

The oldest platypus and its bearing on divergence timing of the platypus and echidna clades

Timothy Rowe^{*†}, Thomas H. Rich^{*§}, Patricia Vickers-Rich[§], Mark Springer[¶], and Michael O. Woodburne^{||}

^{*}Jackson School of Geosciences, University of Texas, C1100, Austin, TX 78712; [†]Museum Victoria, PO Box 666, Melbourne, Victoria 3001, Australia; [§]School of Geosciences, PO Box 28E, Monash University, Victoria 3800, Australia; [¶]Department of Biology, University of California, Riverside, CA 92521; and ^{||}Department of Geology, Museum of Northern Arizona, Flagstaff, AZ 86001

Edited by David B. Wake, University of California, Berkeley, CA, and approved October 31, 2007 (received for review July 7, 2007)

Monotremes have left a poor fossil record, and paleontology has been virtually mute during two decades of discussion about molecular clock estimates of the timing of divergence between the platypus and echidna clades. We describe evidence from high-resolution x-ray computed tomography indicating that *Teinolophos*, an Early Cretaceous fossil from Australia's Flat Rocks locality (121–112.5 Ma), lies within the crown clade Monotremata, as a basal platypus. Strict molecular clock estimates of the divergence between platypus and echidnas range from 17 to 80 Ma, but *Teinolophos* suggests that the two monotreme clades were already distinct in the Early Cretaceous, and that their divergence may predate even the oldest strict molecular estimates by at least 50%. We generated relaxed molecular clock models using three different data sets, but only one yielded a date overlapping with the age of *Teinolophos*. Morphology suggests that *Teinolophos* is a platypus in both phylogenetic and ecological aspects, and tends to contradict the popular view of rapid Cenozoic monotreme diversification. Whereas the monotreme fossil record is still sparse and open to interpretation, the new data are consistent with much slower ecological, morphological, and taxonomic diversification rates for monotremes than in their sister taxon, the therian mammals. This alternative view of a deep geological history for monotremes suggests that rate heterogeneities may have affected mammalian evolution in such a way as to defeat strict molecular clock models and to challenge even relaxed molecular clock models when applied to mammalian history at a deep temporal scale.

Mammalia | Monotremata | phylogeny | molecular clock

The timing of divergence of the two living monotreme clades is of general interest because it bears on basal events in mammalian history and provides independent calibration for understanding temporal aspects of the great radiation of therian mammals. Strict molecular clock estimates of the platypus–echidna divergence time range from 17 Ma to 80 Ma (1–11), with most opinions favoring the younger end of the spectrum (Table 1). Recent discoveries of Mesozoic and earliest Cenozoic fossils hint at a far deeper geological history for monotremes (12, 13); however, these fossils consist mostly of isolated teeth and jaws and their precise relationships are controversial. They are generally relegated to positions at the base of the monotreme stem, and viewed as consistent with a relatively recent divergence between the living platypus and echidna clades.

High-resolution x-ray computed tomography (HRXCT) is enabling a systematic reappraisal of these important and controversial fossils by generating new information on the comparative internal structure of the mandible and dentition (14, 15). In this report, we focus on one such fossil, *Teinolophos trusleri*, and describe new information on derived features of its jaw morphology. We also re-analyzed a large data set of morphological characters relevant to basal mammalian phylogeny, and our results shifted the phylogenetic position of *Teinolophos*, from stem to crown Monotremata. The implications of this seemingly minor adjustment are magnified and amplified by the great antiquity of this fossil. As we report below, this adjustment may

broadly affect our understanding of early mammalian history, with special implications for molecular clock estimates of basal divergence times.

Monotremata today comprises five species that form two distinct clades (16). The echidna clade includes one short-beaked species (*Tachyglossus aculeatus*; Australia and surrounding islands) and three long-beaked species (*Zaglossus bruijnii*, *Z. bartoni*, and *Z. attenboroughi*, all from New Guinea). The platypus clade includes only *Ornithorhynchus anatinus* (Australia, Tasmania). At first glance, the platypus and echidnas may seem as different from each other as they are from therian mammals, yet monotreme monophyly is supported by skeletal morphology (17–22), brain architecture (23, 24), facial electroreceptor arrays of unique structure (25), karyotype (26), and mitochondrial (27, 28) and nuclear gene sequences (29). Monotremes are conventionally recognized as the sister clade to therian mammals, and to retain many plesiomorphic mammalian features that were transformed during therian evolution (30, 31).

Challenges to this conventional view were raised recently, when either an echidna or the platypus was found to be phylogenetically nested within, or as sister taxon to, marsupials. Evidence came from sequence analyses of 18S rRNA (32), and both mitochondrial (9, 32–37) and nuclear genes (7, 38, 39). These findings resurrected the obscure “Marsupionta” hypothesis, which contended that monotremes are derived marsupials who secondarily reacquired such ancient characters as ovipary. Formulated in 1947 by the great morphologist W. K. Gregory (17), this hypothesis has been largely disregarded ever since (29, 31). If true, it would profoundly alter the framework in which mammalian history is understood today.

The Marsupionta hypothesis has been unanimously rejected in favor of the conventional view of monotreme–therian relationships in all recent computed phylogenetic analyses that incorporated fossils and large samples of skeletal characters (18–22, 40–43), including our analysis. The molecular arguments favoring Marsupionta have also been challenged. Some analyses did not simultaneously sample both monotreme clades (9, 32), whereas those that sampled both platypus and echidna clades supported the conventional view of monotreme relationships (11, 27–29, 44). Analyses of large concatenated sets of nuclear

Author contributions: T.R., T.H.R., M.S., and M.O.W. designed research; T.R., T.H.R., P.V.-R., M.S., and M.O.W. performed research; M.S. contributed new reagents/analytic tools; T.R., M.S., and M.O.W. analyzed data; and T.R. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

Data deposition: Digital Morphology data have been deposited online at www.digimorph.org (<http://digimorph.org/specimens/Teinolophos.trusleri/216575>, <http://digimorph.org/specimens/Teinolophos.trusleri/216750>, and <http://digimorph.org/specimens/Teinolophos.trusleri/212933>)

[†]To whom correspondence should be addressed. E-mail: rowe@mail.utexas.edu.

This article contains supporting information online at www.pnas.org/cgi/content/full/0706385105/DC1.

© 2008 by The National Academy of Sciences of the USA

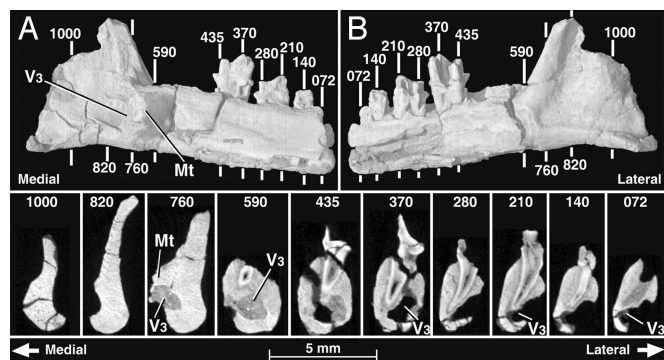


Fig. 2. *Teinolophos trusleri* (NMV P216575). Volumetric reconstruction of left dentary, from HRXCT, in medial (A) and lateral (B) views, and in selected coronal cross sections (slice thickness = 0.019 mm). Medial tubercle (Mt) and mandibular canal (V3) are labeled. Complete CT serial section stacks and volumetric animations are available at <http://digimorph.org/specimens/Teinolophos.trusleri/216575/>.

assemblage was named “Australosphenida,” and this hypothesis of relationships formed the basis for controversial arguments that the tribosphenic molar (57) and middle ear (61, 63) evolved independently in australosphenidans and therians.

For our study, three specimens of *Teinolophos* (specimen numbers: NMV P216750, NMV P216575, and NMV P212933) were scanned at the University of Texas High Resolution x-ray Computed Tomography facility (Figs. 2 and 3). Two were edentulous jaws, and the third was a dentary with three teeth, all from the Flat Rocks locality, Wonthaggi Formation, Bunarong Marine Park, Victoria, Australia, where the type specimen of *Teinolophos* was collected (64). These data were compared with scans of living monotremes including an adult *Ornithorhynchus* and a juvenile still in possession of its deciduous teeth, the fossil platypus *Obdurodon*, the fossil mammaliaform *Morganucodon*, several eutriconodont fossils, several multituberculates, and a large collection of extant therian mammals scanned with HRXCT over the last decade (Fig. 4). The new morphological data were used to modify a large morphological data set published by Luo and Wible (21), which we analyzed using parsimony. Insofar as our results were inconsistent with all strict molecular clock estimates for the echidna–platypus split, we applied three different relaxed clock modes using different

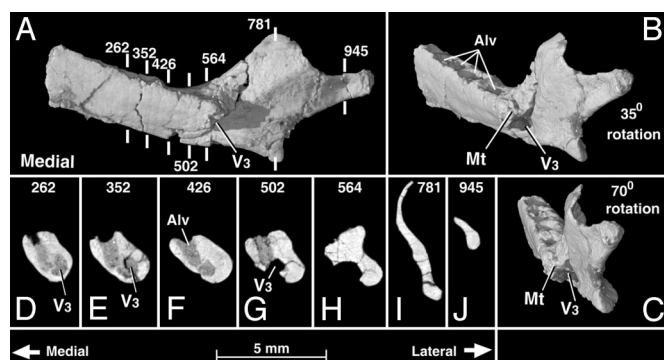


Fig. 3. *Teinolophos trusleri* (NMV P216750). Volumetric reconstruction of right dentary, built from HRXCT, in medial (A) and increasingly oblique views (B and C). (D–J) Selected coronal cross sections (slice thickness = 0.012 mm) of this jaw, with slice sequence positions indicated by numbers and vertical white lines in A to show position of the slice plane. Abbreviations: Alv, tooth alveoli; V3, mandibular canal; Mt, Medial tubercle. Complete CT serial section stacks and volumetric animations are available at <http://digimorph.org/specimens/Teinolophos.trusleri/216750/>.

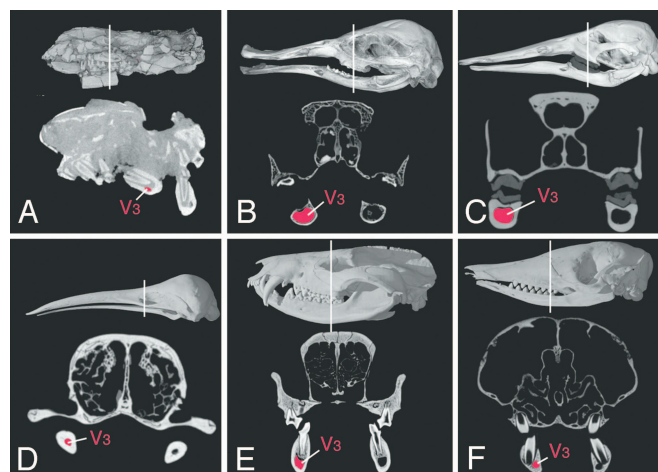


Fig. 4. Comparative diameters of the mandibular canal (in red) shown in HRXCT coronal slice planes, with the location of the slice marked by a white line on three-dimensional reconstructions of complete skulls in lateral view. (A) *Morganucodon* sp. (IVPP 8685), Early Jurassic fossil from China. (B) *Ornithorhynchus anatinus* (AMNH 252512), juvenile specimen still in possession of its deciduous dentition. (C) *Ornithorhynchus anatinus* (AMNH 200255) adult specimen with keratinous adult dentition. (D) *Zaglossus bruijnii* (AMNH 157072) adult specimen. (E) *Didelphis virginiana* (TMM M-2517) adult specimen. (F) *Dasyurus novemcinctus* (TMM M-7417), adult specimen. The mandibular canal is labeled (V3). Images not to scale; scaled imagery and complete CT data sets for each are available at www.DigiMorph.org.

sequences, to evaluate whether any molecular clock models is consistent with the interpretation of a deep geological age for the echidna–platypus divergence. Our matrix, modified character scores, sequence analyses, and methodology are described in [supporting information \(SI\) Text](#).

Results

Our analysis found that *Teinolophos* lies within the monotreme crown, as the most ancient member of the platypus clade, Ornithorhynchidae (Fig. 5). Its precise position among ornithorhynchids was sensitive to different taxon samples, but invariably *Teinolophos* clustered with other ornithorhynchids (see [SI Text](#)). The most compelling evidence to us of its platypus affinities was provided by the HRXCT scans, which revealed the presence of a hypertrophied mandibular canal coursing along the entire length of dentary in a position lateral to the molariform tooth roots, and which exits the ramus medially beneath a large medial tubercle (Figs. 1–3). Among extant mammals, only the platypus has such a hypertrophied canal and medial tubercle (Fig. 4). Whereas diprotodont marsupials have an enlarged canal near the back of the jaw for insertion of the pterygoideus musculature (65), our comparative analysis indicates that only in ornithorhynchids is the mandibular canal hypertrophied along its entire length.

The ornithorhynchid mandibular canal transmits the mandibular artery and hypertrophied mandibular branch of the trigeminal nerve, in support of the electroreceptive bill that gives the duckbilled platypus its common name (66). The bill deploys an array of 60,000 mechanoreceptors along with 40,000 mucous gland electroreceptors. Electroreceptive nerve terminals lie in the ducts of glands that secrete mucous when immersed in water, and they measure electrical profiles of aquatic prey items (25, 67–72). Stimuli received by receptors in the bill are transmitted via comparatively huge mandibular and maxillary branches of the trigeminal nerve to an expansive population of neurons in the S1 somatosensory cortex that are bimodally responsive to both mechanical and electrical signals (25, 69, 70). Echidnas also have

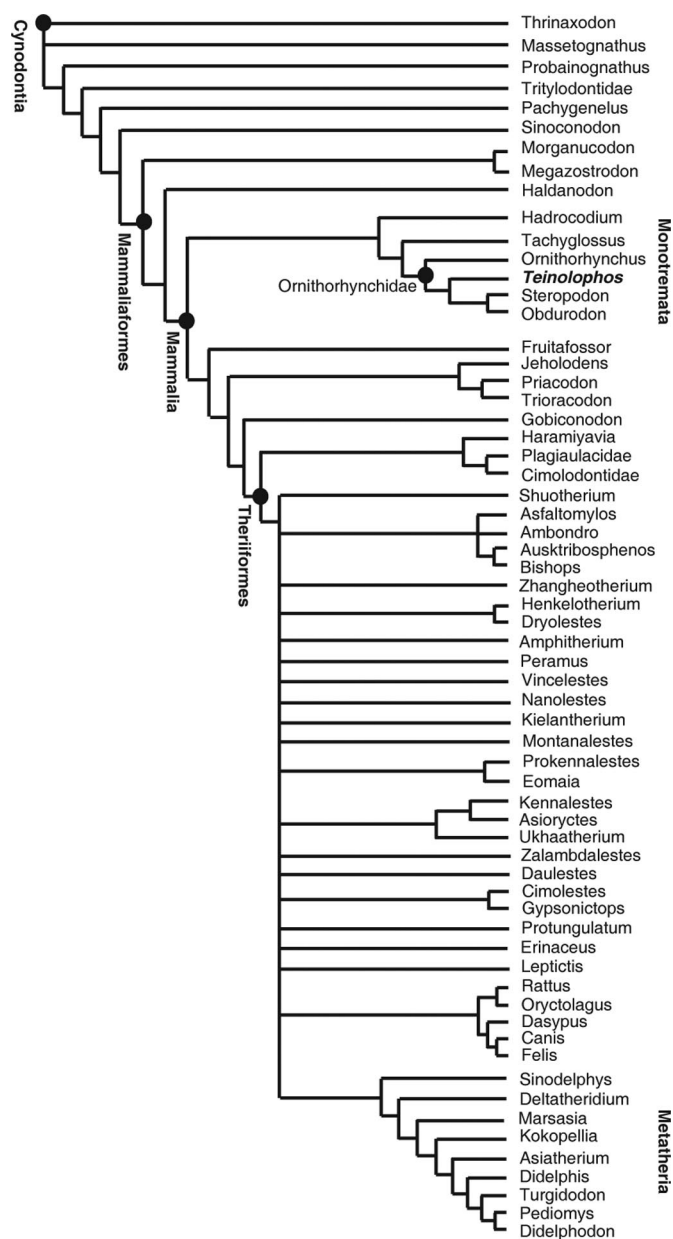


Fig. 5. Cladogram showing relationships of *Teinolophos* to other mammals and their extinct relatives among Cynodontia (see [SI Text](#) for matrix and details of methodology).

electroreceptive capabilities in their beaks (72), but their sensitivity is far less than in the platypus bill. The long-beaked echidnas have only $\approx 2,000$ electroreceptors, whereas the short-beaked echidna has only ≈ 400 (25), which they use in probing moist substrate for food. Both have comparatively narrow mandibular canals, reflecting the plesiomorphic condition that is found in *Morganucodon* and all therians sampled (Fig. 4). Electroreception therefore appears to be an apomorphic characteristic of Monotremata, whereas the evolution of a specialized duckbill for high-resolution aquatic electroreception is unique to the platypus clade. *Teinolophos* preserves the oldest evidence of a duckbill in its hypertrophied mandibular canal.

Our analysis also affirms that the slightly younger (110 Ma) Australian fossil *Steropodon* (12, 73), known from a single broken jaw, is also a platypus. This unique specimen was preserved as an opal infilling of a natural mold, left after the

actual bone and teeth dissolved. However, the dental resemblances to *Teinolophos* and *Obdurodon* are thoroughly documented (40, 41, 59, 60), and it preserves the edge of a large mandibular canal. The Paleocene fossil *Monotrematum* (74), based on three teeth from Argentina, is probably also a member of the platypus clade (Ornithorhynchidae) (31).

Optical data (61) has been interpreted as evidence for the presence of postdentary bones in *Teinolophos*. However, HRXCT data show no evidence of a postdentary trough or postdentary bones, suggesting that *Teinolophos* had a “standard” mammalian middle ear in which the auditory ossicles were separate from the lower jaw and hung suspended beneath the otic capsule, as in the platypus today (75, 76). This finding adds to the mounting evidence (60) that “Australosphenida” is a polyphyletic assemblage, with several of its members (*Teinolophos*, *Steropodon*) belonging to crown monotremes, whereas others (*Ausktribosphenos*, *Bishops*, *Ambondro*, *Asfaltomylos*) clustered consistently with therians. The precise positions of the latter taxa were also sensitive to taxon sampling in our analyses, but invariably they clustered with therian mammals (see [SI Text](#)). Should the Australosphenida hypothesis fail, then so too would assertions based thereupon that the mammalian middle ear and tribosphenic molars evolved convergently (57, 58, 61, 62, 77).

The Flat Rocks locality was dated by using the fission track method at 121–112.5 Ma (64). The finding that *Teinolophos* is a platypus indicates that the platypus and echidna clades diverged during or before the Early Cretaceous. This date is more ancient by a factor of 7 than the youngest, and 50% older than the oldest strict molecular clock estimates (Table 1). The recent characterization of monotreme history as a “long-fuse” clade, whose diversification into platypus and echidna clades postdated the Cretaceous–Tertiary boundary (11), is difficult to reconcile with our more ancient divergence estimate, nor is there evidence of a diversity “explosion” at any time in monotreme history.

Although far older than any previous estimate, the accumulation of anatomical novelty in even the oldest monotreme fossils suggests that our estimate may underrepresent the actual timing of the split between platypus and echidna. Viewing *Teinolophos* and *Steropodon* as platypuses in their ecological aspect suggests that, since the Early Cretaceous, rates of ecological exploitation and morphological diversification among monotremes may have been far slower than is the case in most or all therian clades. The 1,000-fold difference in species diversity found today (5 monotremes vs. 5,362 therian species; ref. 16) may be another indication that monotremes evolved at far slower rates than therians. Several molecular clock studies (6–9) have also suggested the possibility of a molecular evolution rate slowdown in monotremes. A rate slowdown in monotremes will result in estimates for the platypus–echidna divergence that are too young if calibrations are derived from therian taxa with faster rates of molecular evolution.

Given differences in rates of molecular evolution, we applied a relaxed molecular clock method (refs. 78–80; see [SI Text](#)) to reanalyze both the DNA and amino acid sequence versions of van Rheede *et al.*’s (29) data set I for 21 mammalian taxa. Each analysis gave a different estimate. The amino acid data of van Rheede *et al.*’s (29) data set I yielded a point estimate of 88.9 Ma for the platypus–echidna split, with 95% credibility intervals ranging from 130.8 to 55.6 Ma. This result overlaps broadly with the 121–112.5 Ma date for *Teinolophos*. However, the DNA data set of van Rheede *et al.* yielded a point estimate of 79.5 Ma (credibility interval 110.4 to 51.6 Ma). Previously, Woodburne *et al.* (41) reported a relaxed clock point estimate of 63.7 Ma (credibility interval 95.0–39.7 Ma) for the platypus–echidna split based on IGF2 amino acid sequences.

Discussion

Even considering *Teinolophos* as a crown monotreme, the monotreme fossil record remains dismally sparse and open to

interpretation. Our results are consistent with estimates of a Triassic date for the monotreme–therian split (41) (*SI Text*), although as yet we have no Triassic crown-mammalian fossils that would offer direct corroboration. If the new position of *Teinolophos* is upheld, crown monotremes had originated and the platypus and echidna clades were established by the Early Cretaceous.

Monotremes have left only a meager fossil record, but what is known at present is consistent with the view that soon after their divergence, in or before the Early Cretaceous, monotremes settled into rates of molecular and morphological evolution and speciation far slower than in the living clades of therian mammals. Even the monotreme metabolic rates and ventilation rates are much slower than in therian mammals of similar body mass, and their body temperature is lower as well (81). In what measure and to what degree these various rates are coupled or were independently

evolving phenomena remains to be determined. It is also difficult to discern in which respects monotremes are simply expressing plesiomorphic mammalian rates, whether there have been apomorphic slowdowns in monotremes that evolved following their divergence from therians, or to what degree therian history can be characterized by rate accelerations over the ancestral states for mammals. In any case, our results suggest that different mammalian clades were subject to evolutionary rate heterogeneities that are incompatible with strict molecular clocks and difficult to accommodate even when relaxed molecular clock models are applied to mammalian history on a deep temporal scale.

ACKNOWLEDGMENTS. This study was funded by National Science Foundation Grants IIS-0208675 and ATOL 0531767, and the Geology Foundation of the Jackson School of Geosciences, The University of Texas at Austin.

- Clemens WA, Richardson BJ, Baverstock PR (1989) in *Faunas of Australia: Biogeography and Phylogeny of the Metatheria*, eds Walton DW, Richardson BJ, (Austr Gov Publ Serv, Canberra), pp. 527–548.
- Hope RM, Cooper S, Wainwright B, (1989) *Austral J Zool* 37:289–313.
- Westerman M, Edwards D (1992) in *Platypus and Echidna*, eds Augée ML (Roy Zool Soc New South Wales, Sydney), pp 28–34.
- Retief JD, Winkfein RJ, Dixon GH (1993) *Eur J Biochem* 218:457–461.
- Gemmell NJ, Westerman MJ (1994) *Mamm Evol* 2:3–23.
- Cao Y, Janke A, Waddell PJ, Westerman M, Takenaka O, Murata S, Okada N, Pääbo S, Hasegawa M (1998) *J Mol Evol* 47:307–322.
- Kirsch JAW, Mayer GC (1998) *Philos Trans R Soc B* 353:1221–1237.
- Messer M, Weiss A, Shaw D, Westerman M (1998) *J Mamm Evol* 5:95–105.
- Janke A, Magnell O, Wiczorek G, Westerman M, Arnason U (2002) *J Mol Evol* 54:71–80.
- Belov K, Hellman L (2003) *Austral Mamm* 25:87–94.
- Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R, Price SA, Rutter AV, Gittleman JL, Purvis A (2007) *Nature* 446:507–512.
- Archer M, Flannery TF, Ritchie A, Molnar RE (1985) *Nature* 318:363–366.
- Pascual R, Archer M, Jaureguizar EO, Prado JL, Godthelp H, Hand SJ (1992) in *Platypus and Echidna*, eds Augée ML, (Roy Zool Soc New South Wales, Sydney), pp. 1–14.
- Rowe T, Kappelman J, Carlson WD, Ketchum RA, Denison C (1997) *Geotimes* 42:23–27.
- Carlson WD, Rowe T, Ketchum RA, Colbert MW (2003) in *Applications of X-ray Computed Tomography in the Geosciences*, eds Mees F, Swennen R, Van Geet M, Jacobs P (Geol Soc, London), pp 7–22.
- Wilson DE, Reeder DM, eds (2005) *Mammal Species of the World* (Johns Hopkins Univ Press, Baltimore).
- Gregory WK (1947) *Bull Amer Mus Nat Hist* 88:1–52.
- Rowe T (1988) *J Vert Paleo* 8:241–264.
- Rowe T (1993) in *Mammalian Phylogeny*, eds Szalay FS, Novacek MJ, McKenna MC (Springer, New York), pp 129–145.
- Rougier GW, Wible JR, Hopson JA (1996) *Am Mus Novitates* 3138:1–38.
- Luo Z-X, Wible J (2005) *Science* 308:103–107.
- Meng J, Hu Y, Wang Y, Wang X, Li C (2006) *Nature* 444:889–893.
- Macrini TE, Rowe T, Archer M (2006) *J Morph* 267:1000–1015.
- Rowe MJ, Bohringer RC (1992) in *Platypus and Echidna*, ed Augée ML (Roy Zool Soc New South Wales, Sydney), pp 177–193.
- Pettigrew JD (1999) *J Exp Biol* 202:1447–1454.
- Grützner F, Deakin J, Rens W, El-Mogharbel N, Graves JAM (2003) *Comp Biochem Physiol A* 136:867–881.
- Phillips MJ, Penny D (2003) *Mol Phylogenet Evol* 28:171–185.
- Reyes A, Gissi C, Catzeffis F, Nevo E, Pesole G, Sacconell C (2004) *Mol Biol Evol* 21:397–403.
- van Rheede T, Bastiaans T, Boone DN, Hedges SB, de Jong WW, Madsen O (2006) *Mol Biol Evol* 23:587–597.
- Burrell H (1927) *The Platypus* (Angus & Robertson, Sydney).
- McKenna MC, Bell SO (1997) *Classification of Mammals Above the Species Level* (Columbia Univ Press, New York).
- Janke A, Xu X, Arnason U (1997) *Proc Natl Acad Sci USA* 94:1276–1281.
- Zardoya R, Meyer A, (1998) *Proc Natl Acad Sci USA* 95:14226–14231.
- Kumanzawa Y, Nishida M (1999) *Mol Biol Evol* 16:784–792.
- Nilsson MA, Arnason U, Spencer PB, Janke A (2004) *Gene* 340:189–196.
- Penny D, Hasegawa M (1997) *Nature* 387:549–550.
- Penny D, Hasegawa M, Waddell PJ, Hendy MD (1999) *Syst Biol* 48:76–93.
- Vernesson M, Aveskogh M, Munday B, Hellman L (2002) *Eur J Immunol* 32:2145–2155.
- Nowak MA, Parra ZE, Hellman L, Miller RD (2004) *Immunogenetics* 56:555–563.
- Woodburne MO (2003) *J Mamm Evol* 10:195–248.
- Woodburne MO, Rich TH, Springer MS (2003) *Mol Phylo Evol* 28:360–385.
- Ji Q, Luo Z-X, Yuan C-X, Wible JR, Zhang JP, Georgi JA (2002) *Nature* 416:816–822.
- Ji Q, Luo Z-X, Yuan C-X, Tabrum AR (2006) *Science* 311:1123–1127.
- Toyosawa S, O'Huigin C, Figueroa F, Tichy H, Klein J (1998) *Proc Natl Acad Sci USA* 95:13056–13061.
- Murphy WJ, et al (2001) *Science* 294:2348–2351.
- Reisz RR, Müller J (2004) *Trends Genet* 20:237–241.
- Müller J, Reisz RR (2005) *BioEssays* 27:1069–1075.
- Woodburne MO, Tedford RH, Archer A, Turnbull WD, Plane MD, Lundelius EL (1985) *Spec Pub S Austral Dept Mines Energy* 5:347–363.
- Musser AM (2003) *Comp Biochem Physiol* 136:927–942.
- Woodburne MO, Tedford RH, (1975) *Am Mus Novitates* 2588:1–11.
- Woodburne MO, Macfadden BJ, Case JA, Springer MS, Pledge NS, Power JD (1993) *J Vert Paleo* 13:483–515.
- Hopson JA, Crompton AW (1969) *Evol Biol* 3:15–72.
- Kermack KA, Kielan-Jaworowska Z (1971) *Zool J Linn Soc* 50(Suppl 1):103–115.
- Pridmore PA, Rich TH, Vickers-Rich P, Gambaryan P (2005) *J Mamm Evol* 12:359–378.
- Bever GS, Rowe T, Ekale EG, Macrini TE, Colbert MW, Balanoff AM (2005) *Science* 309:1492a.
- Rougier GW, Forasiepi AM, Martinelli AG (2005) *Science* 309:1496.
- Luo ZX, Cifelli RL, Kielan-Jaworowska Z (2001) *Nature* 409:53–56.
- Kielan-Jaworowska Z, Cifelli RL, Luo Z-X (2004) *Mammals from the Age of Dinosaurs* (Columbia Univ Press, New York).
- Rich TH, Vickers-Rich P, Trusler P, Flannery TF, Cifelli R, Constantine A, Kool L, van Klaveren N (2001) *Acta Palaeont Polon* 46:113–118.
- Rich TH, Flannery TF, Trusler P, Kool L, van Klaveren NA, Vickers-Rich (2002) *J Vert Paleo* 22:466–469.
- Rich TH, Hopson JA, Musser AM, Flannery TF, Vickers-Rich P (2005) *Science* 307:910–914.
- Luo Z-X, Cifelli RL, Kielan-Jaworowska Z (2002) *Acta Palaeont Polon* 47:1–78.
- Martin T, Luo ZX (2005) *Science* 307:861–862.
- Rich TH, Vickers-Rich P, Constantine A, Flannery TF, Kool L, van Klaveren N (1999) *Rec Queen Victoria Mus* 106:1–29.
- Gregory WK (1910) *Bull Amer Mus Nat Hist* 27:1–524.
- Zeller U (1989) *U Abh Senckenberg Naturforsch Gesell* 545:1–188.
- Bohringer RC (1992) in *Platypus and Echidna*, ed Augée ML (Roy Zool Soc New South Wales, Sydney), pp 194–203.
- Proske U, Gregory JE, Iggo A (1992) in *Platypus and Echidna*, ed Augée ML (Roy Zool Soc New South Wales, Sydney), pp 204–210.
- Taylor NG, Manger PR, Pettigrew JD, Hall LS (1992) in *Platypus and Echidna*, ed Augée ML (Roy Zool Soc New South Wales, Sydney), pp 216–224.
- Iggo A, Gregory JE, Proske U (1992) *J Physiol* 447:449–465.
- Manger PR, Pettigrew JD (1996) *Brain Behav Evol* 48:27–54.
- Augée ML, Gooden BA (1992) in *Platypus and Echidna*, ed Augée ML (Roy Zool Soc New South Wales, Sydney), pp 211–215.
- Flannery T, Archer M, Rich TH, Jones R (1995) *Nature* 377:418–420.
- Pascual R, Archer M, Jaureguizar EO (1992) in *Platypus and Echidna*, ed Augée ML (Roy Zool Soc New South Wales, Sydney), pp 1–14.
- Rowe T (1996) *Science* 273:651–654.
- Rowe T (1996) in *New Perspectives on the History of Life*, eds Ghiselin M, Pinna G (California Acad Sci, San Francisco), Memoir 20, pp 71–96.
- Rauhut OWM, Martin T, Ortiz-Jaureguizar E, Puerta P (2002) *Nature* 416:165–168.
- Thorne JL, Kishino H, Painter IS (1998) *Mol Biol Evol* 15:1647–1657.
- Kishino H, Thorne JL, Bruno WJ (2001) *Mol Biol Evol* 18:352–361.
- Thorne JL, Kishino H (2002) *Syst Biol* 51:689–702.
- Bech C, Nicol S, Andersen NA (1992) in *Platypus and Echidna*, ed Augée ML (Roy Zool Soc New South Wales, Sydney), pp 134–139.