



## Brain and behaviour of living and extinct echidnas



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### ABSTRACT

The Tachyglossidae (long- and short-beaked echidnas) are a family of monotremes, confined to Australia and New Guinea, that exhibit striking trigeminal, olfactory and cortical specialisations. Several species of long-beaked echidna (*Zaglossus robusta*, *Zaglossus hacketti*, *Megalibgwilia ramsayi*) were part of the large-bodied (10 kg or more) fauna of Pleistocene Australasia, but only the diminutive (2–7 kg) *Tachyglossus aculeatus* is widespread today on the Australian mainland. We used high-resolution CT scanning and other osteological techniques to determine whether the remarkable neurological specialisations of modern echidnas were also present in Pleistocene forms or have undergone modification as the Australian climate changed in the transition from the Pleistocene to the Holocene. All the living and extinct echidnas studied have a similar pattern of cortical gyrification that suggests comparable functional topography to the modern short-beaked form. Osteological features related to olfactory, trigeminal, auditory and vestibular specialisation (e.g., foramina and cribriform plate area, osseous labyrinth topography) are also similar in living and extinct species. Our findings indicate that despite differences in diet, habitat and body size, the suite of neurological specialisations in the Tachyglossidae has been remarkably constant: encephalisation, sensory anatomy and specialisation (olfactory, trigeminal, auditory and vestibular), hypoglossal nerve size and cortical topography have all been stable neurological features of the group for at least 300,000 years.

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### 1. Introduction

The echidnas (short- and long-beaked) belong to the family Tachyglossidae, one of the two extant groups of monotremes, the other being the freshwater semi-aquatic platypus (family Ornithorhynchidae). Extant long-beaked echidnas comprise three species (*Zaglossus bruijnii*, *Zaglossus bartoni* and *Zaglossus attenboroughi*) living only in New Guinea (Flannery and Groves, 1998), whereas the short-beaked echidna, *Tachyglossus aculeatus*, is found in both Australia and New Guinea. The monotremes diverged from the line leading to eutherian mammals at least 125 and possibly as much as 240 million years ago (Musser, 2003; Murphy et al., 2004) (Fig. 1). Apart from their unique significance for mammalian evolution, the nervous systems of modern Tachyglossidae are of interest for several reasons. Firstly, both short- and long-beaked echidnas are suspected to use electroreception within the trigeminal pathways in prey location, as the platypus does (Gregory et al., 1989; Manger and Hughes, 1992; Proske et al., 1998; Pettigrew, 1999). Secondly, the Tachyglossidae have highly specialised

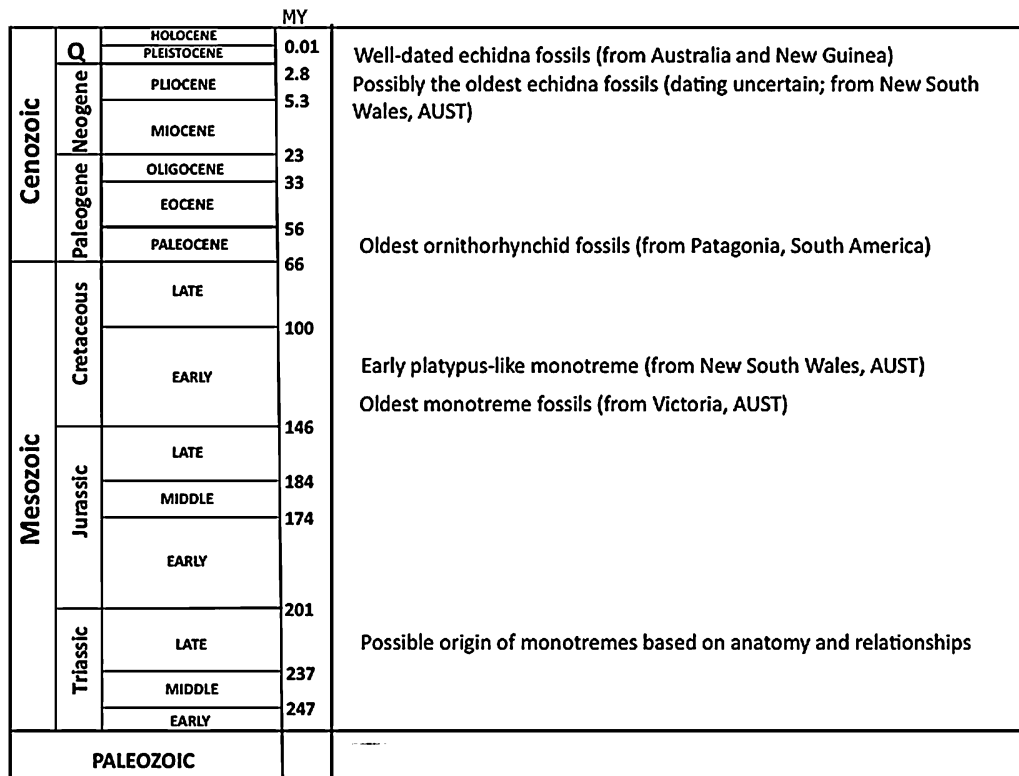
olfactory pathways with gyrified olfactory bulbs (Ashwell, 2006a,b; Ashwell and Phillips, 2006). Finally, studies on the short-beaked echidna show that it has a large gyrified cerebral cortex with motor and sensory areas displaced to the caudal end of the cortical surface (Lende, 1964; Krubitzer et al., 1995; Hassiotis et al., 2003, 2004a,b, 2005) and a large frontal cortical area of unknown function. The gyrified cortex of *T. aculeatus* makes distinct impressions on the interior of the cranial vault so that sulcal boundaries and hence cortical areas can be identified even in dried skulls.

The Tachyglossidae also had representatives among the large fauna of the Australasian Pleistocene (the period from 10,000 years ago to about 2.6 million years ago (mya)), and possibly from the preceding period, the Pliocene (from around 2.6 to 5.3 mya). Fossil limb bones that may be of Pliocene age come from Cooma in New South Wales, although the Pliocene dates are unconfirmed. A posited Miocene date for echidna fossils from Gulgong, NSW (Woodburne et al., 1985) has not been widely accepted, and these bones may instead be Pleistocene in age (Augee et al., 2006).

Pleistocene tachyglossid fossil material includes some well-preserved (and in some cases, well-dated) remains. These include the very large '*Zaglossus hacketti*' (assignment of this specimen to that genus is contentious) (body weight estimated at 30 kg; Johnson, 2006), the slightly smaller *Megalibgwilia ramsayi* (body

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**Fig. 1.** A timeline for monotreme evolution as interpreted from the fossil record and from possible taxonomic relationships. Ages are given in millions of years (MY). Monotremata is a very ancient group whose closest relatives may have been early mammals of Late Triassic–Early Jurassic age. Platypuses (Ornithorhynchidae) and platypus-like monotremes are a much older type than echidnas (Tachyglossidae), with a fossil record that extends back to the Early Cretaceous of Australia. According to the current fossil record, echidnas are primarily a Pleistocene to Holocene group. *Abbreviation:* Q, Quaternary.

Source for geological time scale: Walker et al. (2012).

weight estimated at 10–12 kg; Johnson, 2006), and *Zaglossus robusta*, known from fragmentary remains (possibly referable to *Megalibgwilia*: Griffiths et al., 1991). *Zaglossus* is also known from the Late Pleistocene of New Guinea (see Murray, 1978a,b). In addition, there were ‘megafaunal’ *Tachyglossus* species up to 10% larger than the living *T. aculeatus* (Pledge, 1980). Some *Tachyglossus* fossils are up to 300,000 years of age (Middle Pleistocene: Prideaux, 2006). Large-bodied forms apparently disappeared from the Australian mainland along with other members of the Pleistocene megafauna, so Tachyglossidae in modern mainland Australia is represented only by the diminutive *T. aculeatus* (mean body weight of 3.7 kg). One recent report claims that long-beaked echidnas may have survived in the Kimberley region of north-west Australia until the early 20th century (Helgen et al., 2012). Whether the extinction of large tachyglossids in Australia occurred early or late and was due to human overhunting, climate change and concomitant alteration and reduction of habitat, or some other agency, remains controversial (Johnson, 2006).

There is debate over the taxonomy of extinct long-beaked echidnas. Some palaeontologists follow Griffiths et al. (1991), who divide long-beaked species into two genera, *Megalibgwilia* (the more robust form, with a shorter, somewhat straighter rostrum) and *Zaglossus* (the more gracile form, distinguished by a long and more decurved beak), with different diets proposed for each. Others believe that a single genus, *Zaglossus*, could accommodate all known long-beaked species (e.g., Musser, 2013). Unfortunately, no crania have been found of ‘*Zaglossus*’ *hacketti*, and some palaeontologists believe that, when found, may show this as a distinct genus of long-beaked echidna. Four well-preserved crania have been assigned to *Megalibgwilia* (per Griffiths et al., 1991),

making it possible to ask questions about how the neurology of the Tachyglossidae changed in the transition from the Pleistocene to the Holocene.

Skeletal evidence and field observations suggest that diet and feeding mechanisms differ between the various genera of living and extinct Tachyglossidae (Griffiths et al., 1991). There appears to be some overlap, however, in choice of invertebrate prey recorded between the two extant genera (Griffiths, 1978; Augee et al., 2006; Opiang, 2009). The question of whether dietary specialisations in tachyglossids are reflected in neurological specialisation has never been addressed in detail. Griffiths and colleagues have suggested that the diet of *Megalibgwilia* species consisted of energy-rich scarab beetle larvae of the grasslands of Pleistocene Australia (Griffiths et al., 1991). Climate change causing increased aridity in mainland Australia during the late Pleistocene is believed to have led to their extinction, leaving only the generally myrmecophagous *T. aculeatus*. In fact, Griffiths and colleagues have suggested that the large-bodied *Megalibgwilia* may have been the ancestor of both long- and short-beaked modern echidnas (Griffiths et al., 1991).

Our general aim was to determine whether the unique suite of neurological specialisations of the modern Tachyglossidae was also present in the Pleistocene species, or whether there was a significant change at the end of the Pleistocene. Quantitative analysis and computerised tomography were used to evaluate skeletal material from living and extinct echidnas for evidence of neurological specialisations involving trigeminal, olfactory, auditory and vestibular pathways, as well as control of the tongue. We were interested in determining whether the changing climate of Australia may have induced changes in the neurology of this unique and remarkable group of mammals.

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