Commemoration of Comparative Cardiac Anatomy of the Reptilia I-IV

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Abstract
Our understanding of the anatomy of hearts of ectothermic saurosids, or colloquially "reptiles", was much advanced by the publication of the series of four papers under the heading of Comparative Cardiac Anatomy of the Reptilia in Journal of Morphology between 1971 and 1981. Here, I commemorate the papers, show how they moved our understanding forwards, and briefly describe the state-of-the-art.

KEYWORDS
evolution, heart, Varanus

Fifty years ago, in Sydney Australia, Grahame Webb finished his thesis "The squamate heart" that would become the foundation of the first two of ultimately four papers of the classical series "Comparative Cardiac Anatomy of the Reptilia" published in Journal of Morphology (MacKinnon & Heatwole, 1981; Webb, 1979; Webb, Heatwole, & Bavay, 1971; Webb, Heatwole, & de Bavay, 1974). The culmination of Webb’s efforts was the authoritative and single-authored study on the crocodylian heart from 40 years ago (Webb, 1979), while his thesis supervisor Harold Heatwole, would finish the franchise in 1981 with the authoritative study on the coronary vasculature of non-crocodylian ectothermic sauropsid hearts (MacKinnon & Heatwole, 1981).

The first paper focused on the ventricle of the varanid lizards, or monitors, and emphasizes its prominent septa (Webb et al., 1971). Webb et al. were by no means the first to be intrigued by the monitor ventricle. Physiological experiments started by Harrison (White, 1968) and unequivocally completed by Warren Burggren and Kjell Johansen showed that the monitor ventricle is divided into a high-pressure left side and a low-pressure right side, much like that in mammals (Burggren & Johansen, 1982; Johansen & Burggren, 1984). Thanks to these efforts, the monitor heart is now a key case in textbooks on vertebrate anatomy and physiology to understand the evolution of the four-chambered hearts of mammals (Synapsida) and archosaurs (Sauropsida) from the undivided heart of the ancestral amniotes (Kardong, 2006; Randall, Burggren, French, & Eckert, 2002).

Historically Brücke (Brücke, 1852) and Greil (Greil, 1903), had described the salient anatomical features of the monitor ventricle. However, like so many studies in German, these were largely forgotten, or became illegible, as spoken and written English began to dominate over German and French in scientific communication (Buchanan, 1956; Reese, 1915; White, 1959). The value of the work of Webb et al. was the clear prose and bringing together fragmented literature with inconsistent terminology "The terminology used by Harrison is extremely confusing" (Webb et al., 1974). Further, they also brought back poorly appreciated works, including the marvelous study by Greil (Greil, 1903) from which Webb and colleagues reintroduced the German terms such as Muskelleiste for the so-called muscular ridge, or horizontal septum or folding septum, and the term Bulbuslamelle (which Brücke had given the mundane name of meat-pillar, "Fleischpolster" [Brücke, 1852]). Indeed, Figure 9 of Webb et al. (Webb et al., 1974), which was the prime illustration of the Muskelleiste and Bulbuslamelle, is readily comparable to Figure 5 of plate VIII of Greil (Figure 1). These two septa, the Muskelleiste and the Bulbuslamelle, come together during ventricular contraction and thereby separate the pressures of the left and right side of the ventricle.

The deliberate attempt by Webb et al. to revive lost literature, including works in Latin, French, and Russian, also resulted in the second paper of the series (Webb et al., 1974). This article was a critique of nomenclature and although it focused on Squamata and Rhynchocephalia, its findings and recommendations also apply well to studies of
hearts of Testudines (Jensen, Moorman, & Wang, 2014). The value and appreciation of reviving lost literature is acknowledged by later studies on ectothermic sauropсид hearts, also published in Journal of Morphology (Crossley & Burggren, 2009; Jensen, Abe, Andrade, Nyengaard, & Wang, 2010; Lopez et al., 2003; Starck, 2009; Young, Lillywhite, & Wassersug, 1993), as they cite Webb et al. (MacKinnon & Heatwole, 1981; Webb, 1979; Webb & et al., 1971; Webb et al., 1974), Greil (Greil, 1903), and other classics.

In his final contribution (Webb, 1979), the findings on the crocodylian heart spurred Webb to re-evaluate the previous papers (Webb et al., 1971; Webb et al., 1974). While his description of the crocodylian heart still stands (Cook et al., 2017), the re-evaluations of the noncrocodylian ventricle were largely erroneous (see Jensen et al., 2014 for a detailed discussion). Webb (Webb, 1979) emphasized correctly that it was now shown that the left side of the monitor ventricle has higher pressures than the right (Millard & Johansen, 1974), but he inferred that the monitor setting of "increased muscularization of the caym arteriosum ... applies equally to snakes," p. 232. The python ventricle in fact resembles the monitor ventricle functionally and anatomically, although the python ventricle has a particularly reduced caym venosum, but the ventricle of non-python snakes is essentially an elongated variety of the typical lizard ventricle and not like the monitor ventricle (Jensen et al., 2014). Accordingly, it is only in monitors and pythons that the pulmonary systolic blood pressure is substantially lower than the systolic blood pressure of the systemic circulation, whereas in other noncrocodylian ectothermic sauropсидs the ventricle ejects blood with similar systolic pressure into the both circulations (Jensen et al., 2014). Webb (1979) also thought he had misplaced the caym venosum in 1971 and 1974, and now suggested that the caym venosum was the dorsal part of the caym pulmonale, with the boundary between the two being the Muskelleiste. Moreover, what was previously thought to be the caym venosum was now added to the caym arteriosum and the vertical septum became the dorsal part of the Bulbuslamelle. Unfortunately, these revisions overlooked the founding observations of Brücke (1852) that we still follow (Jensen et al., 2014), namely that the caym venosum is the chamber that (a) receives the systemic venous return in diastole and (b) is sealed by the aortic valves. When Webb was told of his erroneous revisions, because it would be discussed in an upcoming review, the clear and unceremonious prose emerged again "1 ... thought I'd screwed up on the original interpretation which I was keen to try and correct. Seems it created more red herrings" (personal communication, BJ, 2013). In Figure 2, I have reproduced Figure 1b of (Webb et al., 1974) which schematizes the relationship of the major septa, cavities, and valves of the noncrocodylian ventricle, which is among the most definitive overviews of existing information on these structures.

Webb’s 1979 paper concluded with hypotheses on the development of ventricular septation from the vertical septum and the membranous septum (and the Muskelleiste which, it was assumed, would not need to remodel much in order to contribute to the full septum; Webb, 1979). These hypotheses centered around positional changes of the vertical septum and the membranous septum. However, there are crucial developmental processes to the formation of the full ventricular septum that were unknown to Webb and, to be fair, most of the community of comparative vertebrate anatomists and physiologist: first, so-called aortic wedging whereby the aorta moves leftward and connects to the left ventricle (rather than the membranous septum moves) and, second, the rightward expansion of the atroventricular canal that ensures that the right atrium maintains communication with the right ventricle (rather than the muscular septum moves; Anderson, Spicer, Brown, & Mohun, 2014; Lamers, Viragh, Wessels, Moorman, & Anderson, 1995). These processes are emphasized by developmental biologists, whereas positional changes to the ventricular and membranous septa, such as suggested by Webb, are not emphasized or mentioned (Anderson et al., 2014). Recent molecular investigations have attempted to settle the origins of the full ventricular septum of mammals (Synapsida) and archosaurs (Sauropsida). Investigations showing a gradient of the transcription factor...
FIGURE 2  Schematic of the ventricular base of a python (Liasis amethistinus), showing the correct position of Muskelleiste (M), Bulbuslamelle (BU, not original label), and vertical septum (beneath the atrial septum [IAS]), which divide the ventricle into the cavum pulmonale (cp) which leads to the pulmonary artery (P), cavum venosum (cv) which leads to the left (L) and right (R) aorta, and the cavum arteriosum (ca). D = dorsal; l = left; LSAV = left leaflet of the atrioventricular valve; r = right; RSAV = right leaflet of the atrioventricular valve; v = ventral. An earlier version of this schematic appeared in Webb’s thesis from 1969, which in turn appears to be based on cartoons of the heart of the Burmese python by Goodrich (Goodrich, 1919), published 100 years ago this year and shown here on the right. dsv, muscles representing dorsal region of septum ventriculorum (vertical septum); ms, muscular interventricular incomplete septum (Muskelleiste).
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