



## A diverse assemblage of monotremes (Monotremata) from the Cenomanian Lightning Ridge fauna of New South Wales, Australia

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### ABSTRACT

Six species of monotremes, three newly described here, occur in the Cenomanian fossil fauna from Lightning Ridge in northeastern New South Wales, Australia, making it the most diverse monotreme assemblage on record. Four species are known from a single specimen, suggesting that diversity remains underrepresented. No other mammal lineages are known from the deposit, although the absence of smaller taxa is likely due to sampling biases introduced by the opal mining process. Early-Late Cretaceous monotremes thus clearly diversified in Australia during the absence of other large-bodied mammalian competitors; and subsequently occupied a wider range of ecological niches than at any other time in their evolutionary history. One new taxon described herein represents a previously unknown monotreme family that combines marked elongation and torsion of the dentary with teinolophid character states, including the retention of five molars. Another shares dental features with ornithorhynchids, while the third is a possible diminutive steropodontid and simultaneously represents the smallest-bodied post-Barremian monotreme. Additional material of *Steropodon galmani* is also documented, confirming that a Meckelian groove is rudimentary or absent in this taxon, thus adding to the morphological understanding of this unusual monotreme. Lastly, we posit that the loss of teeth in ornithorhynchids may have occurred during the Pleistocene as a result of competition with aquatic hydromyid rodents dispersing to Australia from New Guinea.

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UNTIL the discovery of *Steropodon galmani* Archer, Flannery, Ritchie & Molnar, 1985, the evolutionary history of pre-Oligocene monotremes remained entirely unknown. Over the last few decades a modest diversity of 11 extinct genera (*Patagorhynchus* Chimento, Agnolín, Manabe, Tsuihiji, Rich, Vickers-Rich & Novas, 2023 together with all previously named genera listed by Flannery *et al.* 2022a) ranging in age from the Barremian (Early Cretaceous) to Pleistocene and distributed across Australia, New Guinea and South America, have been documented. Long before even the bare outlines of the pre-

Pleistocene monotreme fossil record was known, Darlington (1957, p. 339) speculated about the group's past diversity, noting: 'It may be guessed that, wherever they originated, monotremes radiated in Australia before marsupials did, and that the old Australian monotreme fauna may have been at least as diverse as the later marsupial fauna...' Darlington's ruminations were based in large part on the contrasting morphologies of the echidnas and platypus. These taxa, however, are now known to be terminal twigs on a deep evolutionary tree that molecular studies suggest diverged between 73–13 million years ago (Ma) (Phillips *et al.* 2009), or around 55 Ma (Zhou *et al.* 2021) depending upon preferred constraints. A much greater morphological diversity of monotremes has now been shown to lie outside of this clade (Flannery *et al.* 2022a). Yet, until now the evidence for Darlington's (1957) vision has been limited. New findings documented here thus

provide the first substantial support for Darlington's (1957) hypothesis.

The Finch Clay facies of the Wallangulla Sandstone Member in the Griman Creek Formation at Lightning Ridge in northeastern New South Wales (Fig. 1) has produced a unique fossil assemblage that inhabited a high palaeolatitude setting around 60°S during the Cenomanian (Kitchener *et al.* 2019). The identified vertebrates included teleosts, chondrichthyans, dipnoans (Kemp & Berrell 2020), turtles (Smith 2010; Smith & Kear 2013), leptocleidian and elasmosaurid plesiosaurs (Kear 2003, 2006, 2016, Kear & Hamilton-Bruce 2011), pterosaurs (Brougham, Smith and Bell 2017), sauropods (Frauenfelder *et al.* 2021), theropods (Brougham, Smith & Bell 2019), ankylosaurs (Bell *et al.* 2018), ornithopods (Bell *et al.* 2018, Bell *et al.* 2019a), crocodylomorphs (Hart 2020), enantiornithine birds and monotremes, amongst other taxa (Bell *et al.* 2019b, Poropat *et al.* 2023). Three monotreme species have been described from the Finch Clay facies: *Steropodon galmani* (Steropodontidae); *Kollikodon ritchiei* Flannery, Archer, Rich & Jones, 1995 (Kollikodontidae); and *Stirtodon elizabethae* Rich, Flannery & Vickers-Rich, 2020a (?Teinolophidae; Flannery *et al.* 2022a).

The Finch Clay facies fossils are preserved in SiO<sub>2</sub>•nH<sub>2</sub>O (hydrated silica dioxide), either as 'potch' or common opal, or as precious opal displaying plays of colour. These formed as pseudomorphs (amorphous potch replacements), or as opal replacements in which silica mineralization was coupled to decomposition. If the opal is translucent, fine internal anatomical details are sometimes visible.

Opalized fossils are also usually three-dimensional and undistorted by compaction or diagenesis, but may show a variable degree of pre-burial weathering. The majority of recovered specimens have passed through mechanical agitators—large rotating barrels that wash out and remove softer sediments to leave tailings of harder claystone and opal, including fossils. This process breaks delicate fossils, rounds edges and often removes the crowns of teeth and other projections. All of the fossil monotreme jaws described herein exhibit fresh breaks due to mechanical excavation and processing. However, alveoli containing remnant claystone indicate that the teeth were lost prior to burial. Notably, the opal-mining process also biases against the recovery of smaller vertebrates, with the smallest mammal remains recovered to date (see below) having posterior molars estimated at almost twice as long as the largest molars of Australian Cretaceous tribosphenidans (Flannery *et al.* 2022b). The Finch Clay facies also produces perinatal (possibly embryonic) ornithopod dinosaurs with an estimated body mass of 113 g (Kitchener *et al.* 2019), and tiny elements from fish, turtles, crocodylomorphs and birds (Bell *et al.* 2019b). We suspect that tribosphenidans were present in the Lightning Ridge faunal assemblage, and that careful excavation may yet yield evidence of them.

We assign all of our named Lightning Ridge mammal taxa to Monotremata based on their very large dental canals and other diagnostic features of the clade. However, the often fragmentary condition of

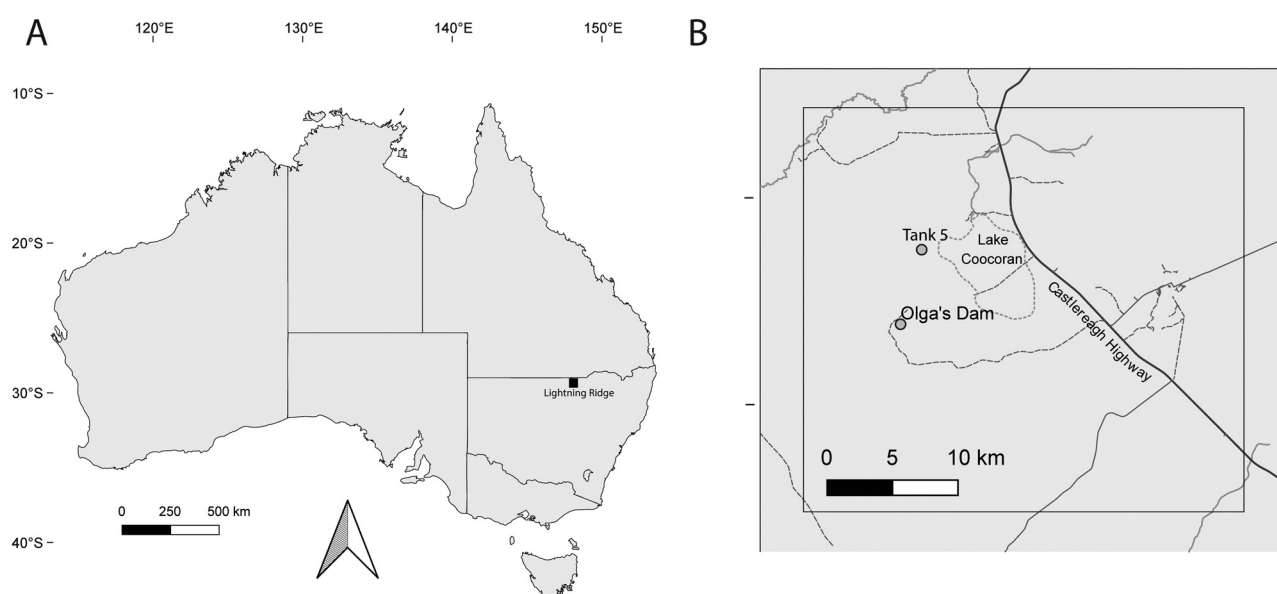


Fig. 1. Map of Australia showing the location of Lightning Ridge and nearby localities. A, Lightning Ridge. B, Tank 5 and Olga's Dam sites. Adapted from Hart *et al.* 2021.

the fossils makes identification of tooth positions difficult. Consequently, we interpret dental homologies based on comparisons with *Teinolophos trusleri* Rich, Vickers-Rich, Constantine, Flannery, Kool & van Klaveren, 1999, which is known from multiple dentaries (Flannery *et al.* 2022a), the tooth-bearing holotype dentary (AM F66763) of *S. galmani*, and the juvenile dentition of *Ornithorhynchus anatinus* Shaw, 1799.

Finally, we have not undertaken a phylogenetic analysis of the Lightning Ridge monotreme fossils because our interests principally lie in taxonomy and zoogeography. The outgroup to Monotremata is disputed, with two very different mammalian groups having been put forward—Southern Hemisphere tribosphenids (Luo *et al.* 2001), and dryolestids (Archer *et al.* 1993). This makes determinations of character state polarity (e.g., molar number) uncertain. Moreover, the very small number of identified taxa and their fragmentary preservation produces excessive missing data that compromises tree resolution (Kearney & Clark 2003). Consequently, we adopt the approach of Flannery *et al.* (2022b) in focusing on only the few unambiguous functional/adaptive character state complexes to diagnose taxa.

### ***Institutional abbreviation***

AM, Australian Museum ('F' prefix denotes the Palaeontology Collection), Sydney, Australia.

### ***Systematic palaeontology***

MAMMALIA Linnaeus, 1758

MONOTREMATA Bonaparte, 1837 or 1838

ORNITHORHYNCHOIDEA superfam. nov.

### ***Diagnosis***

Distinguished amongst other Monotremata by torsion of the dentary, whereby the lingual surface of the distal portions of the dentaries faces dorsally and are dorsoventrally flattened (except Tachyglossidae); and the distal portion of the masseteric canal being divided into three wide moieties (except Tachyglossidae).

### ***Remarks***

Ornithorhynchoidea includes Opalionidae and fam. nov. crown group monotremes: (1) Tachyglossidae, including *Tachyglossus* Illiger, 1811, *Zaglossus* Gill, 1877, *Megalibgwilia* Griffiths, Wells & Barrie, 1991, and *Murrayglossus* Flannery, Rich, Vickers-Rich, Ziegler, Veatch & Helgen, 2022a, all of which have

highly reduced dentaries, but likely split from Ornithorhynchidae during the Cenozoic (Phillips *et al.* 2009); (2) Ornithorhynchidae, which includes *Ornithorhynchus* Blumenbach, 1800 and *Obdurodon* Woodburne & Tedford, 1975, plus the stem ornithorhynchids (*sensu* Flannery *et al.* 2022a) *Monotrematum* Pascual, Archer, Jaureguizar, Prado, Godthelp & Hand, 1992, *Patagorhynchus*, and *Dharragarra* gen. nov.—these taxa share key synapomorphies with crown-group ornithorhynchids. Given that divergences within Ornithorhynchoidea probably occurred during the Cretaceous, multiple clades might be recognized within the systematic scope of Monotremata.

OPALIONIDAE fam. nov.

***Opalios splendens*** gen. et sp. nov.

(Fig. 2A–F)

### ***Diagnosis***

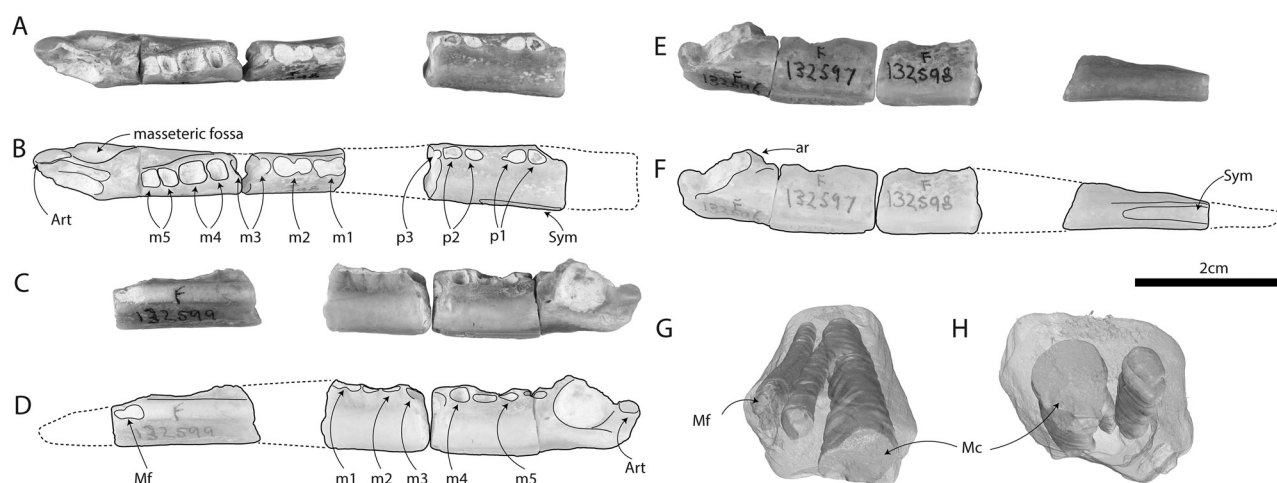
Differs from all monotremes except *Teinolophos trusleri* in possessing five molars rather than four or fewer (Fig. 2A, B). Differs from *T. trusleri* in being much larger and possessing: a lower ascending ramus; an articular facet below the level of the toothrow (Fig. 2C, D); a hemispherical depression for insertion of the masseteric musculature on the buccal side of the dentary (Fig. 2C, D); the anterior portion of the dentary twisted (torsion) such that the lingual surface faces dorsally and the anterior dentary is dorsoventrally flattened (Fig. 2A, B, E, F); a much reduced or absent Meckelian groove (Fig. 2E, F); an extremely dorsoventrally shallow mandibular symphysis (Fig. 2F). Differs from all other monotremes except stem and crown ornithorhynchids by exhibiting torsion of the horizontal ramus of the dentary. We consider *Opalios splendens* to be the basal-most diverging taxon within Ornithorhynchoidea.

### ***Etymology***

The genus name refers to 'opal' in Greek. The species name refers to the large size and spectacular translucency of the holotype (AM F132596–AM F132599), which provides views of its internal structure.

### ***Holotype***

AM F132596–AM F132599, a left dentary broken into four pieces. AM F132596 comprises the posterior-most dentary including the rear margin of the m5 alveolus. AM F132597 includes the m5, m4 and posterior wall of the m3 alveoli. AM F132598 preserves the anterior wall of the m3, as well as m2, m1 and posterior wall of the p4 alveolus. AM F132599 bears



**Fig. 2.** AM F132596-9, dentary of *Opalios splendens* gen. et sp. nov. in **A, B**, occlusal, **C, D**, buccal, and **E, F**, lingual views. The internal morphology of the mandibular canal is shown in both **G**, distal oblique and **H**, mesial oblique views. **G** and **H** are not to scale. Art = articular facet of dentary. Mc = mandibular canal. Mf = mental foramen. Sym = symphysis.

the p1–3 alveoli. The anterior-most part of the dentary is missing.

#### Type locality, unit and age

AM F132596–AM F132599 were found in 2001 during sorting of a tailings heap at the Tank Five processing dam (29.406629°S, 147.779965°E) on the Coocoran Opal Fields west of Lightning Ridge township. The tailings had been deposited by the opal miner Dusan Malinovik, and mined from his claim at the nearby Smith's Opal Field (29.437973°S, 147.771212°E). AM F132596–AM F132599 were recovered over the course of a few days in sequence of AMF132596, AMF132598 (discovered by Clytie Smith of Lightning Ridge), AMF132597 and AMF132599 (discovered by ETS). Although the entire 10 m<sup>2</sup> area was searched over subsequent weeks, no further dentary sections were located. Finch Clay facies, Wallangulla Sandstone Member, Griman Creek Formation; Cenomanian (Upper Cretaceous), 100.2–96.6 Ma (Bell *et al.* 2019b).

#### Description

The ventral margin of the dentary is gently arcuate, flattening anteriorly. The alveolar margins of the molars also form an arc with high points at the anterior and posterior ends of the molar row, as in *Kollikodon ritchiei* (Flannery *et al.* 1995). A shallow groove at the level of the termination of the tooth roots is present on the labial surface (Fig. 2C, D). The total length of the dentary as reconstructed is around 76 mm. The length of three missing sections below m3, below p4, most of p3, and the anterior-most part of the dentary adds some uncertainty to this estimate.

The least problematic of these gaps is that below m3 because both the posterior surface of the posterior alveolus, and the anterior surface of the anterior alveolus is preserved, and the segments of the lingual surface of the dentary almost occlude, constraining the length of the missing portion. The length of the missing section which includes the posterior premolars is more difficult to estimate. Our estimate is based on the contour of the adjacent preserved dentary fragments, and assumes a smooth transition from the circumference of one section to the next. The length of the missing distal section has been estimated by comparing the specimen with the dentaries of both *Ornithorhynchus anatinus* and *Teinolophos trusleri* (Rich *et al.* 2016), in the latter of which approximately 15% of the dentary lies anterior to p1. We thus estimate that the dentary of *Opalios splendens* would have extended approximately a centimetre beyond its anterior-most break.

Judging from their alveoli, the molars all had two roots. The alveolar lengths of the five molars are: m1 4.3 mm, m2 5.1 mm, m3 5.4 mm (estimate), m4 6.4 mm, m5 5.2 mm. Judging from the preserved alveoli, there was a step change in size between the molars and the premolars (as is seen in all monotremes where the dentary is known). Because the alveoli and mandibular canal are filled with white claystone and the specimen is glassy and translucent, features are clearly visible inside the bone, especially in the midsection of the dentary. The tooth roots were apparently short and thick, extending slightly lingual (medial) to the mandibular canal (Fig. 2C). Broken cross-sections indicate that the roots actually contact and press into the top section of the

mandibular canal. Tooth roots of p1 and p2 are extremely short and butt against the mandibular canal.

AM F132596 was damaged in the agitator in such a way that the angle of the ascending ramus cannot be accurately estimated (Fig. 2). Judging from what remains, the ascending ramus would have extended from just posterior to m5 to just anterior to the articular facet, and was modest in height (Fig. 2C, D). A slight ridge is present on the ventrolingual margin of the dentary (Fig. 2E). It is unlikely that this extended into an angle. There is no internal coronoid process. The mandibular condyle is extremely low-set, lying about midway between the dorsal and ventral edges of the horizontal ramus (Fig. 2C, D). The articular surface is situated near the buccal margin of the bone and is elongated anteroposteriorly (length 3.5 mm, width 2.6 mm) with a flat articular surface whose buccal margin is lower than the lingual one. A deep, hemispherical mandibular sulcus (Fig. 2C, D) indicates the insertion point of the masseters. A roughened tubercle is present on the buccal side of the dentary at the rear, onto which a portion of the masseteric musculature presumably attached. There is a well-developed lingual shelf present, dorsal to a shallow groove, which may be a remnant Meckelian groove, or a myohyoid groove. This groove shallows both anteriorly and posteriorly: it does not reach the margin of the mandibular foramen, and attenuates before terminating below m5 (Fig. 2E, F). The mandibular foramen is large and bounded buccally by a ridge, buccal to which is a fossa, presumably for insertion of the mandibular musculature. This fossa extends from a point buccal to the articular facet, anteriorly to the point at which the ascending ramus is visible when viewed lingually (Fig. 2A, B).

AM F132597 fits precisely onto AM F132596. The part of the dentary housing the dental canal bulges in its posterior section. The alveoli indicate that the anterior and posterior alveoli of m5 are subequal in size, while the posterior alveolus of m4 is larger than the anterior one. There are pronounced crenulations or imbrications (irregular vertical striae) on the anterior and lingual walls of the alveoli for m4.

AM F132598 is separated from AM F132597 by a gap where the m3 would have been situated. Both the posterior wall of the posterior alveolus, and the anterior wall of the anterior alveolus of m3, survive. The alveoli of m2 indicate that this tooth was smaller than m4, and that its anterior moiety was narrower than its posterior one. The alveoli for the roots of m1 indicate that it was narrower than the m2, with its

anterior moiety being narrower than its posterior one (Table 1). The anterior root of the m1 is preserved in its alveolus (Fig. 2A).

A gap of uncertain length exists between AM F132598 and AM F132599. *Teinolophos trusleri* has four premolars (Rich *et al.* 2016). We interpret *O. splendens* to have also had four premolars. In *T. trusleri*, the p4 is closely adpressed against m1 (Rich *et al.* 2016). No evidence of p4 survives in *O. splendens*, the section of the dentary that presumably supported it being missing. AM F132599 (the anterior-most preserved fragment of the dentary) has alveoli for three premolars, interpreted here p1–3. The posterior-most root of p2 and the anterior-most root of p1 are preserved. The posterior margin of AM F132599 preserves the anterior alveolus of p3, which is not separated from p2 by a diastema. A diastema of about half a premolar length separates p2 from p1, and a diastema of uncertain length is present anterior to p1. A large dental foramen is present adjacent to the anterior root of p1, and continues anteriorly to where the dentary fragment terminates. The dental foramen is more dorsally placed than in *O. anatinus*. A narrow symphyseal region, 9.2 mm long, is preserved on the ventrolingual margin of the anterior end of AM F132599. There is no indication that the distal portions of the dentaries diverged to support the broad bill, as occurs in *O. anatinus*, and it seems likely that the mandibular symphysis in *O. splendens* extended to the mandibular tip, as it does in *T. trusleri* (Rich *et al.* 2016).

When the fragments of the dentary are assembled, it is evident that the horizontal ramus displays torsion (its long axis is vertically oriented under the molars, but twisted anticlockwise in the holotype left dentary to an angle of around 90° below p1). The symphyseal regions of the dentaries would have aligned closely, although they are not sutured. The lingual side of this anterior-most preserved section of the dentary has a peculiar rough, dimpled surface texture, extending posteriorly to m1 on AMF192598. Because of torsion, this dimpled section would have formed part of the floor of the oral cavity. Strong texturing of the surface of the dentary at this location is unusual, and its functional significance remains unknown.

The mandibular canal can be seen in cross section in several fragments. A CT scan reveals that it trifurcates anteriorly, a branch exiting at the dental foramen, while a smaller dorsal branch and a much larger ventral branch do not exit at a foramen but can be seen in cross section at the anterior-most break of the dentary (Fig. 2G).

**Table 1.** Measurements for monotreme specimens mentioned in the text.

|  | Measurement (mm) |
|--|------------------|
| <i>Opalios splendens</i> . Holotype. AMF 132599 –132599.     |                  |
| Length of preserved portion of dentary                       | 66.0             |
| Estimated length of complete dentary                         | 76.0             |
| AM F132597   |                  |
| Depth of dentary below posterior alveolus m5                 | 9.2              |
| Width of dentary at posterior alveolus m5                    | 6.4              |
| Length of alveoli for m5                                     | 5.1              |
| Length posterior alveolus of m5                              | 3.6              |
| Width of posterior alveolus of m5                            | 3.5              |
| Length of anterior alveolus of m5                            | 2.6              |
| Width of anterior alveolus of m5                             | 4.0              |
| Length of anterior alveolus of m4                            | 2.3              |
| Width of anterior alveolus of m4                             | 3.0              |
| Length of m4   | 6.4              |
| AM F132598   |                  |
| Depth of dentary at posterior alveolus of m1                 | 8.9              |
| Width of dentary at posterior alveolus of m1                 | 5.6              |
| Length of alveoli of m2                                      | 5.2              |
| Length of posterior alveolus of m2                           | 3.2              |
| Width of posterior alveolus of m2                            | 3.2              |
| Length anterior alveolus of m2                               | 2.3              |
| Width anterior alveolus of m2                                | 2.7              |
| Length of alveoli of m1                                      | 4.3              |
| Width of posterior alveolus of m1                            | 2.8              |
| Length of anterior alveolus of m1                            | 2.4              |
| Width of anterior alveolus of m1                             | 2.5              |
| AMF 132599.  |                  |
| Dentary depth below anterior root ant premolar               | 7.8              |
| Length of alveoli, p2  | 6.1              |
| Length of alveoli, p1  | 5.8              |
| Length of diastema one.                                      | 3.2              |
| Length of diastema two (incomplete)                          | 3.7              |
| Dentary width below the anterior root of p1                  | 4.4              |
| <i>Dharragarra aurora</i> . Holotype. AM F97262              |                  |
| Depth of dentary below posterior alveoli of m2               | 7.7              |
| Width of dentary at posterior alveoli of m2                  | 5.7              |
| Dentary depth at anterior alveolus of m2                     | 7.4              |
| Dentary width at anterior alveolus of m2                     | 5.5              |
| Dentary depth at posterior margin of dental foramen          | 7.1              |
| Dentary width at posterior margin of dental foramen          | 4.8              |
| Width of alveolus of m3                                      | 2.1              |
| Estimated length of alveolus of m3                           | 2.4              |
| Length of alveoli of m2                                      | 7.2              |
| Length of posterior alveolus of m2                           | 4.6              |
| Width of posterior alveolus of m2                            | 3.5              |
| Length of anterior alveolus of m2                            | 2.6              |
| Width of anterior alveolus of m2                             | 3.5              |
| Length of alveoli of m1                                      | 7.0              |
| Length of posterior alveolus, of m1                          | 4.2              |
| Width of posterior alveolus of m1                            | 4.0              |
| Length of anterior alveolus of m1                            | 2.3              |
| Width of anterior alveolus of m1                             | 3.1              |
| Alveolar length of p4  | 4.1              |
| Alveolar length of p3  | 5.4              |
| Alveolar length of p2  | 4.8              |
| Dentary depth below posterior root of p4                     | 8.1              |
| Dentary width below posterior root of p4                     | 5.1              |
| <i>Parvopalus clytiei</i> . Holotype. AM F 161198            |                  |
| Total length of dentary fragment                             | 14.7             |
| Depth of dentary below posterior alveolus of posterior molar | 4.8              |
| Width of dentary below posterior alveolus of posterior molar | 3.2              |
| Length of alveoli of posterior molar                         | 3.2              |
| Length of posterior alveolus of posterior molar              | 1.8              |
| Width of posterior alveolus of posterior molar               | 1.9              |
| Length of anterior alveolus of posterior molar               | 1.3              |
| Width of anterior alveolus of posterior molar                | 2.3              |
| <i>Steropodon galmani</i> . Holotype. AM F66763              |                  |

(continued)

**Table 1.** Continued.

|  | Measurement (mm) |
|--|------------------|
| Depth of dentary below posterior of m3                                 | 8.3              |
| Breadth of dentary below posterior of m3 (broken so this is a minimum) | 5.7              |
| m3 length  | 5.0              |
| m2 length  | 6.6              |
| m1 length  | 7.3              |
| AM F 97263   |                  |
| Depth of dentary at anterior alveolus m3                               | 7.2              |
| Width of dentary at anterior alveolus m3                               | 5.9              |
| Length of alveoli for m2   | 7.5              |
| Length of posterior alveolus of m2                                     | 3.9              |
| Width of posterior alveolus of m2                                      | 3.6              |
| Length of anterior alveolus of m2                                      | 3.0              |
| Width of anterior alveolus of m2                                       | 3.7              |
| AM F161197   |                  |
| Depth of dentary below posterior root of m3                            | 7.7              |
| Width of dentary at posterior root of m3                               | 6.1              |
| Length of alveoli of m3  | 5.1              |
| Length posterior of alveolus of m3                                     | 3.2              |
| Width of posterior alveolus of m3                                      | 2.1              |
| Length of anterior alveolus of m3                                      | 2.6              |
| Width of anterior alveolus of m3                                       | 3.3              |
| Approximate length of alveoli of m2                                    | 7.4              |
| Length of posterior alveolus of m2                                     | 4.4              |
| Width of posterior alveolus of m2                                      | 3.3              |

**Remarks**

Because the four fragments that comprise the dentary were recovered separately, a rationale for their association is required. Opalized vertebrate bones are generally uncommon in the Finch Clay facies of the Griman Creek Formation, and mammalian fossils are extremely rare (Bell *et al.* 2019a). The discovery of four dentary fragments at a single location is unique in our experience, and is almost certainly the result of breakage during the mining process of the original, more complete specimen. The only other fossils recovered from this site were plant scraps, unionid bivalves and a megaraptorid theropod tooth. All four fragments were collected from approximately 10 m<sup>3</sup> of tailings and all share the distinctive translucent ‘amber’ coloured opal, fine preservation of external and internal details, and a very large mandibular canal.

The posterior-most three fragments share molar alveoli that are similar in depth and overall morphology. Two of the fragments (AM F132596 and AM F132597) can be unequivocally fitted together, the break between them being sharp and unabraded. AM F132598 cannot be fitted with these, being separated by a missing segment of the dentary below the m3. A larger gap separates AM F132599 from AM F132598, but the appearance of the opalization, the alveoli, and the proportions of the mandibular canal between this piece and AM F132598 are consistent with them being part of the same dentary.

*Opalios splendens* is the second monotreme known (after *Teinolophos trusleri*; Rich *et al.* 2016) to possess five molars. Archer *et al.* (1993) argued that Dryolestida is the outgroup to Monotremata. Many dryolestoids have five or more molars, implying that this state may be plesiomorphic for Monotremata. Luo *et al.* (2001), however, countered that southern hemisphere tribosphenids, which have three molars, form a clade with monotremes, implying that the presence of five molars may be a secondary reversion.

There is no morphological overlap between the only known specimen (a P4) of *Stirtodon elizabethae* (which was tentatively referred to Teinolophidae by Flannery *et al.* 2022a) and *O. splendens*, thus direct comparisons are not possible. But the P4 of *S. elizabethae* is far larger, broader and more robust than any lower premolar of *O. splendens*. It is highly likely that *S. elizabethae* was a very large monotreme (Flannery *et al.* 2022a), and far larger than *O. splendens*. *Opalios splendens*, however, represents a larger animal than *T. trusleri*, the only other teinolophid known. *Teinolophos trusleri* is unique among monotremes in retaining a well-developed Meckelian groove (Flannery *et al.* 2022a). Both taxa have five molars, with diastemata between most premolars (see Rich *et al.* 2016, Flannery *et al.* 2022a). As noted above, though, *O. splendens* differs from *T. trusleri* in lacking a diastema between p3 and p2.

Kollikodontids have highly specialized bunodont molars and a relatively narrow mandibular canal (Flannery *et al.* 2022a). Steropodontids have relatively tall, narrow dentaries with a well-developed ascending ramus (Flannery *et al.* 2022a). Both steropodontids and kollikodontids have a lower molar number (three and four, respectively), and in both the posterior-most molar is markedly reduced in size relative to the anterior ones (Flannery *et al.* 2022a). While m5 is smaller than m4 in *O. splendens*, the size difference is less than that seen between the posterior and penultimate molars in these two other families (Table 1).

**Comparisons with other ornithorhynchoids.** *Opalios splendens* is larger than *Dharragarra aurora* gen. et sp. nov., being similar in size to *Ornithorhynchus anatinus* (dentary length ~76 mm versus 73.4–94.0 mm based on a sample of 13 *O. anatinus* individuals from the AM collections). The most striking differences between *O. splendens* and *D. aurora* are, in the latter, the absence of m4–5, the reduction of m3, the absence of diastemata between the premolars, and the reduced size of p1. Partial dentaries of the ornithorhynchids *Obdurodon insignis* Woodburne & Tedford,

1975, and *Obdurodon dicksoni* Archer, Jenkins, Murray, Hand & Godthelp, 1992, were described in detail by Musser & Archer (1998), Archer *et al.* (1992) and Archer *et al.* (1992). *Obdurodon insignis*, *O. dicksoni* and *O. anatinus* are unique amongst monotremes in possessing a deep masseteric foramen and an internal coronoid process on the dentary (Archer *et al.* 1992). *Obdurodon dicksoni* is unique amongst crown ornithorhynchids in possessing a prominent ascending ramus (Archer *et al.* 1992); however, this is anteroposteriorly shorter than that of *O. splendens*. It also has a prominent dentary angle (Archer *et al.* 1992), a feature that is absent in *O. splendens*. *Obdurodon insignis*, by comparison, had a lower ascending ramus and seems to have lacked, or had only a rudimentary, dentary angle (Musser & Archer 1998).

The horizontal ramus of the dentary in *O. anatinus* is sinuous in shape when viewed laterally, the anterior ('bill-covered') section being sharply deflected ventrally, and the region posterior to the posterior horny masticatory pad is deflected dorsally. The dentary is also strongly sinuous in the labiobuccal plane, the section of the dentary bearing the anterior horny pad being deflected labially. In *O. splendens* the mandibular symphysis, which is shallow but distinct, likely extended to the anterior tip of the dentary, while in *O. anatinus* it terminates around 15–20 mm posterior to the dentary tip, allowing the dentaries to separate and flare laterally to support the bill. Only the posterior part of the dentary is known for the species of *Obdurodon* (Archer *et al.* 1992, 2012, Musser & Archer 1998), but what is preserved is similar to that of *O. anatinus* in having the region posterior to the molars being deflected dorsally. By contrast, the horizontal ramus of the dentary in *O. splendens* is almost straight in the dorsoventral and labiobuccal planes. The modest lateral broadening of the dentary anteriorly suggests that if a bill were present, it was far narrower than in *O. anatinus*. In the species of *Obdurodon* and *O. anatinus*, the articular facet is positioned high above the horizontal ramus and is transversely broad (Archer *et al.* 1992, Musser & Archer 1998). In *O. anatinus* there is no ascending ramus. In *O. splendens*, the articular facet is located below the level of the tooth crowns, is small, anteroposteriorly elongated, and a modest ascending ramus is present. In *O. anatinus*, a foramen is present on the ventral surface of the dentary near its tip. Two branches of the mandibular canal continue anteriorly to the dental foramen in *O. splendens*, indicating that additional foramina existed anterior to the preserved

part of the dentary (Fig. 2H). The larger of the two branches is positioned ventrally, suggesting that, as in *O. anatinus*, a foramen exited the dentary on its ventral surface (Fig. 2G). The anterior end of the dentary is flattened and spatula-like in *O. anatinus*, while in *O. splendens* it is thicker and narrower.

Potential synapomorphies demonstrating a relationship of *O. splendens* with other Ornithorhynchoidea include: reduction of the ascending ramus of the dentary; presence of a deep hemispherical fossette for an enlarged masseter; torsion of the horizontal ramus of the dentary; and horizontal flattening of the anterior part of the dentary. However, *O. splendens* also possesses character states present in tachyglossids, including: an anteroposteriorly elongated articular facet of the dentary; and relatively narrow rostrum. This character state combination is evident in either crown tachyglossids or ornithorhynchids, but not both, indicating that *O. splendens* is likely placed outside of the crown group. The presence of five molars with premolars separated by diastemata are possibly plesiomorphic features otherwise seen only in *T. trusleri* (Rich *et al.* 2016, Flannery *et al.* 2022a), suggesting that ornithorhynchoids may derive directly from ancestors with a teinolophid-like morphology.

Family ?ORNITHORHYNCHIDAE Gray, 1825

***Dharragarra aurora*** gen. et sp. nov.

(Fig. 3A–F)

2013, (b) (occlusal view, left dentary, steropodontid, Musser, p. 8.

2022a, gen. nov. ?Ornithorhynchidae (stem), Flannery *et al.*, p. 5.

### Diagnosis

Differs from teinolophids in lacking a Meckelian groove, possessing dentary torsion and three molars, and in lacking diastemata between the premolars. Differs from kollikodontids in possessing an enlarged mandibular canal, in possessing three rather than four molars and in possessing dentary torsion. Differs from Steropodontids in possessing dentary torsion, having a dorsoventrally flattened dentary, and a more reduced posterior molar. Differs from *Opalios splendens* in having three molars rather than five, and in lacking diastemata between p1 and p2. Amongst ornithorhynchoids, *Dharragarra aurora* differs from the species of *Obdurodon* and *Ornithorhynchus* in having molars with two roots rather than more than two; from *Patagorhynchus pascuali* in being larger; from *Monotrematum sudamericanum* in being smaller.

### Etymology

The genus name derives from ‘*Dharragarra*’, meaning platypus in the Gamilaraay, Yuwaalaraay and Yuwaalayaay languages (Ash *et al.* 2003). The species name is Latin for ‘dawn’.

### Holotype

AM F97262, a partial left horizontal ramus with roots for m3, p1, p3 and p4, and alveoli for m1–2 and p3 (Fig. 3).

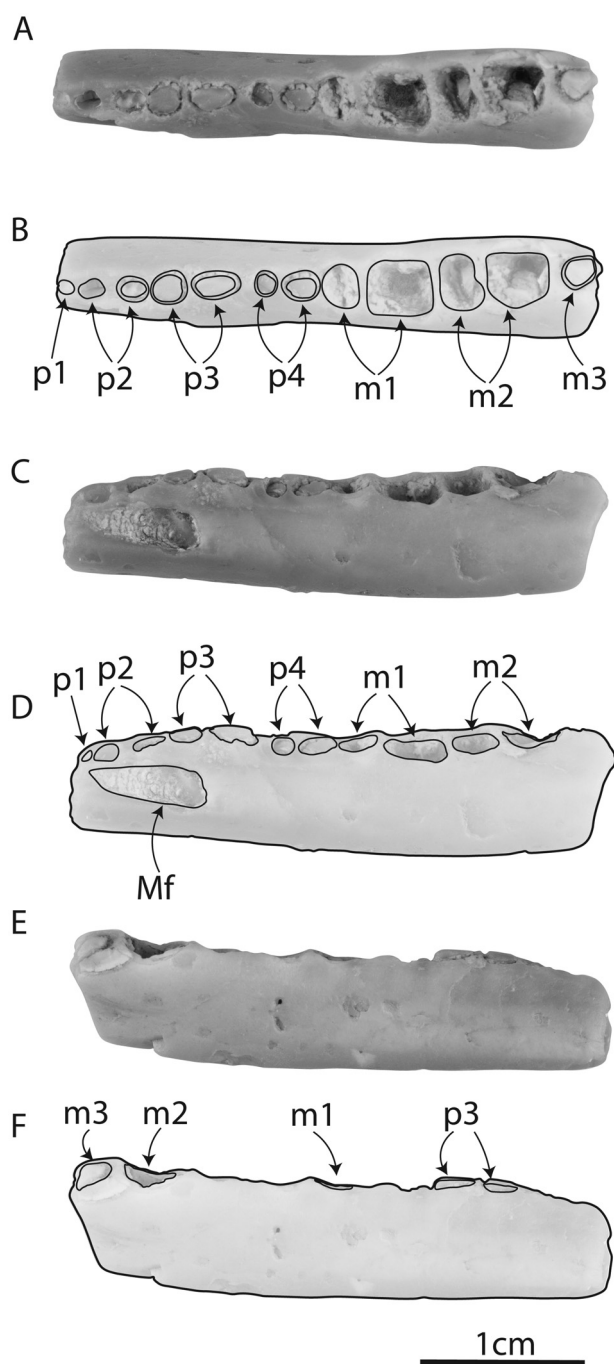
### Type locality, unit and age

AM F97262 was found in 2002 on a tailing heap at Tank Five (29.406629°S, 147.779965°E) on the Coocoran Opal Fields, and originated from the nearby Smith’s Opal Field. Finch Clay facies, Wallangulla Sandstone Member, Griman Creek Formation; Cenomanian (Upper Cretaceous), 100.2–96.6 Ma (Bell *et al.* 2019b).

### Description

AM F97262 is preserved in opaque, dark grey ‘potch’ and consists of the horizontal ramus from the posterior end of the molar row to the posterior root of p1 (Fig. 3). Its length is 32.6 mm. No tooth crowns are preserved. An alveolus retaining a root indicates the presence an m3 (Fig. 3A, B) which is much reduced relative to the more anterior molars. The root of m3 suggests that the tooth was similar in size to that in species of *Obdurodon* and juvenile *Ornithorhynchus anatinus* (Flannery *et al.* 2022a). The alveoli of m2 indicate that it was smaller than m1, and that its posterior moiety was larger than the anterior one (Fig. 3A, B). The alveoli for m1 show that its anterior moiety was markedly smaller than the posterior one. The roots and alveoli of the premolars suggest that the molar–premolar boundary was clearly differentiated, as in all monotremes where that region is known (Flannery 2022a). All premolars were narrower than the molars. Both roots of p4 are preserved, indicating that it was smaller than the p3 (Fig. 3A, B). The roots of p3 indicate that it was the largest premolar, and that its crown was narrow. The roots of p2 are similar in size and morphology to those of p4. A much smaller root, which is preserved at the anterior margin of the holotype, is identified as probably the posterior root of p1. A subtle depression, positioned on the lingual surface of the dentary below m2–3, may be a remnant of a Meckelian or myohyloid groove (Fig. 3E, F). The dental canal is large in diameter and limits the depth of the dental alveoli towards the anterior margin of the preserved section of





**Fig. 3.** AM F97262, dentary of *Dharragarra aurora* gen. et sp. nov. in A, B, occlusal, C, D, buccal and E, F, lingual views. Mf = mental foramen.

the jaw, making it doubtful that any teeth, except possibly remnant or procumbent ones, were present anterior to the p1. There are no diastemata separating any of the teeth in the preserved part of the dentary, apart from a very small gap between p3 and p4 (Fig. 3A, B). A very large dental foramen exits the labial side of dentary ventral to the alveoli of p3 (Fig. 3C, D). This is slightly posterior to its position in *O. splendens* (where it exits below p1). This apparent

difference, however, may be due to breakage of the buccal wall of the foramen. An enlarged dental canal continues anterior to this point, suggesting that a second, more anteriorly positioned foramen was present.

The preserved part of the horizontal ramus is nearly straight in both the buccolingual and dorso-ventral planes (Fig. 3). There is, however, some torsion of the dentary, which is broken off at p1, at which point the horizontal ramus is twisted through 55°. It is likely that the degree of torsion increased anteriorly, but this is impossible to substantiate due to breakage. The preserved fragment is heavily abraded, and there is no indication of a mandibular symphysis.

#### Remarks

We refer *Dharragarra aurora* to ?Ornithorhynchidae because, like *Monotrematum sudamericanum*, the species of *Obdurodon* and *Ornithorhynchus anatinus* (juveniles only) it has only three lower molars, the posterior-most of which is highly reduced (see Flannery 2022a). Because it is Cenomanian in age, *D. aurora* likely predates the split between tachyglossids and ornithorhynchids (Phillips *et al.* 2009, Zhou *et al.* 2021). It may thus be a stem ornithorhynchid (*sensu* Flannery *et al.* 2022a). All such possible stem ornithorhynchids are classified as ?Ornithorhynchidae in this work.

No direct comparisons with *Sundrius zieglerei* Rich, Flannery, Evans, White, Ziegler, Maguire, Poropat, Trusler & Vickers-Rich, 2020 are possible. The lower premolars of *D. aurora* are, however, far smaller, less robust and broader than the P4 of *S. zieglerei*. *Teinolophos trusleri* is far smaller than *D. aurora*, and has a distinct Meckelian groove which is absent (or much less marked) in *D. aurora*. As in *T. trusleri*, however, the p3 is larger than the p4 (see Rich *et al.* 2016, Flannery *et al.* 2022a).

#### Comparisons with other ornithorhynchoids.

*Dharragarra aurora* contrasts with *Opalios splendens* in its reduced molar number and lack of diastemata between the premolars. It is difficult to compare the degree of dental torsion in these taxa, but marked torsion exists in *O. splendens* (ca 90°), while in *D. aurora* around 55° of torsion is evident at the point where the dentary is broken. *Dharragarra aurora* shares an enlarged dental canal, a prominent dental foramen and torsion of the horizontal ramus of the dentary as potential synapomorphies with other (non-tachyglossid) ornithorhynchoids. The presence of three lower

molars with the posterior-most being reduced in size and likely single rooted, are shared with the species of *Obdurodon*, *Ornithorhynchus anatinus*, and probably *Monotrematum sudamericanum* (Flannery *et al.* 2022a). We consider the presence of a highly reduced m3 to be a unique synapomorphy uniting this group.

The only other Late Cretaceous ornithorhynchoid is *Patagorhynchus pascuali* Chimento, Agnolín, Manabe, Tsuihiji, Rich, Vickers-Rich & Novas, 2023, from the early Maastrichtian deposits of Patagonia (Chimento *et al.* 2023). The holotype of this taxon was identified as an m2 by Chimento *et al.* (2023). However, its anterior moiety is markedly narrower than the posterior one, and the partial alveolus anterior to the molar is too small to support a molar root, but is consistent in size with that of the posterior alveolus of a premolar (see Chimento *et al.* 2023). These features are consistent with the single preserved molar being an m1 rather than an m2—a designation adopted here.

Because *P. pascuali* is known from a single molar with an adhering dentary fragment, and *D. aurora* is known only from a near complete horizontal ramus of a left dentary that lacks molar crowns, few direct morphological comparisons can be made between these taxa. The m1 of *P. pascuali* is double-rooted as is that of *D. aurora*. The m1 also has shallow molar roots and a smaller anterior moiety than the posterior moiety. The p4 is likewise markedly smaller and narrower than the m1, although the m1 of *P. pascuali* is 5.8 mm in length (see Chimento *et al.* 2023), while the alveolar length of the m1 in *D. aurora* is 7.2 mm. As tooth crown length is usually greater than alveolar length, it is likely that *D. aurora* was somewhat larger than *P. pascuali*. In addition, the chronostratigraphical and palaeogeographical gap between *P. pascuali* and *D. aurora* spanning ~22 Ma from southern South America to Eastern Australia prompts us to classify these two taxa as separate genera.

Similarly, few direct comparisons can be made with *M. sudamericanum*. Pascual *et al.* (2002) report that *M. sudamericanum* probably had three lower molars, with m3 being reduced in size, and m1 and m2 double-rooted—features all shared with *D. aurora*. By contrast, the species of *Obdurodon* and *O. anatinus* have multi-rooted m1 and m2 (Flannery *et al.* 2022a). In *Obdurodon dicksoni* the P4 is larger than P3, and it seems likely that the lower premolars had a similar size relationship (Archer *et al.* 1992). This is in marked contrast with *D. aurora*, where the p3 is larger than the p4. Furthermore, a very short diastema separates P3 and P4 in *O. dicksoni*, and there are no teeth anterior to P3 (Archer *et al.* 1992).

On the other hand, *D. aurora* lacks diastemata between premolars and p1–2 are undoubtedly present.

Only juvenile *O. anatinus* have teeth: M1–2, an upper premolar and m1–3 (m3 being highly reduced: Flannery *et al.* 2022a). *Dharragarra aurora* shares the same lower molar formula, but has four lower premolars while *O. anatinus* lacks lower premolars. The preserved segment of the horizontal ramus of *D. aurora* is nearly linear in both the buccolingual and dorsoventral planes, which is in stark contrast with the equivalent segment in *O. anatinus*, where the posterior portion is deflected dorsally, and distal portion deflected ventrally. In *D. aurora*, the dentary is broken off at p1, a point at which the degree of torsion is 55°. In *O. anatinus*, torsion of the dentary commences around one third of the distance posteriorly from its anterior tip, resulting in a twisting of the long axis of the dentary (in cross-section) so that the lingual segment is twisted anticlockwise through around 90°. It is possible that a similar degree of torsion existed in *D. aurora*.

STEROPODONTIDAE Archer, Flannery, Ritchie & Molnar, 1985

***Steropodon galmani*** Archer, Flannery, Ritchie & Molnar, 1985

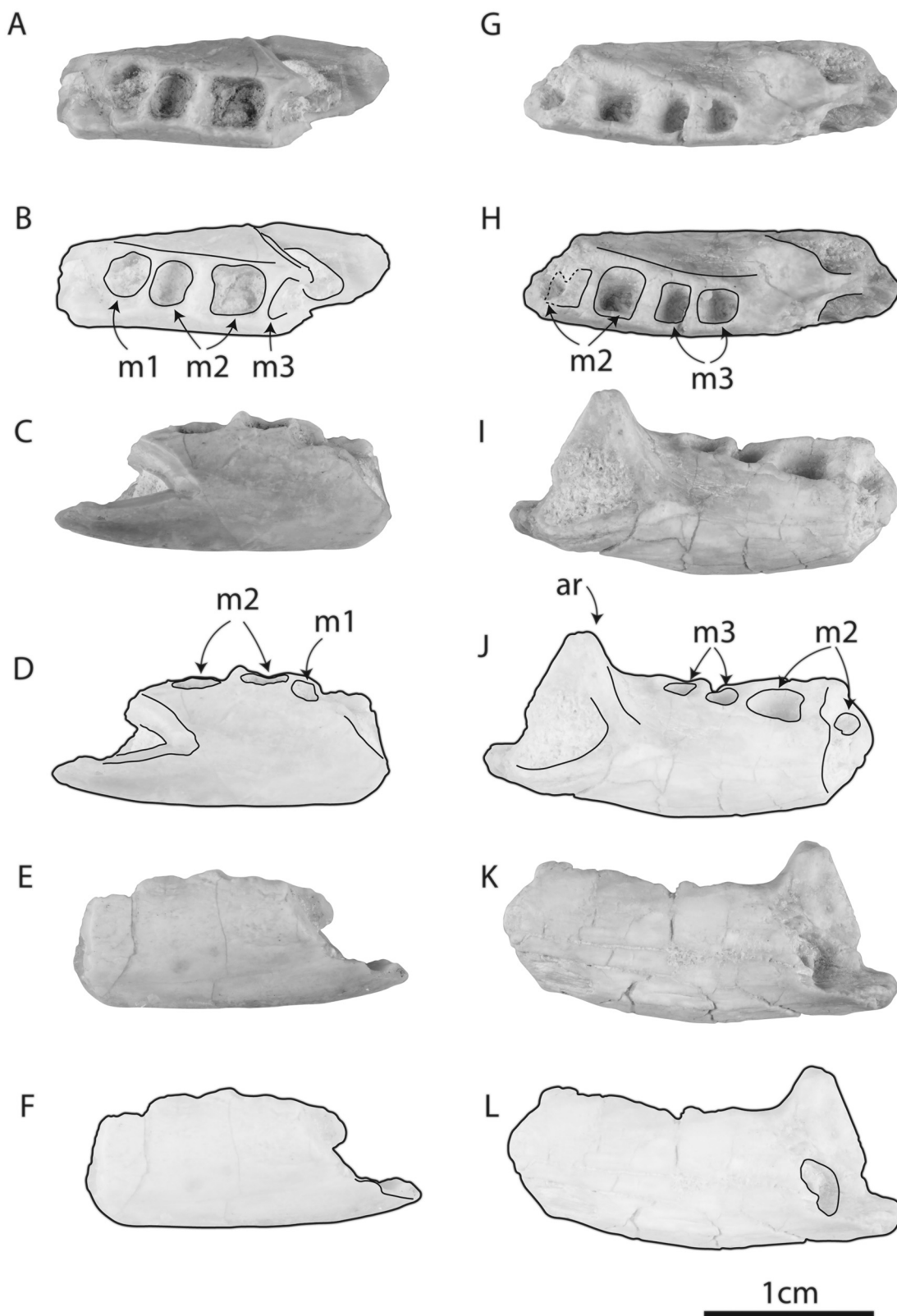
(Fig. 4)

#### ***Referred material***

AM F161197, a partial right dentary with the base of the ascending ramus and large dental canal, hosting alveoli for m3, the posterior alveolus of the m2, and the posterior surface of the anterior alveolus of m2. AM F97263, a right dentary fragment preserving the anterior wall of anterior alveolus of the m3, both alveoli of m2, the posterior alveolus and part of the anterior alveolus of the m1.

#### ***Type locality, unit and age***

AM F161197 was recovered from a tailing heap at Tank Five (29.406629°S, 147.779965°E), ~5 km from Olga's Dam. AM F97263 was also found at Tank Five but derived from a different tailings heap. Consequently, AM F161197 and AM F97263 are from separate sites on nearby opal fields, probably within a few kilometres of the Tank Five processing dam. The holotype of *Steropodon galmani* (AM F66763) was found in one of the older opal fields near Lightning Ridge, ~35–40 km from Tank Five. AM F161197 and AM F97263 are therefore the first records of *S. galmani* from the Coocoran Opal Fields. Finch Clay facies, Wallangulla Sandstone Member, Griman Creek Formation; Cenomanian (Upper Cretaceous), 100.2–96.6 Ma (Bell *et al.* 2019b).



**Fig. 4.** *Steropodon galmani* AM F97263 in A, B, occlusal, C, D, buccal and E, F, lingual views. *Steropodon galmani* AM F161197 in G, H, occlusal, I, J, buccal and K, L, lingual views.

**Description**

AM F161197 closely resembles the holotype of *Steropodon galmani* (AM F66763) in size and

morphology. However, AM F161197 preserves the dentary further posteriorly than does AM F66763 (Fig. 4). AM F161197 is preserved in opaque, whiteish

‘potch’ and exhibits surface weathering equivalent to level WS2 on the 6-stage scale of Behrensmeyer (1978). Unusually, this includes desiccation cracks, which are also often observable on unionid bivalve shells from the Finch Clay facies (ETS pers. obs.). The molar alveoli of AM F161197 are approximately square in dorsal profile, and the alveoli for the m3 indicate that it was smaller than the m2, as in AM F66763. The preserved segment of the ascending ramus rises at an angle of  $\sim 70^\circ$ . Judging from its preserved portion, the ascending ramus of AM F161197 was prominent and robust. The masseteric sulcus is moderately deep, suggesting a well-developed masseteric musculature. The posterior molar is situated well anterior to the ascending ramus, with a broad valley separating it from the ascending ramus. The opening of the mandibular canal is 3.2 mm in diameter (Fig. 6B). Posteriorly, the dentary fragment terminates in a break. There is no indication of a dentary angle, although if commencing well posteriorly, it could have been broken away. A slight depression on the lingual side of the horizontal ramus posterior to the m3 might be a remnant of a Meckelian or myohyoid groove.

AM F97263 provides almost no additional information, as it replicates the morphology of AM F66763 and AM F161197. The diameter of the mandibular canal at the posterior break of the dentary is 2.9 mm. There is a slight depression on the lingual surface that may be a remnant of a Meckelian or myohyoid groove. The horizontal ramus is shallower than in AM F66763 and AM F161197, and may be a result of intraspecific variability.

### Remarks

AM F161197 and AM F97263 add considerably to knowledge of the Meckelian groove in *Steropodon galmani*. AM F66763 is widely considered to have possessed a Meckelian groove (e.g., Luo 2007, Luo *et al.* 2001, 2002, 2007, 2017, Kielan-Jaworowska *et al.* 2004, Rougier *et al.* 2007, Wible *et al.* 2009), but recent re-examination has revealed post-mortem damage to the dentary above the Meckelian groove suggesting that this feature is actually a crack (see Flannery *et al.* 2022a). Notably, AM F161197 and AM F97263 both lack corresponding structures, although they do possess corresponding shallow depressions on the lingual sides of their dentaries.

*Steropodon galmani* differs from ornithorhynchoids in possessing a narrow and deep horizontal ramus of the dentary, and a prominent ascending ramus that in addition to its tribosphenic-like (but not tribosphenic)

lower molars (see Flannery *et al.* 2022b), could suggest that *S. galmani* was a terrestrial omnivore.

### ?STEROPODONTIDAE

#### *Parvopalus clytiei* gen. et sp. nov.

(Figs. 5A, B, 6A)

### Diagnosis

Attributed to Monotremata on the basis of its enlarged mandibular canal and squared molar alveoli profile. Provisionally attributed to Steropodontidae based on its deep, narrow, horizontal ramus and prominent ascending ramus (rising at an angle of  $\sim 70^\circ$ ); well-developed masseteric sulcus; and posterior molar positioned well anterior to the ascending ramus. *Parvopalus clytiei* is one of the smallest-known monotremes with the exception of *Teinolophos trusleri* (molar alveolar length of 3.2 mm versus molar tooth lengths of 1.1–1.7 mm: Flannery *et al.* 2022a). Differs from *Steropodon galmani* in being much smaller; possessing a more prominent ventral margin of the masseteric sulcus; and posterior alveoli of the posterior-most molar being larger than the anterior one indicating no reduction in posterior molar size. Differs from teinolophids in lacking a Meckelian groove, and from ornithorhynchids and kollikodontids in having a deeper, narrower dentary.

### Etymology

Genus name is Latin for ‘small opal’. Species is named for Clytie Smith (Lightning Ridge), who has recovered many opal fossils at Lightning Ridge.

### Holotype

AM F161198, partial left dentary, preserving the posteroventral margin of the ascending ramus to the posterior alveoli of the penultimate molar.

### Type locality, unit and age

Found in 1999 in a tailings heap at Olga’s Dam (29.464407°S, 147.777180°E),  $\sim 5$  km south of Tank Five on the Coocoran Opal Fields. AM F161198 originated from a small field known as CC’s, which is near Smith’s Opal Field. Finch Clay facies, Wallanguilla Sandstone Member, Griman Creek Formation; Cenomanian (Upper Cretaceous), 100.2–96.6 Ma (Bell *et al.* 2019b).

### Description

AM F161198 has alveoli for the posterior-most molar (alveolar  $l = 3.2$  mm) and the rear surface of the posterior alveolus of the penultimate molar (Fig. 5). The alveoli penetrate the dentary to the level of the dental

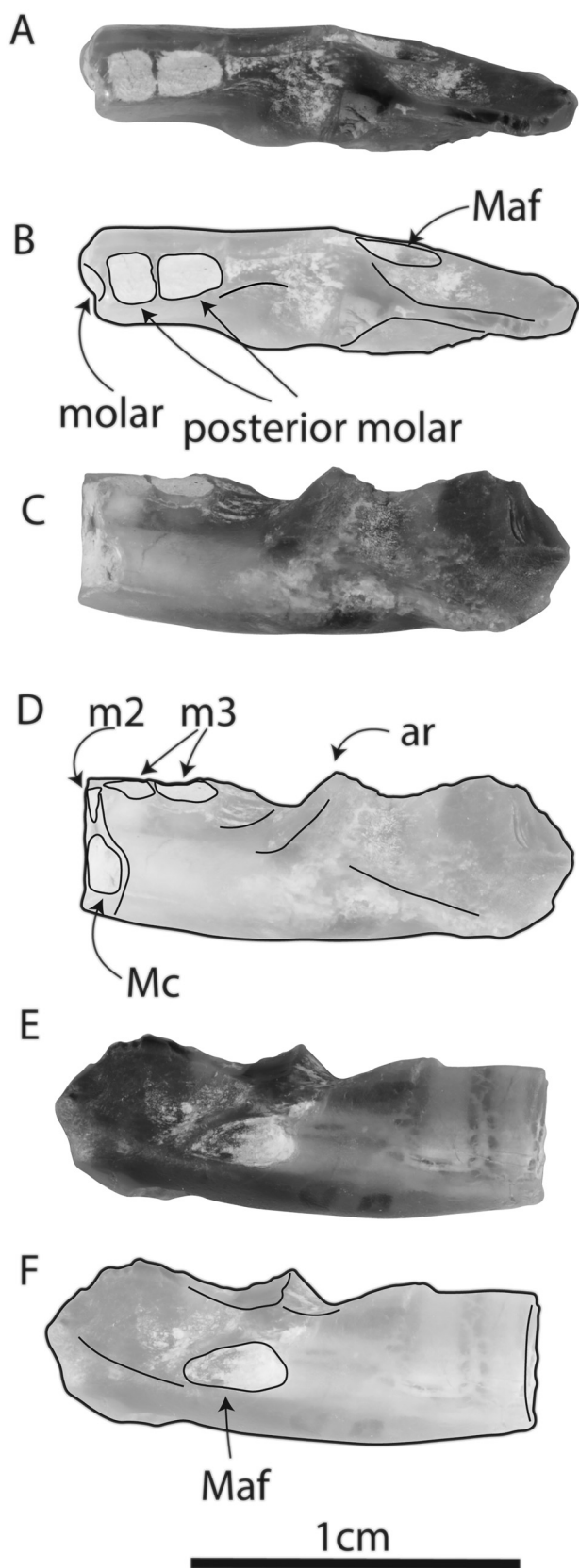


Fig. 5. AM F161198, dentary of *Parvopalus clytiei* gen. et sp. nov. in A, B, occlusal, C, D, buccal and E, F, lingual views. Maf = mandibular foramen. Ar = ascending ramus.

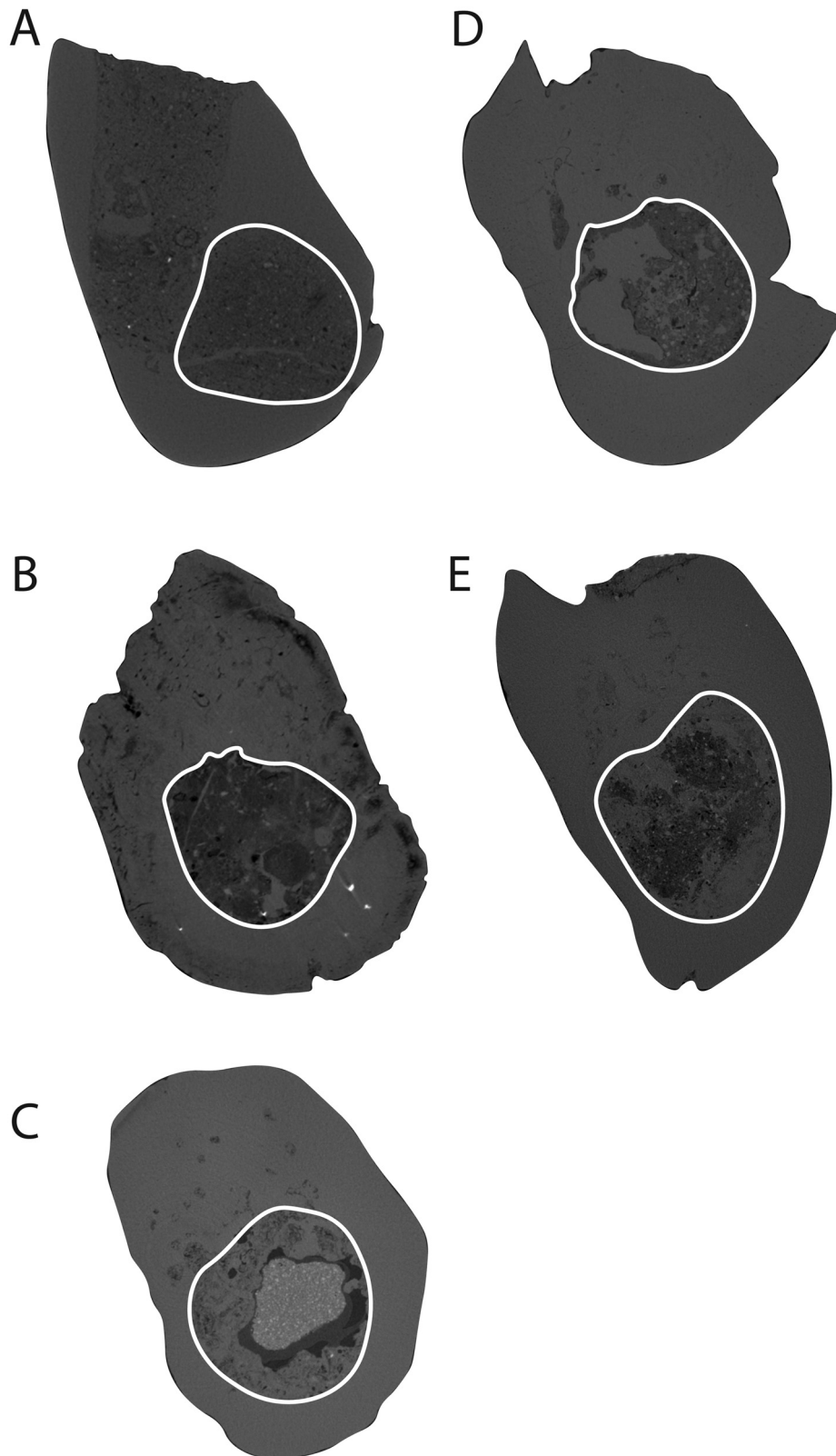
canal, passing the upper part of the canal on its buccal side (Fig. 6A). The mandibular foramen is moderately enlarged (1.6 mm in diameter) and the dental canal is large, being 2 mm in diameter below the posterior of the most anterior molar alveoli. The mandibular foramen is located lingual to the anterior margin of the ascending ramus about half-way between the dorsal and ventral margins of the horizontal ramus. There is no dentary angle. The base of the ascending ramus is stout, and similar in form to that of *Steropodon galmani* (see Archer *et al.* 1992). The remnant of a prominent ridge at the base of the masseteric sulcus is truncated by a break (Fig. 5). The alveoli of the posterior-most molar are located well anterior to the anterior edge of the ascending ramus, as in *S. galmani* (see Archer *et al.* 1992). The prominent mandibular canal enters the horizontal ramus immediately ventral to the leading edge of the ascending ramus.

#### Remarks

*Parvopalus clytiei* is the smallest known mammal fossil from the Lightning Ridge faunal assemblage. The largest molar of the tribosphenidan *Bishops whitmorei* Rich, Flannery, Trusler, Kool, van Klaveren & Vickers-Rich, 2001 (m2) is 1.8 mm long, and this species has an estimated bodyweight of ~40 g (Flannery *et al.* 2022b). The alveoli for the roots of the posterior molar of *P. clytiei* are 3.2 mm in length. Mammalian molar crowns are usually longer than the molar alveoli, thus the posterior molar of *P. clytiei* is likely to have been almost twice as long as the largest molar of *B. whitmorei*. The dentary of *P. clytiei* is deep, unlike the dorsoventrally flattened dentaries of ornithorhynchids (see Flannery *et al.* 2022a).

#### Discussion

The geologically oldest documented monotreme taxon, *Teinolophos trusleri*, from the uppermost Barremian–lowermost Aptian ‘Wonthaggi Formation’ of the Bass Coast in southeastern Australia, suggests that monotremes originated in high-palaeolatitude environments of Australo-Antarctic Eastern Gondwana during or before the Early Cretaceous (Flannery *et al.* 2022a). By the early-Late Cretaceous (Cenomanian, around 30 Ma later), the groups had clearly diversified in multiple lineages represented by Kollikodontidae, Steropodontidae, Teinolophidae and Ornithorhynchoidea. In the early Maastrichtian, at least one monotreme lineage (*Patagorhynchus pascuali*



**Fig. 6.** Cross sections of the mandible scaled to similar sizes. **A**, *Parvopalus clytiei* (AM F161198) at the anterior of m3, **B**, *Steropodon galmani* (AM F161197) in between m2 and m3, **C**, *Dharragarra aurora* (AM F97262) in between m2 and m3, **D**, *Steropodon galmani* (AM F97263) in between m2 and m3, **E**, *Opalios splendens* (AM F132598) in between m1 and m2. The white line indicates the mandibular canal.

attributed to ?Ornithorhynchidae) had reached South America (Chimiento *et al.* 2023). It therefore seems possible that the Turonian altithermal could have facilitated a trans-Antarctic migration of monotremes coincident with other biotic elements, such as angiosperms (Cantrill & Poole 2002).

The fossil record of ornithorhynchids stem spans an interval of some 40 Ma from the Cenomanian to Palaeogene, and is sourced entirely from southern polar habitats (Flannery *et al.* 2022a, Chimiento *et al.* 2023). A chronostratigraphical hiatus in occurrences then occurs from the early Paleocene (~64 Ma) to late Oligocene (26 Ma) (see Woodburne *et al.* 1994). The crown ornithorhynchids *Obdurodon* spp. and *Ornithorhynchus anatinus*, which occur from the Oligocene to today, share a number of synapomorphies including: molars with more than two roots; reduction or loss of the ascending ramus; and presence of an internal coronoid process on the dentary (see Flannery *et al.* 2022a). These are unique to crown group ornithorhynchids, which notably all occurred in higher latitude settings extending up to 15°S (Carrick *et al.* 2008).

Edentulous ornithorhynchids, represented solely by *O. anatinus*, are known only from the Pleistocene to today, while toothed ornithorhynchids are known from the Oligo-Miocene. A limb fragment attributed to *Ornithorhynchus* (AMF 162429) by Rich *et al.* 1991, from the Pliocene Bow Local Fauna of New South Wales (Musser 2013) may represent either *Ornithorhynchus* or *Obdurodon*, or some other taxon. The holotype of *Ornithorhynchus agilis* De Vis, 1885, a junior synonym of *O. anatinus* (Archer *et al.* 1978), is an anterior dentary section lacking teeth from Pleistocene deposits at King Creek near Pilton on the Darling Downs in Queensland. It is the oldest evidence for an edentulous ornithorhynchid. If tooth loss in ornithorhynchids occurred in the Plio-Pleistocene, the lower molar row of ornithorhynchids remained largely unchanged for ~95 Ma, with the m3 being present but highly reduced, and the anterior molars being low-crowned. The advantages of tooth loss in *Ornithorhynchus* are uncertain, but could be linked to dispersal of the Australo-New Guinean Water-rat (or Rakali) *Hydromys chrysogaster* Geoffroy, 1804. This large (*ca* 1 kg) aquatic, carnivorous rodent is of equivalent size to *O. anatinus*. The hydromyid clade originated in New Guinea around 8.5 Ma, with migration of the *H. chrysogaster* lineage to Australia sometime during the Pleistocene (Roycroft *et al.* 2022). The diet of *H. chrysogaster* includes fish, freshwater mussels, parastacid crayfish, spiders and insects

(Woollard *et al.* 1978). *Ornithorhynchus anatinus* alternatively feeds on softer-bodied prey, such as worms, insect larvae and freshwater crustaceans (Bethge 2002). We therefore consider it plausible that competition between the ancestors of *O. anatinus* and *H. chrysogaster* may have trophically displaced harder-bodied prey from the diet of ornithorhynchids. Softer food items are more easily processed with horny pads rather than a battery of molars.

The higher-level mammalian clade diversification occurred during the Jurassic, and a trend for the development of larger body masses was evident by the Cretaceous (Close *et al.* 2015). All mid-Cretaceous and later monotremes are relatively large, the earliest being *Kryoryctes cadburyi* Pridmore, Rich, Vickers-Rich & Gambaryan 2005 and *Sundrius zieglerei* from the lower Albian Eumeralla Formation of Victoria (Pridmore *et al.* 2005, Rich *et al.* 2020). Coeval tribosphenidan mammals are otherwise comparatively smaller-bodied (Flannery *et al.* 2022b), and we suspect might have been present within the Lightning Ridge faunal assemblage but have not yet been detected because of size-related sampling biases. Whatever the case, the only fossil mammals thus far recovered from the Cenomanian deposits of Australia are monotremes, with 10 craniodental fragments (Table 2) and three isolated vertebrae (see Smith 1999, p. 97) recovered from the Finch Clay facies to date.

The Cenomanian Mata Armarella Formation of Argentina is stratigraphically contemporaneous with the Finch Clay facies of the Griman Creek Formation, and was laid down at similar palaeolatitudes (56.5°S: Martin *et al.* 2022). The corresponding Mata Armarella Formation fossil mammal assemblage includes only seven isolated dental fragments, yet these reflect a far more diverse higher-level clade fauna comprising ?Docodonta, Tribosphenida, Meridiolestida and Dryolestida (Martin *et al.* 2022). The docodontan and meridiolestidan are larger-bodied, and similar in size to the monotreme remains recovered from the Finch Clay facies. The absence of comparable lineage abundance, if not representatives of the gondwanatherian, docodontan and meridiolestidan clades in the Cretaceous of Australia, is therefore striking, and

**Table 2.** Number of known specimens per monotreme taxon, Lightning Ridge local fauna.

| Family             | Genus              | Species            | No. of known specimens |
|--------------------|--------------------|--------------------|------------------------|
| ?Teinolophidae     | <i>Stirtodon</i>   | <i>elizabethae</i> | 1                      |
| Kollikodontidae    | <i>Kollikodon</i>  | <i>ritchiei</i>    | 2                      |
| Steropodontidae    | <i>Steropodon</i>  | <i>galmani</i>     | 3                      |
| ?Steropodontidae   | <i>Parvopalus</i>  | <i>clytiei</i>     | 1                      |
| ?Ornithorhynchidae | <i>Dharragarra</i> | <i>aurora</i>      | 1                      |
| Opalionidae        | <i>Opalios</i>     | <i>splendens</i>   | 1                      |

should be expected given the number of specimens now recovered at Lightning Ridge. Indeed, even Early Cretaceous mammal assemblages from high-palaeolatitudes in the Northern Hemisphere have higher relative clade diversity. For example, the Hauterivian–Barremian Ilek Formation in Siberia (~54.2°N palaeolatitude) has yielded up to 38 reported mammal fossils representing potentially five order-level groups including Symmetrodonta, ?Tinodontidae (basal to Symmetrodonta), Multituberculata, Eutriconodonta, and Docodonta (Averianov *et al.* 2005, Lopatin *et al.* 2005, 2009). Likewise, the famous lower Aptian Jehol Biota from the Yixian and Jiufotang formations in China has produced 18 species allocated to four clades: Triconodonta, Multituberculata, Symmetrodonta and Eutheria (Bi *et al.* 2018, Zhou 2014, Mao *et al.* 2021, Wang *et al.* 2022). High southern palaeolatitude climatic and geographical isolation might explain the unusually low clade-level taxonomic diversity in the Finch Clay facies at Lightning Ridge, with these barriers preventing dispersal across the Eastern Antarctic landmass. It is therefore significant that monotremes were an apparently endemic southern polar group, as suggested by their geologically earliest radiations from the Barremian to Paleocene (Flannery *et al.* 2022a).

In closing, a substantial Turonian-to-Eocene chronostratigraphical gap still exists in our understanding of monotreme evolution, from which not a single monotreme fossil has yet been discovered. As a consequence, it is unclear whether a diverse monotreme fauna survived the end-Cretaceous mass extinction event, and subsequently persisted (and perhaps ecologically radiated) prior to the arrival of marsupials in Australia by ~54 Ma (Godthelp *et al.* 1992). Filling this mysterious interval of monotreme diversity and adaptive development should be a primary focus for research in the future.

## Conclusions

- The co-occurrence of six morphologically distinct fossil mammal taxa (three named herein) in the Lightning Ridge faunal assemblage from the Finch Clay facies of the Griman Creek Formation provides the first indication that Australia was home to a hitherto cryptic diversity of monotremes during the mid-Cretaceous (as predicted by Darlington 1957).
- The newly described *Opalios splendens* is annectant between a teinolophid-like ancestral monotreme morphotype and more derived ornithorhynchoids.

- *Dharragarra aurora* demonstrates that the lower molar formula typical of Cenozoic ornithorhynchids was established by the Cenomanian.
- New specimens of *Steropodon galmani*, along with the new small-bodied taxon, *Parvopalus clytiei*, expand current knowledge of morphological diversity in Cenomanian monotremes.
- The loss of teeth in ornithorhynchids may have been related to ecological displacement caused by the arrival of aquatic rodents in Australia during the Pleistocene.

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No potential conflict of interest was reported by the author(s).

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