

PRIMITIVE MARSUPIAL TAPIRS (*PROPALORCHESTES*  
*NOVACULACEPHALUS* MURRAY AND *P. PONTICULUS* SP.  
NOV.) FROM THE MID-MIOCENE OF NORTH  
AUSTRALIA (MARSUPIALIA: PALORCHESTIDAE).

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ABSTRACT

The upper molar dentition of *Propalorchestes novaculacephalus* demonstrates a transitional state between the bilophodont marsupial tapirs and the selenodont wynyardiids. Although *Propalorchestes* had developed bilophodont crowns, the metacone and stylar cusp D remained sufficiently differentiated to verify the development of bilophodonty in diprotodontoid (vombatimorphian) marsupials from a selenodont condition, in which the primary buccal cusp is formed by stylar cusp D rather than the metacone.

KEYWORDS: Palorchestinae, Wynyardiidae, molar evolution, diprotodontoid systematics, Bullock Creek Local Fauna, Riversleigh "Systems" Fauna.

INTRODUCTION

A cranial fragment from the Bullock Creek Local Fauna indicated that tapir-like marsupials (Palorchestinae) were already highly modified forms by mid-Miocene times and that they differed in many significant respects from the palorchestid *Ngapakaldia tedfordi* Stirton (Murray 1986). Several years had elapsed since the cranium of *Propalorchestes* was described before any palorchestine dentitions from the Camfield Beds came to light. What was thought to be the first to be recovered, a right maxillary fragment containing one and a half molars, was actually preceded several years by a dentary collected by Dr Thomas Rich in 1982, from the Horseshoe West locality of the Camfield beds. The dentary and maxilla fragment are well-matched and of the correct proportions to belong to the same species as the edentulous cranium. Casting further afield, Dr Mike Archer and Ms Sue Creagh assembled a small assortment of isolated teeth and dentary fragments from Riversleigh which have palorchestid features.

The total collection of late Oligocene to mid-Miocene palorchestine material consists of only eight specimens: three dentary frag-

ments, a maxilla, a cranial fragment and three isolated teeth. Despite the sparseness and fragmentary condition of the sample, it substantially improves our resolution of the systematics of the marsupial tapirs and moreover, adds a previously unknown transitional element to the interpretation of the phylogeny of bilophodont dentitions within the Vombatimorphia.

The "diprotodontoid" (vombatimorphian) affinity as opposed to a macropodoid (Owen 1874; Raven and Gregory 1946) affinity of palorchestids was first noted by Woods (1958). Since then, palorchestid *affines* possessing vombatimorphian character complexes were diagnosed by Stirton (1967) (*Ngapakaldia*, *Pitikantia*). However, the molar crown morphology of these genera showed few synapomorphic features to unite them with members of the genus *Palorchestes*. *Ngapakaldia* is usually treated as a plesiomorphic sister group of the apparently more derived Palorchestinae (Stirton *et al.* 1967). However, Archer (1984) correctly observed that there is very little to support an even monophyletic union of the two groups or the state of the morphocline for their dental and cranial characters.



Evidence is presented indicating that the distinctive upper molar morphology of *Propalorchestes* more closely resembles that of a wynyardiid than any other described, potentially antecedant, vombatimorphian group. Moreover, if the transitional state of the dentition is taken as an indication of the polarity of the morphocline, the Subfamiliae Incertae palorchestids (*Ngapakaldia*, *Pitikan-tia*) must represent a more derived state, indeed, if they are even to remain within the Family Palorchestidae.

The following abbreviations are used in the text: NTM, Northern Territory Museum; NMV, Museum of Victoria (formerly National Museum of Victoria); AR, Palaeontology Laboratory University of New South Wales; CPC, Commonwealth Palaeontological Collection.

## SYSTEMATICS

### Family Palorchestidae Archer and Bartholomai Subfamily Palorchestinae Tate Genus *Propalorchestes* Murray

*Propalorchestes* Murray, 1986:195.

**Type species.** *Propalorchestes novaculacephalus* Murray, 1986:195.

**Additional species.** *Propalorchestes ponticulus* n. sp.; *Propalorchestes* cf. *ponticulus*.

**Diagnosis.** To the diagnostic features given in Murray (1986) I add the following: dentary shorter, thicker, more massive relative to size of dentition than in *Palorchestes painei*; intercoronoid sulcus absolutely and relatively wider and deeper, forming a definite crest extending to below  $M_2$ , defining a deep subalveolar fossa. Horizontal ramus deepens anteriorly in contrast to attenuated depth of ramus in *Palorchestes painei*. Lower molars absolutely smaller and much smaller relative to the size of the horizontal ramus. Crowns lower, interloph valleys less steeply inclined toward the buccal and lingual sides than in *Palorchestes painei*. Anterior cingulum thicker, buccal cingulum more clearly defined than in *Palorchestes painei*. Maxilla relatively shorter, wider and deeper than in *Palorchestes* spp., zygomatic root of maxilla thicker and projects laterally perpendicular to the tooth row in contrast to a definite posterior slant of the process in *Palorchestes* spp. Anterior surface of infraorbital fossa flat; infraorbital fo-

ramen higher and relatively larger than in any *Palorchestes* species. Upper molars trapezoidal in outline shape, metaloph markedly narrower than protoloph. Buccal cingulum absent. Styler cusp E well developed; styler cusp D forming primary buccal cusp of metaloph, metacone reduced to a swelling between the metaconule ("hypocone") and styler cusp D. Conspicuous postmetacrista slants buccally from the metacone to the base of styler cusp E.

### *Propalorchestes novaculacephalus* Murray (Figs 1-2, 3A-B)

*Propalorchestes novaculacephalus* Murray, 1986:195-211, figs 1-6.

**Type material.** HOLOTYPE - NTM P8552-10: left and part of the right side of neurocranium including most of the zygomatic arch and latex endocast (Murray 1986: figs 1-6). PARATYPES - NTM P862-27: right maxilla with  $M^{2-3}$  (Fig. 1A-B). NMV P187282: right dentary, containing  $M_{3-5}$  (Fig. 2A-B), Camfield Beds, Northern Territory. AR 9682: isolated right  $M^3$ , damaged on the buccal side, Riversleigh Queensland (Fig. 3B).

**Type locality:** Camfield Beds "...16 miles Southeast of Camfield Homestead in the north central Northern Territory" (Plane and Gatehouse 1968).

**Formation.** Camfield beds, light coloured calcareous sandstone, siltstone and limestone with basal ferruginization and silification at the top.

**Age.** Mid-Miocene, determined on the basis of the stage of evolution of diprotodontid species (Woodburne *et al.* 1985).

**Description.** **Lower molars:**  $M_{2-5}$  essentially homomorphic; lower molars rectangular, shallowly waisted at the midvalley and equidistant between the trigonid and talonid (Fig. 2A-B). Relatively long and narrow (length to width proportions about 1.5: 1.0). Molar gradient a very slight increase from front to back, ( $M_3$  is 98% of the length of  $M_5$ ). Molars are about 15% shorter than *Palorchestes painei* and much smaller than in other *Palorchestes* species.

Breached lophids have crescentic, slightly oblique cementum exposures with basinlike expansions on the protoconid and hypoconid. Protoconid large, offset anterolabially and divided anteriorly from the metaconid by a deep sulcus originating from a fossette developed in the lingual margin of the precingulid.



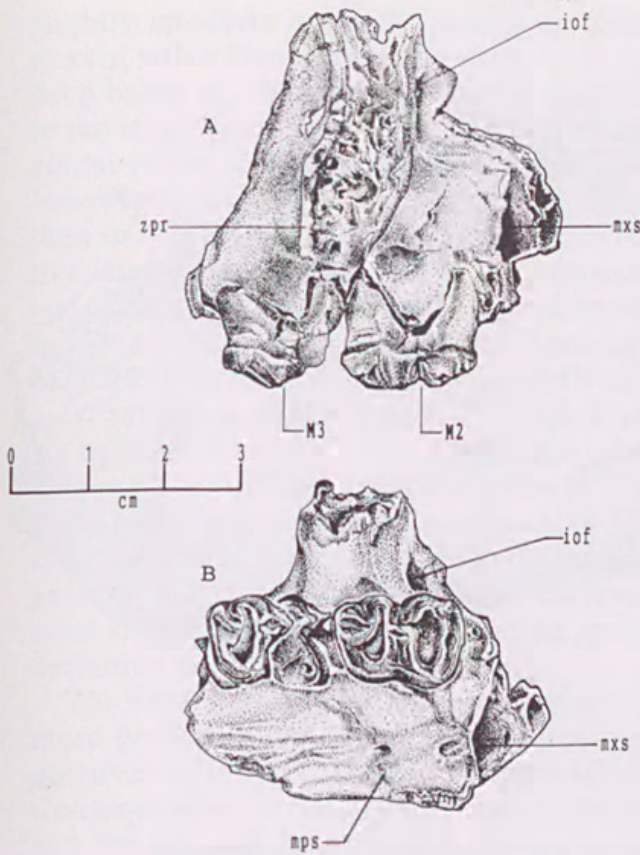


Fig. 1. Maxilla fragment of *Propiorchestes novaculacephalus*, paratype NTM P862-27. A, lateral aspect; B, ventral aspect. Abbreviations: ioof, infraorbital foramen; mxs, maxillary sinus; zpr, zygomatic process; mps, maxillopalatine suture.

In worn molars this sulcus results in a narrowing of the lophid by an invaginated crescent of enamel similar to the neomorphic cuspid described in *Muramura williamsi* (Pledge, 1987).

Precingulid extends from labial side of anterior portion of protoconid, ascending and expanding slightly to the midline of the crown then descending abruptly before reaching the lingual side of the crown. The area of maximum expansion and height of the precingulid forms a small cuspid (paraconid). Cristid obliqua (midlink) broad, low, complete, situated near the longitudinal midline of each molar.

Faint, rounded labial cingulid present on all molars; interlophid valley on either side of the midlink broad, shallow and gently tilted towards the margins of the crown. Anteroposteriorly deep, rounded postcingulid extending slightly higher up the crown lingually than labially; connected to the middle of the hypolophid by a stout post-link demarcated on either side by deep, crescentic sulci. (Measurements approximate;  $M_3$  length 16.6; anterior width 10.6; posterior width 10.0;  $M_4$

length 16.5, anterior width 10.0; posterior width 11.0;

$M_5$  length 17.1; anterior width 11.0; posterior width 11.2).

**Upper molars:**  $M^2$  broad, bilophodont, low crowned and trapezoidal in occlusal outline with the proto-loph markedly wider than the metaloph (Figs 1A-B, 3A). Labial side of the crown composed of four styler cusps. Moieties deeply divided labially by a sulcus extending from the midlink down to the cementoenamel contact of the crown. Proto-loph broader and wider than metaloph; precingulum wide and deep anteroposteriorly, merging anterolabially with a short postparastylar crest terminating in a small paraconal facet.

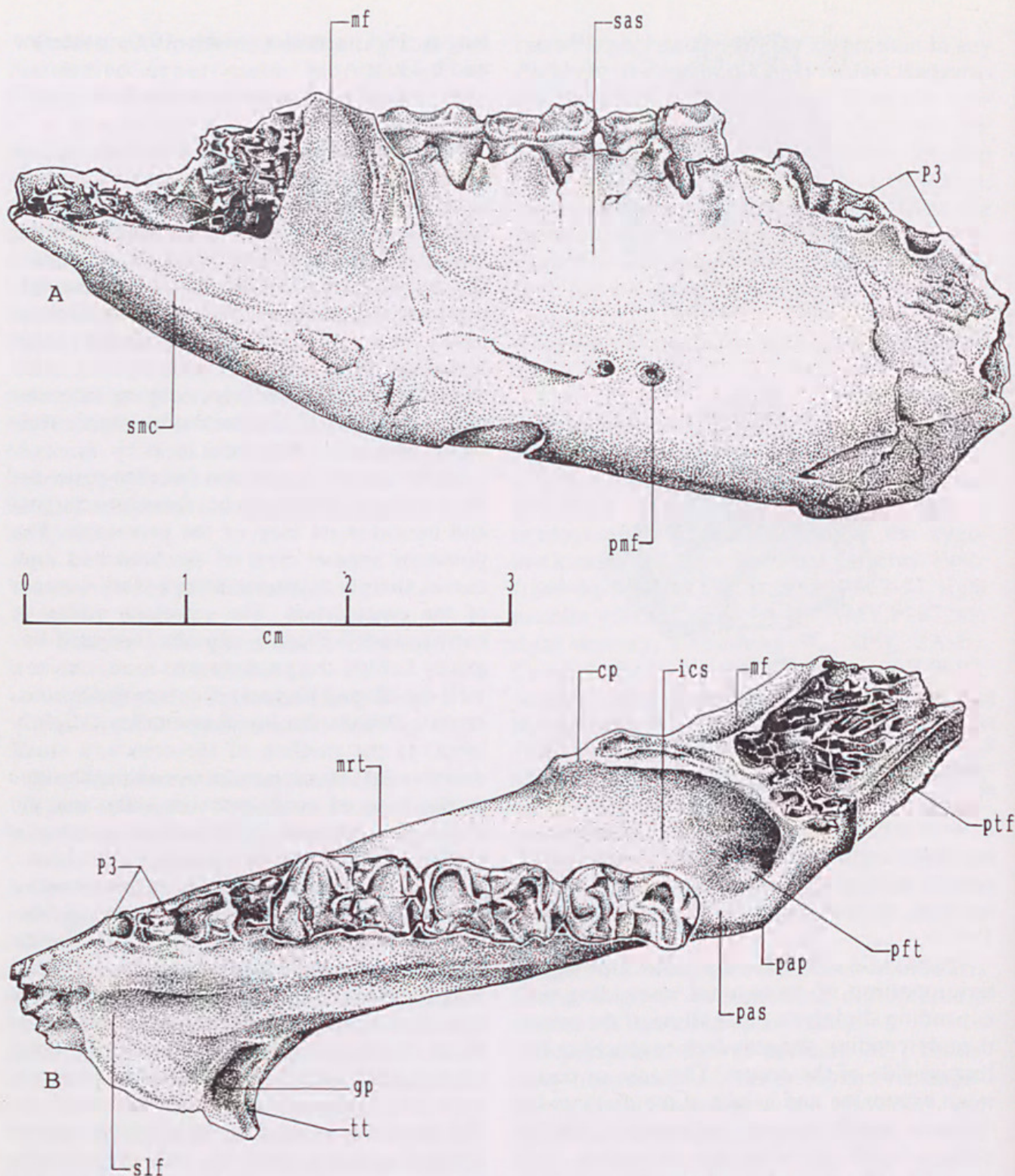
Stylar cusp C, separated from the paracone by a shallow labial sulcus, forms the largest and buccal-most cusp of the proto-loph. The posterior enamel crest of the breached loph curves sharply mesiad to form a short remnant of the centrocrista. The interloph valley is narrow and V-shaped, slightly expanded lingually behind the protocone to terminate at a well-developed lingual cingulum (postproto-crista). Within the interloph valley, slightly labial to the midline of the crown, a small rhomboidal fossa separates two enamel bulges at the base of each loph lingually and the remnant centrocrista labially, forming a double midlink-like structure.

The posterior moiety of the crown retains a strong triangular outline due to the prominence distobuccally of stylar cusp E. The labial cusp of the metaloph is composed of stylar cusp D which is separated from stylar cusp E by a deep sulcus. The metacone is represented by an enamel thickening about midway along the metaloph, and is connected to stylar cusp E by a long, obliquely oriented postmetacrista. The posterior surface of the metaloph angles anterolingually towards the metaconule ("hypocone") presenting a smooth, steeply angled face, emarginated by a well-developed postcingulum, situated low on the crown.

$M^3$  is similar to  $M^2$ , with a slightly narrower metaloph and a less obliquely oriented and less prominent, though still remarkably robust, postmetacrista. (Measurements:  $M^2$  length 16.8; anterior width, 13.2; posterior width, 12.0;  $M^3$  estimated length, 15.7; posterior width, 11.6).

A possible  $M^4$  is represented by a system C Riversleigh specimen (AR9682, paratype). This isolated, lightly worn crown (16.0 mm





**Fig. 2.** Right dentary of *Propalorchestes novaculacephalus*, paratype NMV P187282. **A**, lateral aspect; **B**, dorsal aspect. Abbreviations: **mf**, masseteric fossa; **sas**, subalveolar sulcus; **smc**, submassteric crest; **pmf**, posterior mental foramen; **ics**, intercoronoid sulcus; **cp**, coronoid process; **mrt**, mid-ramal torus; **pft**, pit for fleshy temporalis muscle; **ptf**, pterygoid fossa; **pap**, postalveolar process; **pas**, postalveolar shelf; **slf**, sublingual fossa; **tt**, transverse torus; **gp**, genial pit.

long) shows all of the previously noted features in a slightly more suppressed form than the  $M^3$  of the holotype. Because the  $M^3$  of NTM P862-27 shows a similar reduction of its features, a gradient along the molar row is likely. However, AR9682 could also be interpreted as a slightly more derived  $M^3$  of *Propalorchestes novaculacephalus*.

**Dentary:** The right horizontal ramus of *Propalorchestes novaculacephalus* (NMV P187282) is distinctive in its robustness and strong angularity. Compared to *Palorchestes painei*, *P. novaculacephalus* is slightly shorter, but significantly thicker (23.8 mm thick below  $M_{3-4}$ ), and markedly triangular in section. In contrast to *P. painei*, the dentary



slightly increases in depth towards the symphysis, rather than tapering forward (42.0 mm deep below  $P_3$ ; 40.0 mm below  $M_5$ ). Relative to the length, depth and thickness of the horizontal ramus, the cheek teeth of *P. novaculacephalus* are proportionally much smaller than in *P. painei*. The 18.0 mm wide furrow-like intercoronoid sulcus, which is a conspicuous feature of palorchestines, is exceptionally broad in *P. novaculacephalus* and is continued forward to form a wide, sloping, shelf-like crest extending 25.0 mm from the molar alveoli to the mid region of the dentary. In other *Palorchestes* species a notable, though less distinguished (due to the weakness of the coronoid crest) subalveolar fossa is likewise present. In *P. novaculacephalus*, the coronoid crest is prominent and sharp; grading into a definitive mid-ramal torus below  $M_3$ .

The lower portion of the ascending ramus is more produced laterally, and more confined dorsoventrally than in other palorchestines. Consequently, the masseteric fossa is deeper and the submasseteric crest ascending to the posterior masseteric eminence is thicker and more prominent. The pterygoid fossa is relatively deeper and more confined than in *P. painei*. As in other palorchestines, the digastric fossa is shallow and indistinct.

The postalveolar shelf is significantly shorter than in other palorchestine species. The postalveolar crest is higher, more robust and more laterally deflected. A distinct 10.0 mm diameter fossa for the fleshy temporalis insertion in the posterior end of the intercoronoid furrow in *P. novaculacephalus* is absent or indistinct in *Palorchestes* species.

*Propalorchestes novaculacephalus* has large, deep genial pits in the lower mid-posterior surface of the dentary symphysis, and a thick, though short transverse torus. *Palorchestes painei* has small genial pits located relatively higher on the posterior surface of the symphysis. No transverse torus is present. The dentary symphysis of *P. novaculacephalus* is shorter, more rounded, relatively deeper than in *P. painei* and apparently slightly less decurved.

Relative to the posterior margin of the symphysis and in combination with its less horizontal inclination, the diastema was perhaps shorter in *P. novaculacephalus* than in *P. painei*. The diastemal crest descends towards the incisor alveolus less steeply than in *P.*

*painei*, but overall, the dentaries of the two species appear to have been very similar.

**Maxilla:** The maxilla (paratype NTM P862-27) containing previously described  $M^{2-3}$ , corresponds in size and robusticity to the dentary (Fig. 1A-B). The occlusal surfaces and theotics of the assigned upper and lower dentitions match closely. Although there are no contact points with the cranium (holotype, NTM P8552-10) the maxilla readily corresponds to the projected missing proportions in relation to its shape and the thicknesses of its broken margins.

Compared to the same region in other *Palorchestes* species, the mediolateral thickness of the maxilla above  $M_2$  is much greater in *Propalorchestes novaculacephalus* due to the formation of a large sinus. This sinus is not present in *P. parvus* and is either reduced or absent in *P. painei*. The expanded maxillary antrum creates a conspicuous swelling beneath the infraorbital foramen in *P. novaculacephalus*, and a deep groove for the emergent infraorbital nerve is inscribed on its external surface. Unlike *P. parvus*, in which the facial plane slants posteriorly, the anterior surface of the zygomatic root abruptly projects at a right angle to the surface of the maxilla. In some respects, *P. novaculacephalus* more closely resembles *P. painei*, in which the zygomatic roots and jugals must have presented a broad, flat facial plane extending around the orbits and nearly up to the corresponding lateral expansions of the frontal crests. However, the entire facial plane of *P. painei* also retreats more than in *P. novaculacephalus*. The relatively large diameter of the infraorbital nerve canal and foramen (10.0 mm by 8.0 mm) and its slightly elevated position compared to *P. parvus*, are also common to *P. painei*.

Judging from the more anterior position of the maxillopalatine suture, which transects the palate between  $M^2$  and  $M^3$ , the palate must have been proportionally different from *P. painei*. This could, of course, indicate that the molar series is  $M^{3-4}$ , but relative to the zygomatic root, the position of the molars correspond closely to  $M^{2-3}$  in *Palorchestes painei*. However, assuming that a more primitive condition was manifest, similar to that of *Muramura williamsi* (Pledge, 1987), the position of the molars relative to the maxillary process of the zygoma in *P. novaculacephalus* might eventually be found to differ substan-



tially from that of *Palorchestes* species. In any case, I have taken the least speculative course, and await the resolution of the problem from a more complete specimen.

The internal surface of the maxilla preserves the contour of the internal nares, which was relatively more expanded than in the corresponding regions of *P. parvus*.

*Palorchestes painei* appears to show an intermediate condition between *P. novaculacephalus* and *P. parvus*. Overall, the maxillary fragment indicates that the midfacial region in *P. novaculacephalus* was relatively more laterally expanded and deeper than in any species of *Palorchestes* and perhaps that the palate was shorter. The large infraorbital foramen and deep, broad, perpendicular facial plane of the zygoma, ostensibly for the attachment of nasolabialis musculature, strongly suggest the presence of a trunk-like appendage in this species.

There is however, an indication that the narial aperture may have been much wider transversely and perhaps relatively shorter than in *P. painei*. In all *Palorchestes* species, the plane of the zygoma slopes posteriorly about 10 degrees relative to the occlusal line, whereas in *Propalorchestes novaculacephalus* it slopes to about the same extent anteriorly, as in more typical diprotodontoid marsupials. This indicates that the nasofrontal region projected more anteriorly than in *Palorchestes painei*, which would result in a greater overhang of even highly reduced nasal bones. As no portion of the rostrum of this species has been recovered, I can only conclude that while *Propalorchestes novaculacephalus* probably had a well-developed tapir-like trunk, its proportions and perhaps its extent of mobility differed somewhat from the more evolved *Palorchestes* species.

In conjunction with its cranial morphology (holotype NTM P8552-10), *Propalorchestes novaculacephalus* had a deep cranium, with a high, narrow braincase and robust, wide zygomatic arches which terminated abruptly in a wide, flat facial platform for the attachment of the facialis muscles of the trunk. The rostrum was probably relatively broader, shorter and less downturned than in *Palorchestes painei*. The fragmentary remains of this species indicate that the more primitive palorchestines had fully developed, by mid-Miocene times, a characteristic masticatory complex which is distinctive for the subfamily (Murray 1986).

Indeed, no other species within this lineage shows this constellation of characters as conspicuously, relative to the size of its dentition and braincase. Presumably, as palorchestines increased in size, an allometric adjustment of the adductor complex resulted in the moderation of some of these features in later forms.

***Propalorchestes ponticulus* n.sp.**  
(Fig. 3C)

**Type material.** HOLOTYPE - AR1802: isolated right  $M_2$  (Fig. 3C), D-site (System A, Archer *et al.* 1989) Riversleigh, Queensland.

**Provisionally referred material.** AR11302: ? $M_5$  (Fig. 3E,F), Wayne's Wok Locality (System B, Archer *et al.* 1989) Riversleigh Queensland. AR1779: dentary fragment (Figs. 3D; 4A-C), fully fused symphysis with portion of  $M_2$ , no site designated, Riversleigh, Queensland. SGM1008: fragment of dentary, hemimandibles fully fused at the symphysis with  $P_3$ - $M_{2,3}$  crowns sheared off (Fig. 4D-F), Sticky-Beak locality (System A, Archer *et al.* 1989), Riversleigh Queensland.

**Type locality.** "D-Site", northern tip of Carl Creek Limestone exposures, 2.4 km South of Verdon Creek (Tedford, 1966).

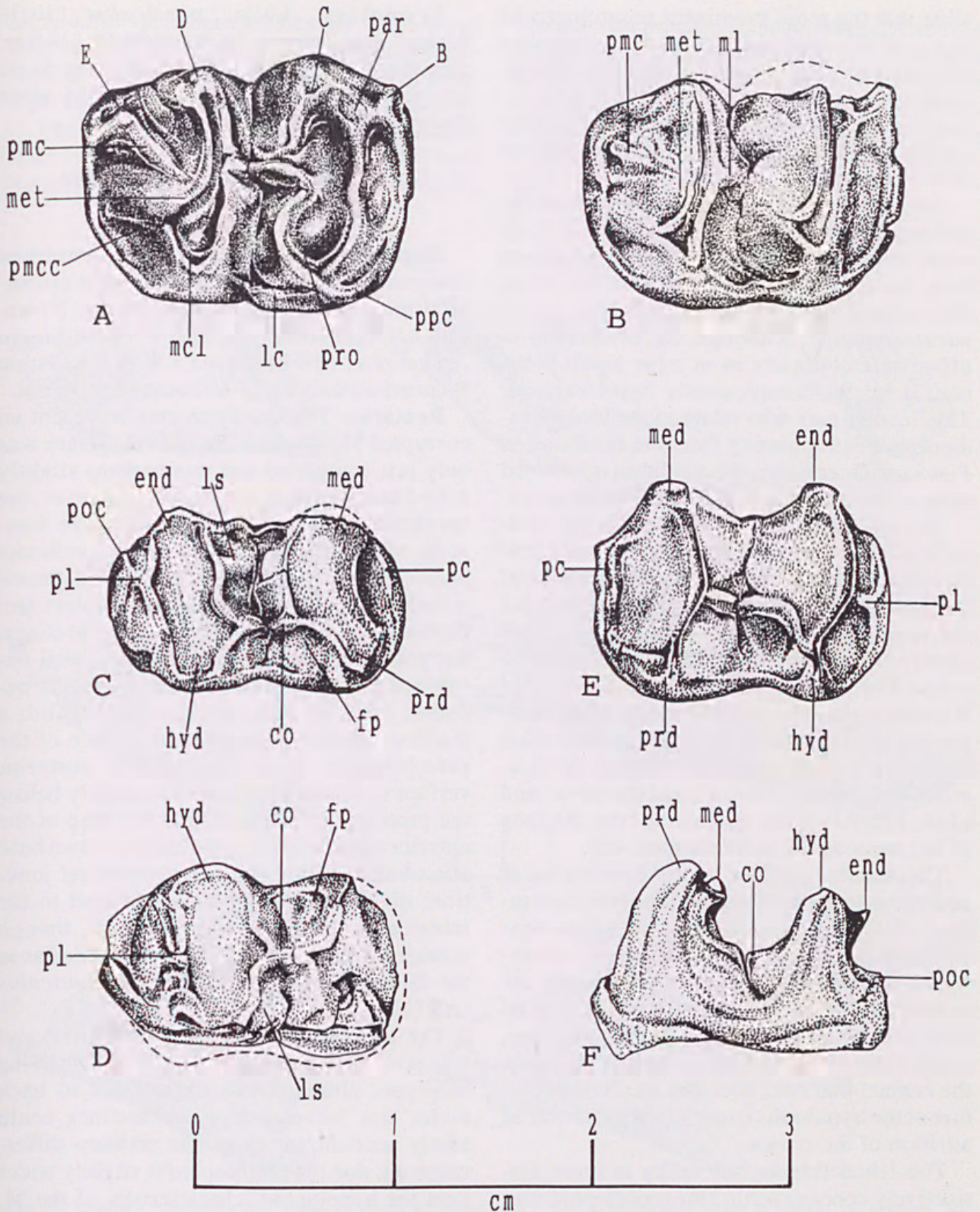
**Formation.** Carl Creek Limestone: mottled, vuggy cream and yellow limestone.

**Age.** Late Oligocene or early Miocene (Tedford 1966; Archer *et al.* 1989).

**Diagnosis.** Smallest palorchestine, with cheek teeth similar in size to *Pitikantia*; characteristic, nearly equal-sized, narrow lophids and anterior displacement of the protoconid; low, centrally divided and labially situated cristid obliqua, weaker than in other palorchestines, deep, tapering postcingulid and hindlink. Differs from other palorchestines but resembles *Pitikantia dailyi* in having a more labially situated cristid obliqua, deeply notched in the interlophid valley and traversing a narrower declivity between the lophids; differs from *Pitikantia dailyi* in having a secondary swelling on the anterolingual side of the hypolophid, in having a clearly defined preprotocristid immediately mesial to the protoconid and a broad shallow sulcus in the middle of the anterior surface of the protolophid of  $M_2$ .

**Description.** Considered to be an  $M_2$  on the basis of its narrow interproximal facet and less expanded protoconid (Fig. 3C); it is also pos-





**Fig. 3.** Upper and lower molars of *Propalorchestes* species. **A**, upper right second molar of *Propalorchestes novaculacephalus*, paratype NTM P862-27; **B**, upper right third or fourth molar of *Propalorchestes novaculacephalus*, paratype AR9682; **C**, lower right second molar of *Propalorchestes ponticulus* sp. nov., holotype AR1802; **D**, lower left second molar of *Propalorchestes* cf. *ponticulus*, SGM 1008; **E**, occlusal aspect of left lower ?fifth molar of *Propalorchestes* cf. *ponticulus*, AR11302; **F**, labial aspect of left lower ?fifth molar of *Propalorchestes* cf. *ponticulus*, AR11302. Abbreviations: **E**, stylar cusp E; **D**, stylar cusp D; **C**, stylar cusp C; **B**, stylar cusp B; **par**, paracone; **ppc**, preprotocrista; **pro**, protocone; **lc**, lingual cingulum (postprotocrista); **mcl**, metaconule ("hypocone"); **pmcc**, postmetaconulecrista; **met**, metacone; **pmc**, postmetacrista; **ml**, "midlink"; **end**, entoconid; **ls**, lingual swelling of the base of the hypolophid; **med**, metaconid; **pc**, precingulid; **prd**, protoconid; **fp**, fossa behind protoconid; **co**, cristid obliqua; **hyd**, hypoconid; **pl**, postlink; **poc**, postcingulid.



sible that the more prominent preprotocrisid is a gradient-related feature, as no complete *Propalorchestes novaculacephalus* cheek-tooth series is known. Compared to *P. novaculacephalus*, the roots are small relative to the crown and less divergent from one another anteroposteriorly.

Judging from the narrower interloph valley, and depth of the breached lophids, the lophids were relatively high and steep. The crown base lacks the distinctive narrow swellings above the cemento-enamel junction in *P. novaculacephalus*. Although the protoconid is offset anterobuccally as in other palorchestines, it is not conspicuously hypertrophied. This feature may also relate to the molar gradient, but extrapolating from the condition in *P. novaculacephalus*, the condition is adduced to be a characteristic of the entire molar series.

The cristid obliqua is divided in the mid-valley rather than continuous as in *P. novaculacephalus*. It is situated in the buccal third of the interlophid valley rather than traversing the longitudinal midline of the tooth. This feature is also present on the  $M_2$  of *Pitikantia dailyi*. The anterior surface of the protolophid is concave due to a shallow sulcus commencing immediately above the precingulum. This concavity is accentuated by a distinct but low, broad and steep preprotocrisid (forelink) and a low, broad swelling emanating from the base of the metalophid on the lingual side.

The anterior surface of the hypolophid is analogous to the protolophid. The labially situated cristid obliqua delineates a shallow concavity in the middle third of the tooth, accentuated lingually by a distinct swelling of the enamel on the anterior surface of the lingual third of the hypolophid. The lingual swelling, resembling a faint mid-link, was a low bulge in the enamel that only becomes an obvious feature of the hypolophid structure after advanced attrition of the crown.

The labial interlophid valley is more distinctively concave behind the protolophid than in *P. novaculacephalus*. This indicates that the posterior surface of the protolophid was more hollowed-out and probably more posteriorly recurved on the labial protolophid apex than in *P. novaculacephalus*. Like *P. novaculacephalus*, the interloph surface was less cambered labially and lingually than in other palorchestines. A short, weak lingual cingulum is present. (Measurements: length, 14.5; anterior width 9.2; posterior width, 10.5).

**Etymology.** Latin, *ponticulus* "little bridge" in reference to the weaker, shorter, partially divided midlink and alluding to its apparent phyletic position relative to other palorchestids.

*Propalorchestes cf. ponticulus*  
(Figs 3D-F, 4)

**Material.** AR11302: a perfectly preserved lower molar crown of a palaorchestine marsupial from the Wayne's Wok Locality, Riversleigh, Queensland (Fig. 3E,F). According to Archer *et al.* (1989) Wayne's Wok is a system B (provisionally early-Miocene) equivalent.

**Remarks.** The specimen may represent an encrypted  $M_5$  in which the enamel surface was only just completed and was perhaps slightly dehydrated before fossilization. However, the specimen preserves, in a conservative way, some of the key features of *Propalorchestes ponticulus* and is therefore assigned provisionally to that species. These characters are: protolophid offset as in typical palorchestines, but not greatly enlarged at the base, well developed preprotocrisid, which however, becomes faint as it reaches the precingulid; a shallow sulcus on the anterior surface of the protolophid; a somewhat hollow posterior surface of the protolophid immediately below the protolophid; a swelling at the base of the anterior surface of the hypolophid; crown base not swollen above the cemento-enamel junction; divided cristid obliqua confined to the labial side of the interloph valley, though stronger, higher and not situated as labiad as in the holotype of *Propalorchestes ponticulus* (AR1802).

The crown is slightly longer (0.3mm) and relatively broader anteriorly (0.8mm) than the holotype, although the slight front to back molar size increase in palorchestines could easily account for this. The primary differences are that the protolophid is slightly wider than the hypolophid (characteristic of the  $M_5$  of *Palorchestes* species), and that the floor of the interloph valley is more cambered on either side of the midlink. (Measurements: length 15.1, anterior width, 10.0, posterior width, 9.6).

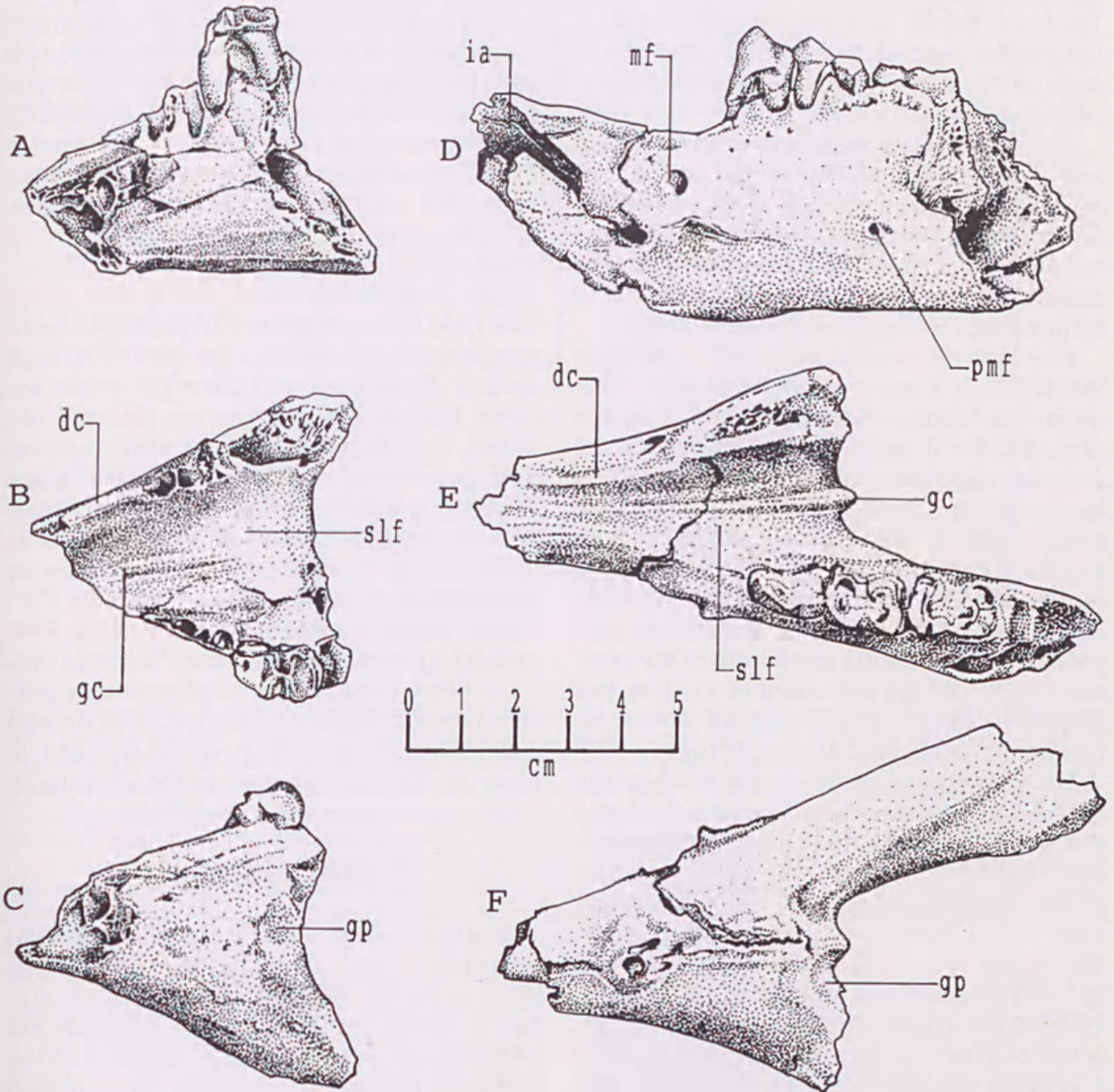
Though slightly smaller and otherwise less derived than other palorchestine species, the lophids of *P. ponticulus* are high, sulcate anteriorly and recurved posteriorly as in the later palorchestines. Because all of the *P. novacu-*



*lacephalus* specimens are heavily worn, it can only be inferred that they were similarly high-crowned but larger, thicker, with a wider interloph valley and a relatively larger protoconid.

The provisionally referred specimen AR1779 is a dentary fragment with both hemimandibles fully fused at the symphysis.

The anterior portion of the protolophid and the lingual sides of both lophids of  $M_2$  are broken and the lophids are severely worn. Based on the size of the crown base and roots, the Riversleigh  $M_2$  is slightly smaller than the  $M_2$  of the Camfield *P. novaculacephalus* (Figs 3D, 4A-C).



**Fig. 4.** Dentary fragments of *Propalorchestes* cf. *ponticulus*. These specimens share a variety of features with *Pitikantia*, *Ngapakaldia* and *Propalorchestes*. **A**, anterior portion of the dentary of AR1779, lateral aspect; **B**, dorsal aspect of AR1779; **C**, ventral aspect of AR1779; **D**, lateral aspect of SGM 1008. Abbreviations: **dc**, diastemal crest; **gc**, genial crest; **gp**, genial pit; **slf**, sublingual fossa; **ia**, incisor alveolus; **pmf**, posterior mental foramen. The profile of the dentaries more closely resemble those of the genera *Ngapakaldia* and *Pitikantia* than the genus *Palorchestes*; like the former genera, there is an apparently greater front-to-back molar gradient and the incisor implantation is more like that of *Ngapakaldia* than *Palorchestes*. Like *Propalorchestes* and *Palorchestes*, the dentary symphysis is fully ankylosed, with a long, deep sublingual fossa, but the genial pits are located on the ventral surface rather than posterior to the symphysis. Because A-C (AR1779) retains a lower second molar that resembles the holotype of *P. ponticulus*, and because the dentary morphology of D-E (SGM 1008) closely resembles AR1779, I have provisionally included them in the species *P. ponticulus*. These fragments support a close relationship of *Pitikantia*-like forms to the palorchestines and may represent a stage of evolution close to their divergence.



The remnants of the crown reveal a narrower, steeper interloph valley than in *P. novaculacephalus* and the presence of an enamel bulge on the anterior surface of the base of the entoconid is only just apparent. The midlink is short, though well-developed and situated immediately labial of the midline of the tooth. The dentary fragment is more informative. The portions in common with *P. novaculacephalus* indicate that AR1779 was not as deep or thick transversely through each hemimandible.

The symphysis is shallower posteriorly and less steeply inclined. The genial pits are located on the ventral surface of the symphysis rather than comparatively high up on the posterior surface. As in later palorchestines, the diastemal crests are prolonged anteriorly to form a deep, U-shaped sublingual trough.

The provisionally referred specimen SGM1008 is a more complete dentary fragment, but lacking cheek tooth crown details (Fig. 4 D-F). It is therefore aligned with the formerly described specimen on the basis of its overall morphological similarity and the comparison of the sizes of the cheek tooth alveoli. Although the  $P_3$  crown is damaged on the lingual side, the occlusal and lateral profile of the tooth, combined with its size and proportions, the steepness and breadth of the anterior cuspid and the indication of a sulcus just lingual to the preprotocristid all favour an incipiently palorchestine morphology.

The proportions of the crown bases of the molars and their alveoli indicate that the molar gradient was very slight, as in all palorchestines. The lateral surface of the anterior portion of the horizontal ramus is flat, moderately deep with a broad, rounded inferior border. The gently upturned symphysis is long, and narrows gradually towards the incisor alveoli. The incisor alveoli are large, vertically oriented, oval cavities separated throughout their considerable depth by a thin bony septum. The implantation angle of the incisors was shallow, but due to a lack of symphyseal deflection, typical of *Palorchestes* species, SGM1008 had only moderate procumbency of the incisors, comparable to that of *Pitkandia dailyi* (Stirton, 1967). As in all known palorchestines, the diastema is exceptionally long and forms a narrow trough extending to the base of the incisor crowns.

In contrast to *P. novaculacephalus*, the genial pits are located on the ventral surface of

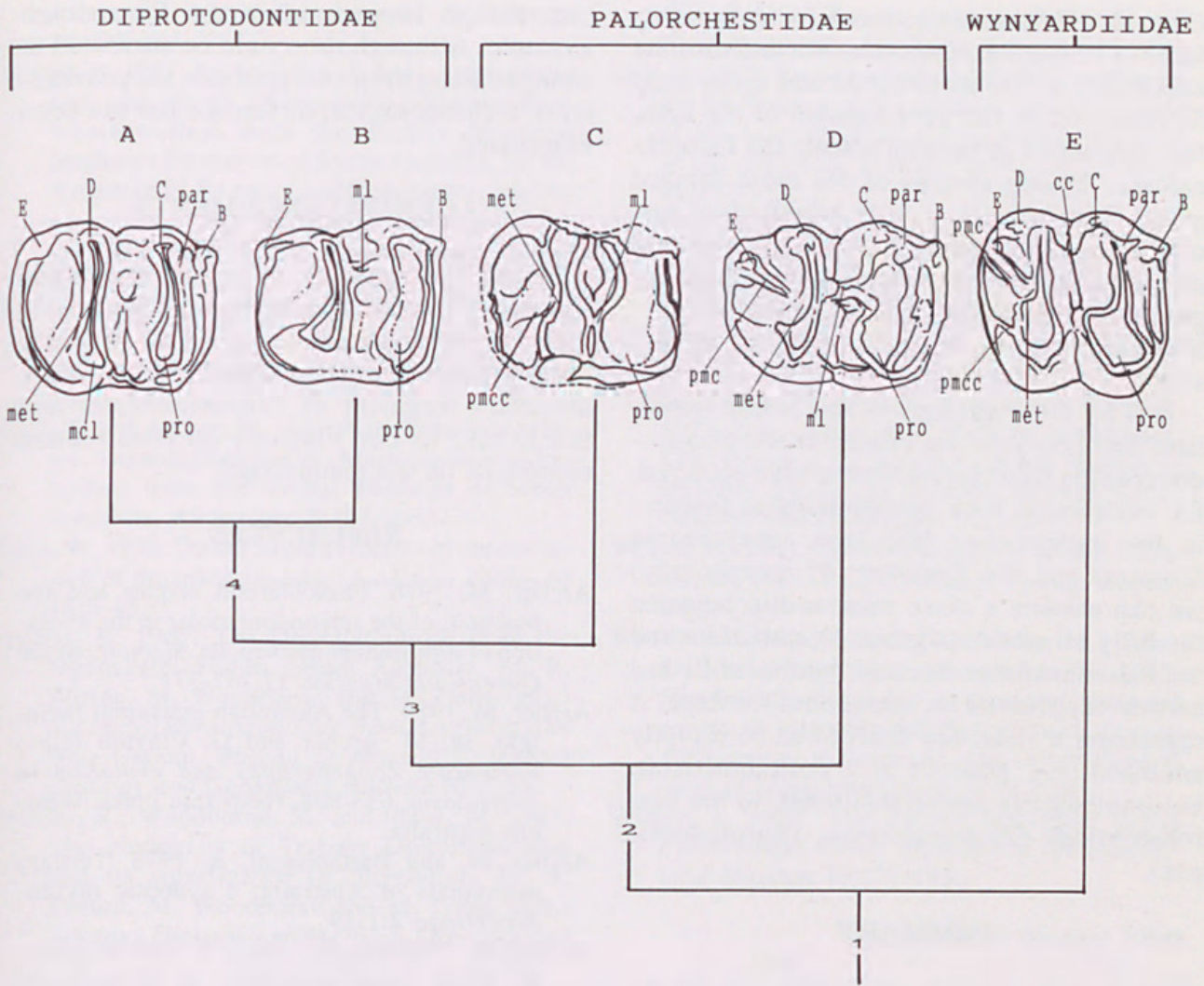
the symphysis as in AR1779. These are separated by a prominent genial crest that extends anteriorly within the sublingual sulcus to below the  $P_3$ . A remnant of this crest is visible in AR1779, immediately anterior to the level of  $P_3$ , and as the posterior portion of the symphysis is severely weathered, the genial crest must have been equally well developed.

Although the fossil material is fragmentary, I am confident that the presence of these two palorchestine species in the lower Oligocene and mid-Miocene of Australia will eventually be confirmed by more complete specimens. *Propalorchestes ponticulus* is a less robust form, that could be ancestral to *P. novaculacephalus* as the specimens appear to be confined to system B and A faunas at Riversleigh. Experience with other genera from Camfield, Riversleigh and Wipajiri (*Wakaleo* spp., *Neohelos tirarensis*) has shown that such species distinctions as I have just made become blurred when larger samples are obtained. It is therefore with the same reservation that Murray and Megirian (1990) place upon the distinction of *W. vanderleueri* from *W. oldfieldi* that I designate *P. ponticulus* as distinct from *P. novaculacephalus*. A closer relationship of SGM 1008 to the genus *Pitkandia* cannot be ruled out. However, that Riversleigh specimen differs from *Pitkandia dailyi* in being more robust, in possessing a posterior mental foramen, in having an apparently more strongly ankylosed symphysis and in showing some differences in the cheektooth crown proportions and morphology.

## CONCLUSIONS

Tedford *et al.* (1977) first noted that wynyardiid upper molars show a transitional stage in the development of bilophodont molars in which the labial side of the lophs are composed of stylar cusps B, C and D, with the metacone and paracone taking up a median position within gradually evolving transverse crests. This evidence supported the observations of Winge (1941), Ride (1971) and Archer (1976) that a selenodont pattern resembling phascolarctids and peramelids, gave rise to the highly developed, albeit superficially uncomplicated bilophodonty characteristic of, for example, the nototherine and zygomaturine Diprotodontidae. The traditional descriptive nomenclature (Stirton *et al.* 1967) applied to the Diprotodontidae assumed that the hy-





**Fig. 5.** Phenogram depicting a hypothesis of the evolution of bilophodont "diprotodontoids" from a selenobilophodont ancestor partially based on the morphology of the second upper molar. **A**, *Neohelos* (Zygomaturinae); **B**, *Pyramios* (Diprotodontinae); **C**, *Ngapakaldia* (Subfamily Incertae); **D**, *Propalorchestes* (Palorchestinae); **E**, *Muramura* (Wynyardiidae, Subfamily Incertae). **1**, (symplesiomorphic) expression of "posterobuccal triangle"; **2**, (synapomorphic) loss of "posterobuccal triangle"; **3**, (synapomorphic) suppression of the metacone; **4**, (synapomorphic) widening of interloph valley and transverse expansion of lophs. The postulated connection between *Propalorchestes* and wynyardiids is deduced from phenetic resemblances; possible synapomorphies include the robust, elongated postmetacrista and the distinct swelling in the middle of the protoloph that could have been a precursor to the double midlink complex (?centrocrista + postparacrista) in *Propalorchestes*. These resemblances are more compelling than with other selenodont vombatimorphians or phascolarctomorphians.

pocone and the metacone formed the respective lingual and buccal cusps of the metaloph.

Tedford *et al.* (1977: fig. 3A-D) illustrated a series of second upper molars of a wynyardiid, two vombatoids and a phascolarctid from the Pinpa Local Fauna. This series clearly demonstrated the cusp homologies from a selenodont phascolarctid in which the hypocone was not present, to an incipiently bilophodont wynyardiid, that unambiguously demonstrated the intraloph position of the metacone, absence of the hypocone and labial position of styler cusp D, to form the metaloph of the molar, with the metaconule as the proxy "hypocone".

Although wynyardiids such as *Muramura williamsi* Pledge (1987) and *Namilamdeta snideri* (Rich and Archer, 1979) are incipiently bilophodont, they retain a predominately selenodont pattern. The possibility of paraphyletic bilophodonty could not be ruled out, particularly with respect to the diprotodontids, among which no clear representation of the conspicuous posterobuccal triangle of cusps (D, E and metacone) remains.

*Propalorchestes novaculacephalus* is fully bilophodont but retains the "posterobuccal triangle" of the wynyardiids and demonstrates the reduction of the metacone and hypertrophy of the metaconule to form the metaloph



(Fig. 5). Moreover, a hypso-bilophodont pattern, in which the postmetacrista and discrete expression of the metacone and stylar cusp D, obscured by the development of the loph, had developed in parallel among the Palorchestinae. Among species of the more derived genus *Palorchestes*, a fully bilophodont pattern is present, and only by tracing the specific details of its transformation can the homologous structures relating to the obfuscated selenodont heritage of the lineage be understood.

It is by close analogy to this subtle transition, that I consider the characteristic bilophodonty of the Diprotodontidae to have occurred. By association with synapomorphic features in the basicranium (the large epitympanic fenestra) and the dentition ( $P^3$  morphology) we can assume a close relationship between the fully bilophodont genus *Ngapakaldia* and the Palorchestinae. Because *Ngapakaldia* has further suppressed its selenodont heritage, it represents a state, too derived to be directly ancestral (e.g. absence of a postmetacrista), but immediately post-transitional, to the diprotodontidae (Zygomaturinae, Diprotodontinae).

### SUMMARY

The genus *Propalorchestes* was initially diagnosed on the basis of a cranial fragment representing a primitive palorchestine. Dentitions assigned to this genus are likewise plesiomorphic, and show the transition between selenodont wynyardiid or wynyardiid-like dentitions and the fully evolved bilophodont dentitions that characterize members of the family Diprotodontidae. Derived palorchestids paralleled the diprotodontids by also incorporating stylar cusp D into the metaloph while suppressing the metacone; therefore little, if any, indication of this state is evident in the later Tertiary genus *Palorchestes*.

Palorchestine palorchestids were present in the late Oligocene as evinced by *Propalorchestes ponticulus*. In retaining a remnant metacone and a large postmetacrista, *Propalorchestes novaculacephalus* from the mid-Miocene (post-Wipajiri) Camfield beds appears be less derived than the Riversleigh system C specimen. The distinctive features of the upper molar crowns observed for *P. novaculacephalus* from Camfield are obviously pres-

ent, though suppressed in the Riversleigh example. Although this could be attributed to changes along the molar gradient, the possibility of a chronological difference has not been eliminated.

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