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Short communication

History of reptile placentology II: Wilhelm Haacke's 1885 account of lizard viviparity

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ABSTRACT

As viewed from a modern perspective, Wilhelm Haacke's 19th century research on Australian lizards of the genus *Tiliqua* made significant contributions to our understanding of viviparity and placentation in squamate reptiles. He recognized the close structural relationship between the fetal membranes and the uterus through which maternal support of the embryos is accomplished. He also described the placental vasculature, the vestigial nature of the eggshell, and the lack of an egg tooth in viviparous embryos, and challenged the traditional concept of "ovoviviparity." In recognizing that viviparity had evolved independently in reptiles and mammals, Haacke's work foreshadowed the outpouring of research on comparative placentation of the past 50 years.

1. Introduction

The German biologist Wilhelm Haacke (1855–1912) is a notable 19th century zoologist whose scientific contributions are not widely recognized. Haacke is chiefly remembered (if at all) for his demonstration of oviparity in the mammalian echidna (Hall, 1999). However, he also made significant contributions to evolutionary ideas of the late 19th century (Levit and Olsson, 2006). Furthermore, he was among the very first to recognize the structural relationship through which viviparous female lizards sustain their developing embryos—in a description published in *Zoologischer Anzeiger* in 1885.

This paper is part of a series that traces the history of our understanding of reptile placentation–the structural/functional relationship by which pregnant lizards and snakes (squamate reptiles) maintain their developing embryos. The first paper in the series focused on the earliest study of a reptile placenta, published by Cesare Studiati in 1855 (Blackburn et al., 2015). The present contribution considers the second such work, Haacke's (1885a) study of the viviparous Australian shingleback lizard, *Tiliqua rugosa* (Gray 1825). Haacke's work is of particular interest given the important role that studies of Australian lizards have played in our understanding of viviparity and placentation (Blackburn, 2000a; Shine, 2014; Thompson et al., 2002; Weekes, 1935).

2. Haacke's career and contributions

Johann Wilhelm Haacke (Fig. 1A) was a naturalist, teacher, and administrator who published broadly in the zoological and evolutionary literature. Limited information on his life and career is available (Debus, 1968; Levit and Olsson, 2006; Uschmann, 1959, 1966). Born in Lower Saxony, Haacke studied zoology at the University of Jena under the eminent scientist Ernst Haeckel, and earned his doctorate in 1878. Haacke briefly held assistantship positions at Jena (1878) and University of Kiel (1880). In 1881, he emigrated to New Zealand, a common professional destination for German-speaking scientists at that time (Braund, 2005). From 1882 to 1884, Haacke served as the first director of the South Australian Museum in Adelaide. His tenure began in controversy, when he exchanged quantities of the Fijian anthropological collection for natural history specimens, including reptiles (Jones, 1993). In 1885, Haacke joined the Australasian Geographical Society's expedition to New Guinea, a venture that brought biological, geological, and ethnological specimens back to Australia (Dwyer et al., 2015).

Following his return to Germany, Haacke served as director of the Zoologischer Garten in Frankfurt (1888–1893). There he greatly expanded the reptile and bird collections. During summer months, when the monkeys could be housed outside, he converted the monkey house to an outstanding exhibit of (non-avian) reptiles and amphibians. For winter months, he constructed a *Wärmetisch* to keep these ectotherms warm (Niekisch, 2010). In 1890 Haacke defended his *Habilitation* (second thesis) at the Tech-

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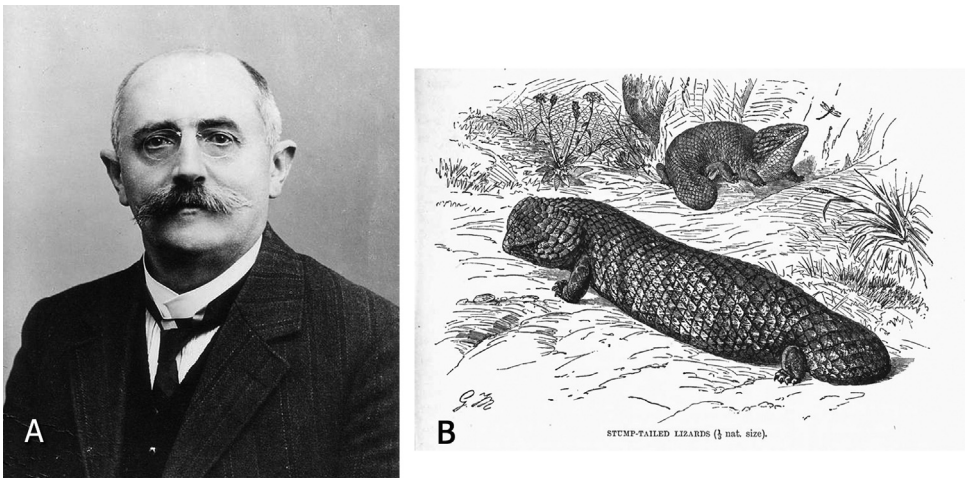

Fig. 1. A. Wilhelm Haacke (1855–1912). B. Contemporaneous illustration of the stump-tailed lizard, *Tiliqua rugosa* (as *"Trachysaurus rugosus"*). From Lydekker (1896).

nische Hochschule in Darmstadt. To gain more time for his writing, he left his position in Frankfurt for one at Darmstadt where he taught zoology as a lecturer for several years. During this period, he advanced a Lamarckian concept of evolution for which he coined the term "orthogenesis," followed by an attempt to reconcile science with religion (Haacke, 1893, 1895). These works caused an irreparable breach with Ernst Haeckel, his former mentor (Levit and Olsson, 2006). Although Haacke had hoped for a professorship in zoology, such a position failed to materialize (Levit and Olsson, 2006). For the remainder of his career, he worked as a school teacher and an independent scholar.

Haacke's biological research was phylogenetically and conceptually diverse. His dissertation and other early work focused on developmental morphology in corals and jellyfish (Haacke, 1879). Following his move to Australia, his research was extended to vertebrates, and he published papers on reproduction and development in reptiles and other animals. These included his documentation of oviparity in the prototherian echidna and his reports of viviparity in a scincid lizard and in a chondrichthyan skate (Haacke, 1883, 1884, 1885b,c). An internet search reveals that among his ensuing publications were a variety of papers on reproduction, physiology, taxonomy, development, genetics, and animal husbandry. He also contributed books on zoology, biogeography, embryology, and mechanisms of inheritance (Uschmann, 1966), in addition to his 3-volume *Das Thierleben der Erde* (Haacke and Kuhnert, 1901) and his aforementioned works on evolution and philosophy.

3. Haacke's reports of viviparity

By the 1880s, little was known about reptile viviparity, and even less about placental structure and function. Live-bearing reproductive habits had been documented in various lizard and snake species, particularly in Europe and the American continents (e.g., see Cuvier, 1829; Duméril and Bibron, 1834-1854; de Jacquin, 1787). However, by the late 1800s, scant information on reproduction in Australian lizards was available (Shea, 2004).

Haacke's (1883, 1885a) accounts of viviparity among Australian lizards – both of which were published in *Zoologischer Anzeiger*—chiefly focused on *T. rugosa* (as "*Trachydosaurus asper,*") which he referred to as the *Stummelschwanzeidechsen* ('stump-tailed lizard') (Fig. 1B). ("*Trachydosaurus*" is now regarded as a synonym of *Tiliqua,* and "*asper,*" is a subspecies of *T. rugosa:* see Cogger, 2014; Cogger et al., 1983; Shea, 1990). Lizards of the species *T. rugosa* are large, slow-moving skinks with robust bodies and short limbs and tails. (For general information, see Bull, 1994; Greer, 1989; Cogger, 2014). They are omnivorous, and occupy a range of terrestrial habitats, including sandy deserts, woodlands, and coastal heaths. Common names for this species include Shingleback (in reference to its large, rough body scales), Pinecone Lizard, and Sleepy Lizard (Uetz and Hošek, 2015).

Haacke determined that female *T. rugosa* give birth to their young after a gestation of about three months. Based on dissections of more than 30 pregnant females, he described a litter size of 1–3 offspring. These figures lie within the range of 1–4 neonates now known to be characteristic of the species (Bull, 1994). Haacke's contributions were presented as supportive responses to a paper on maintenance of this species in captivity (von Fischer, 1882). His rationale was that the combination of viviparity, a long gestation length, and sexual dimorphism made this Australian lizard suitable for transport back to Europe for captive breeding and embryological study. In his second paper, Haacke (1885a) extended his observation of live-bearing reproduction to the Australian lizard to *T. scincoides* (White, 1790) (as "*Cyclodus boddaertii*:" see Cogger et al., 1983), based on the observation of a pregnant female that contained 4 embryos. He also speculated that this pattern occurs within *Egernia* (Gray, 1838) (as "*Silubosaurus*:" for taxonomy, see Cogger et al., 1983; Mitchell 1950; Uetz and Hošek, 2015).

Haacke's reports are among the earliest to describe live-bearing reproduction in Australian lizards. They were preceded by an 1866 report of live-bearing habits in *Tiliqua scincoides* (Krefft, 1866). Although two subsequent sources claimed that *T. scincoides* is actually oviparous (Lucas and Frost, 1893; Lucas and Le Souëf, 1909), the presence of viviparity had already been well- established and was later confirmed (Flynn, 1923). Recognition of viviparity in Australian lizards apparently proceeded slowly over the ensuing decades, since Harrison and Weekes (1925) noted the addition of only 7 more live-bearing species to those that Haacke had documented.

4. Maternal—fetal relationship in *Tiliqua*

Zoologists of the 19th and early 20th centuries often tried to distinguish live-bearing species according to whether or not an eggshell surrounded the embryo as it developed in the maternal reproductive tract (Blackburn, 1994). According to this perspective, live-bearing reptiles were only 'ovoviviparous,' since the females simply retained eggs in their oviducts until hatchling without providing physiological support. By this criterion, only eutherian mammals were to be considered to be truly "viviparous."