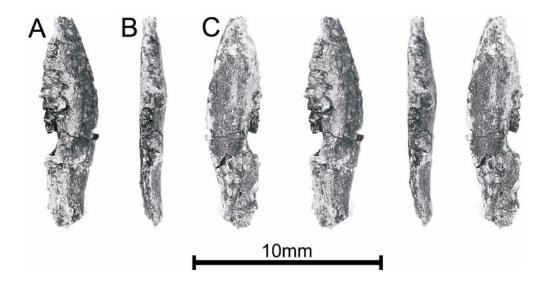


Fig. 3.11. NMV P208484, referred specimen of *Bishops whitmorei*, right mandibular fragment with m2 and alveolus for m3. **A**, labial view; **B**, dorsal view; **C**, lingual view; **D**, occlusal view of m2. Specimen also figured in Rich et al. (2001a: figs. 2d-f, 4a).



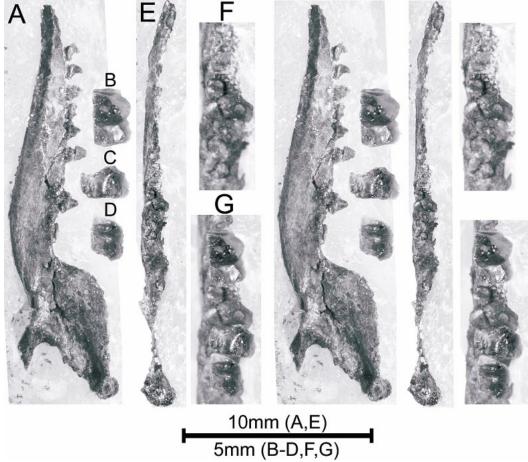


Fig. 3.13. NMV P210070, referred specimen of *Bishops whitmorei*, right mandible with p1–6, m1–3. p6–m3 damaged. **A,** lingual view; **B,** occlusal view of m1; **C,** occlusal view of m2 talonid; **D,** occlusal view of m3; **E,** dorsal view; **F,** dorsal view of m1–3 region of mandible as currently preserved with trigonid of m1 in place; **G,** same view as F, with teeth pictured in B–D superimposed in approximate position they originally occupied on the mandible. Specimen also figured in Rich et al. (2001a: fig. 3).

CONCLUSIONS

There are 47 Early Cretaceous mammalian assemblages from the world tabulated in Kielan-Jaworowska et al. (in press). Of these only nine have six or more mammalian taxa recognized in them, and all but two of these (Synclinal d'Anoual, Morocco, and Flat Rocks) are in Laurasia. Therefore, the presence of at least six, and possibly as many as eight, mammalian taxa is indicative

of the importance of the Flat Rocks site for elucidating a critical phase in mammalian history on the Gondwana land masses during the Early Cretaceous. It was during this time that a number of major groups have been hypothesized to have arisen (Cifelli, 1993). The fact that this diversity has been established from a collection of just 23 specimens is strong evidence that if this locality is worked long enough in the existing

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Fig. 3.12. NMV P209975, referred specimen of *Bishops whitmorei*, right mandibular fragment with heavily worn posterior root of p6, m1–2, and worn m3. **A**, labial view; **B**, dorsal view; **C**, lingual view. Specimen also figured in Rich et al. (2001a: figs. 2a–c).

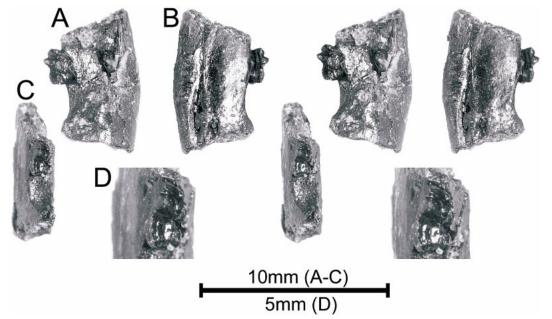


Fig. 3.14. NMV P208582, Ausktribosphenidae, unnamed genus and species, right mandibular fragment with worn m3. **A,** labial view; **B,** lingual view; **C,** occlusal view; **D,** occlusal view of m3.

manner it will eventually yield as diverse an assemblage of fossil mammals as have been found in the more prolific Mesozoic mammal localities elsewhere. The controversial nature of the ausktribosphenid relationships hints that like some of the other tetrapods previously found in these same rocks, such as the youngest record of temnospondyls (Warren et al., 1997), more surprises are in

store when the mammalian fauna from Flat Rocks becomes better known. Even though achieving this goal will require an immense amount of labor, the favorable aspects of the Flat Rocks site are that there is an extensive amount of fossiliferous rock yet to be examined there and it is only about 120 km from Melbourne, thus easy and inexpensive to access.

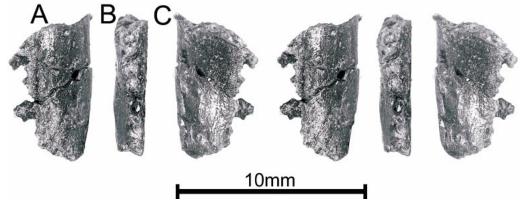


Fig. 3.15. NMV P208483, Tribosphenida, unnamed genus and species, left mandibular fragment with two alveoli for a premolar, followed by a premolar, followed by two alveoli for most posterior premolar or most anterior molar, and trigonid of molar. A, labial view; B, dorsal view; C, lingual view.

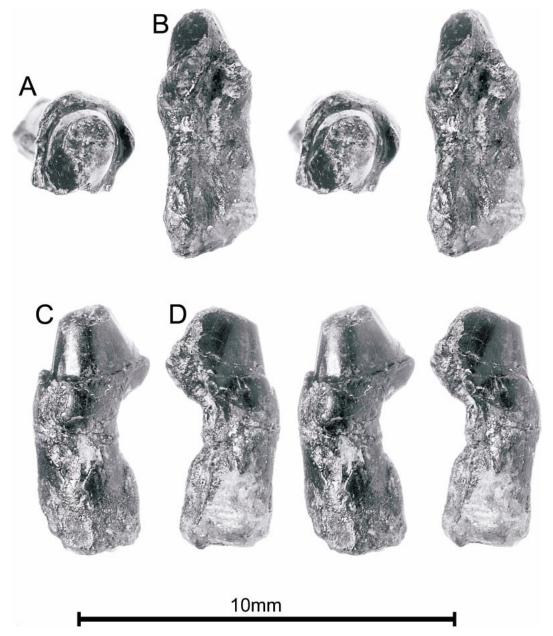


Fig. 3.16. NMV P208383, Mammalia incertae sedis, premolar? **A**, occlusal view with anteroposterior axis vertical; **B**, internal view of root and broken cross section of tooth; **C**, lateral or medial view; **D**, medial or lateral view.

ACKNOWLEDGMENTS

When we were students, Malcolm not only stimulated our interest in the history of Mesozoic mammals but also supported our earliest extensive fieldwork in rocks of this age at Como Bluff, Wyoming. That laid the foundation for our program to understand the Mesozoic history of land mammals and birds in Australia, which with the discovery of the first specimens by us 25 years after we had initially set foot on the continent, is now finally getting under way.

We wish to thank Mr. Steven Morton, who took and skillfully manipulated the photographs. He was ably assisted by Mrs. Lesley Kool. Dr. Richard Cifelli generously provided an advanced copy of his tabulation of Mesozoic mammal localities, table XX, in the chapter on Mesozoic mammal distributions in Kielan-Jaworowska, Cifelli and Luo (in press).

Discussions with Susan Evans, Jason Head, Lou Jacobs, Mike Polcyn, and Oliver Rieppel about NMV P208185 and NMV P210005 were most helpful in trying to ascertain what these two specimens might be.

The fossils that are central to this report are now available for study only because for over a quarter of a century the Committee for Research and Exploration of the National Geographic Society steadfastly supported the fieldwork necessary to first find the fossil sites and then to carry out the necessarily prolonged excavations of them. Funds for the preparation of the fossils during those years has come primarily from the Australian Research Council.

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