

History of reptile placentology, part III: Giacomini's 1891 histological monograph on lizard placentation



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ABSTRACT

By the 1890s, placental arrangements had been documented macroscopically in lizards and fishes, but placental studies on such species lagged far behind research on mammals. In 1891, the biologist Ercole Giacomini (at the University of Siena, Italy) published the first histological analysis of a reptile placenta. Focusing on a placentotrophic lizard (*Chalcides chalcides*) with a morphologically complex placenta, Giacomini documented the histological and cellular bases for placental nutrient transfer and gas exchange. In conjunction with a follow-up study in 1906, he demonstrated that placental structure is correlated with function and can vary dramatically between related species. Giacomini's work was highly influential in showing that placentation in lizards had converged evolutionarily on that of mammals, while establishing reptile placentology as a highly promising area for future research.

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1. Introduction

During the 18th and 19th centuries, evidence for viviparity in diverse vertebrate groups led biologists to explore the means by which pregnant females maintain their developing embryos [1–6]. Although mammals were a major focus of study, viviparous fishes also were shown to have macroscopic specializations for maternal-fetal nutrient transfer [5–7]. In contrast, live-bearing squamate reptiles (lizards and snakes) received very little attention in this regard; their specializations for fetal maintenance were primarily microscopic and therefore difficult to recognize. The advent of histological techniques in the late 1800s began to provide biologists with a mechanistic understanding of how maternal - fetal nutrient transfer was accomplished in reptiles and other viviparous vertebrates [6–13].

In this context, Ercole Giacomini's (1891) work on placentation in the lizard *Chalcides chalcides* [14] represents one of the most important contributions in the history of placentology. Focusing on a lizard with an extreme form of placentotrophy [15], his was the very first study to use histological techniques to reveal the cellular basis for placental nutrient transfer in a reptile. Coupled with a

subsequent study in 1906 [16], he demonstrated that microscopic structure of placentas can correlate with function and vary dramatically between closely related species. During the first few decades of the 20th century, Giacomini's work stimulated a wealth of research on comparative placentation and development. It also helped to establish a placental category that continues to be recognized as one of the most specialized ever to have evolved among reptiles. Nevertheless, Giacomini's placental work is seldom cited in literature from the past 50 years, and his contributions remain unrecognized in the current English-language literature, due to their inaccessibility coupled with barriers of language.

This paper is the third in a series devoted to reconstruction of the history of reptile placentology [17,18]. Having translated Giacomini's 1891 and 1906 placental works from their various presentations in Italian, French, and German [14,16,19,20], herein we summarize their content, significance, and historic contribution to our understanding of placentation in vertebrates.

2. Giacomini's career and scientific contributions

Information on Ercole Giacomini's life and professional career is scarce and scattered. The summary below draws on a retrospective published on the centennial of his birth [21], a commemorative tribute in the *Archivio Zoologico Italiano* [22], an extensive listing in the *Dizionario Biografico degli Italiani* [23], and archival information

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from the University of Bologna and the Unione Zoologica Italiana [24,25].

Ercole Giacomini (Fig. 1) was born in Foligno, Italy, on 19 May 1864, and was the second-youngest of five children. He grew up under humble economic circumstances; his father worked as an artisan and died when Ercole was just 14. In 1885, he enrolled in a program in medicine and surgery at the University of Perugia, where he gained strong interests in zoology and comparative anatomy while studying under Prof. Andrea Batelli. In 1886, while a student at Perugia, he dissected pregnant *Chalcides* (“Seps”) *chalcides* and observed the placental connections that he later studied in detail (see Ref. [14] p. 203 footnote). After a year at the University of Florence, in 1889 he moved to the University of Siena to complete his study program, having been attracted by the reputation of the newly-appointed Professor of Anatomy Giulio Chiarugi. After graduation in 1890, Giacomini began his academic career. He eventually married Chiarugi's sister Erminia, with whom had two sons. During World War I, he served as a volunteer at a military hospital in Bologna.

Giacomini was first appointed as a prosector at the University of Siena, and in 1891 was commissioned to teach anatomy, physiology, and zoology which he did for the next several years. Following a year of teaching anatomy and entomology at the University of Perugia (1903), he accepted the position in Comparative Anatomy at the University of Bologna, where he spent the rest of his career. Although placed in retirement in 1935, he continued to do research and publish until 1939. Throughout his career, Giacomini was very active professionally. He served as secretary of the Academy of Sciences of the Institute of Bologna for more than 40 years. A member of the Unione Zoologica Italiana from its inception in 1900, he served as its president from 1935 to 1937 [26]. He also served as president of the Società Medica Chirurgica of Bologna, and of a local section and the national congress of the Società Italiana di Biologia sperimentale. In recognition of his scientific contributions, Giacomini was awarded a gold medal by the Società Italiana delle Scienze as well as the Gualtiero Sacchetti Prize by the University of Bologna. A street in Bologna bears his name (Via Ercole Giacomini) as does a public square in Foligno, the city of his birth (Piazza Ercole Giacomini) [27]. A volume of the *Archivio Zoologico Italiano* (vol. 40, 1955) was published in his honor, and Giacomini was featured on the cover of the *Italian Journal of Zoology* in 1998 [28].

A comprehensive list of Giacomini's publications [29] reveals that he published nearly 150 papers during his career, between 1888 (midway through his undergraduate career) and 1939. Conducted in the tradition of comparative anatomy, his publications primarily investigated morphology and embryology to address issues of structure and function. His research methods usually involved descriptive anatomy at macroscopic through microscopic levels; however, he also included physiological and other experimental techniques. In his research, he drew upon an extraordinary breadth of research organisms and organ systems [29]. The many aspects that he studied over the years included (a) the digestive tract of reptiles [30]; (b) salivary glands of birds; (c) neuromuscular junctions; (d) avian air sacs; (e) Jacobson's organ and terminal nerve; (f) the sympathetic nervous system in lungfishes (which he discovered); (g) structural homologies of the adrenal system in fishes, amphibians, and other vertebrates [31]; (h) effects of thyroid hormones on amphibian metamorphosis, fish development, and avian plumage; and (i) ovarian structure and function in reptiles, birds, dolphins, and sharks. Much of his other reproductive research is considered below.

3. Historical context

By the late 19th century, viviparity had been widely documented among lizards and snakes [6,32,33], including certain lizards of the skink family [15,34,35]. In addition, Studiati's 1851 study of the viviparous Italian skink *Chalcides chalcides* had revealed that the females ovulate very small (~3 mm) eggs, from which the author inferred that they provide the nutrients for embryonic development via a placenta [15,17]. At the time of Giacomini's 1891 study of this species [14,19], no other non-mammalian vertebrate had been shown to be so highly placentotrophic – making it an ideal species for study. Meanwhile, Haacke's 1888 macroscopic description of the placental membranes in another lizard had raised questions about how oviductal embryos were sustained in viviparous reptiles [18,35].

Giacomini's study of placentation in *Chalcides chalcides* (Fig. 2: Ref. [36]) was the first independent research project of his career, and he soon followed it with several related investigations. These included four papers on the vascular supply to the fetal membranes of reptiles [37–40], one on embryonic withdrawal of the yolk sac

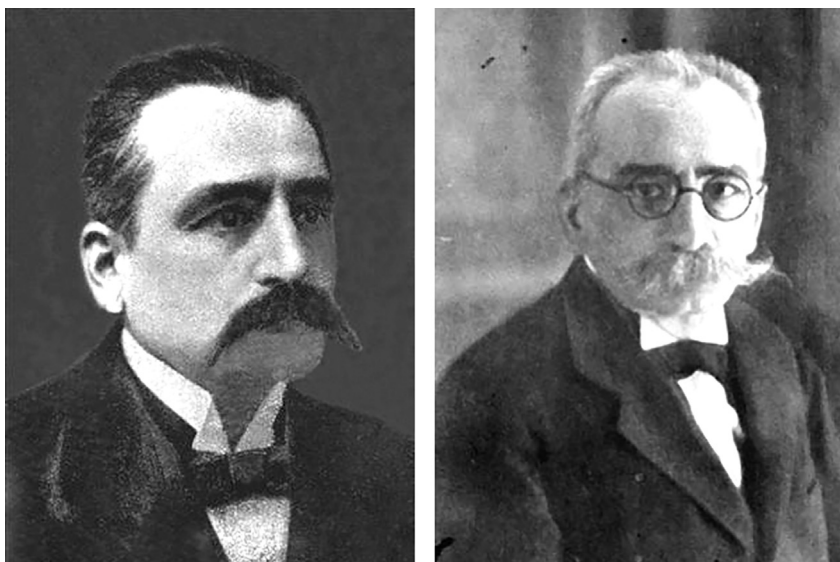


Fig. 1. Ercole Giacomini, at two stages of his career.

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