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Classics Revisited

Hans Strahl's pioneering studies in comparative placentation

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ABSTRACT

Hans Strahl, a contemporary of Duval and Hubrecht, made many important contributions to comparative placentation. Despite this he is not well known and some of his original observations tend to be attributed to later authors. Strahl published a classification of placental types based on their shape and relationship to maternal tissues. This greatly influenced the work of Otto Grosser, who became better known in part because his work was more accessible to other scientists and clinicians. Strahl described the development of the fetal membranes across a broad range of mammalian orders extending his observations beyond parturition to the post partum involution of the uterus. He paid close attention to structures designed for histotrophic nutrition including the areolae of moles, haemophagous organs of carnivores and tenrecs and chorionic vesicles of lemurs and lorises. We here provide a summary of some of the most important findings made by Strahl including work on placentation in carnivores and higher primates that remains unsurpassed.

1. Introduction

The introduction of paraffin embedding by Edwin Klebs in 1869 [1] allowed thin tissue sections to be cut and stained. Other innovations included differential staining, the rotary microtome for creating serial sections, and improvements to the microscope such as the introduction of achromatic lenses. Together these technical improvements laid the groundwork for the rapid advances made by embryologists in the late nineteenth and early twentieth century. A.A.W. Hubrecht from Utrecht, Otto Grosser in Vienna, and Mathias Duval in Paris are names familiar to many scientists. In addition, J.P. Hill of London is among those acknowledged by students of marsupial placentation. Equally important, yet largely forgotten, are the contributions of Hans Strahl of Marburg and Giessen (Fig. 1). Strahl made several important discoveries in the realm of comparative placentation that often are credited to later workers. In an attempt to redress the balance, we highlight some of Strahl's findings and assess his standing among contemporaries as well as his legacy. We have kept biographical details to a minimum as a full account is available elsewhere [1,2].

2. Early life

Hans Strahl was born in Berlin in 1857. He lost his father at an early age and was raised by his mother and two close friends of the family; Rudolph Wagener and Nathanael Lieberkühn had the official status of adoptive father and legal guardian. In 1867, all four moved to Marburg where Lieberkühn and Wagener held academic appointments at the Institute of Anatomy. With this background it is perhaps not surprising that Strahl studied medicine and pursued an academic career. He achieved his habilitation at the remarkable age of 24 with a thesis on the early development of reptiles [3]. When Lieberkühn died, Strahl undertook to finish an uncompleted paper on the green border of the dog placenta [4]. Thus began a lengthy period of research on the comparative anatomy of the uterus and placenta. Strahl continued his work at Marburg until 1895, when he was called to the Chair of Anatomy at Justus Liebig University in Giessen.

3. Placentation in carnivores

Strahl completed and illustrated Lieberkühn's paper on the green border of the dog placenta [4] which showed extravasation of maternal blood and uptake of the erythrocytes by tall, columnar trophoblast cells. Although he followed with papers of his own on dog [5,6] and cat [7], and later described the placenta of an African civet (*Civettictis civetta*) [8], Strahl is best remembered for his work on the domestic ferret (*Mustela putorius furo*) [9–11]. He showed that the large blood-filled sacs of mustelid placentae are haemophagous organs equivalent in function to the green border of the dog placenta [10]. Although such organs had been described for the European otter (*Lutra lutra*) and other species by Bischoff [12], the latter erroneously thought they contained fetal blood.

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Fig. 1. Hans August Balthazar Strahl (1857–1920).

A controversial view espoused by Strahl [7] was that uterine epithelium made an important contribution to the structure of the carnivore placenta. In light of the contrary opinion held by contemporary authors, including Duval [13] and Grosser [14] (see also [15]), he chose to revisit the issue in his later paper on the ferret [11]. The conclusion he reached was a compromise in which he envisaged both the uterine epithelium and the trophoblast contributing to the network of cells surrounding the maternal capillaries. More recent authors accept that the uterine epithelium of the ferret undergoes initial syncytialization, forming a multinucleate layer referred to as "symplasma" (e.g. [16]). However, contrary to Strahl [11], they regard syncytialization as a prelude to degeneration of this cell layer. There are multinucleated masses or giant cells close to the barrier that Wislocki and Dempsey [17] argue are maternal, but these are not thought to be epithelial in origin.

4. Placentation in the mole and tenrec

Early embryologists were interested in insectivores because they were regarded as mammals with many primitive traits. Hubrecht [18] chose to work with the European hedgehog (*Erinaceus europaeus*) in which development of the fetal membranes is quite difficult to follow as it is complicated by secondary interstitial placentation of the blastocyst. Strahl [19,20] was more fortunate in choosing the European mole (*Talpa europaea*), where establishment of a yolk sac (choriovitelline) placenta followed by a chorioallantoic placenta is far easier to follow [21]. Among the special features described by Strahl [19] were the areolae (*Plazentardrüse*), which are thought to play an important role in histiotrophic nutrition of the embryo [22]. They are formed of columnar trophoblast above the openings of uterine glands (Strahl's figure is reproduced in ref. [21]).

In addition, Strahl [8] described the placenta of the tail-less tenrec (*Tenrec ecaudatus*) collected on Madagascar by Alfred Voeltzkow. This paper appeared well before the better known description by Goetz [23], although the latter author certainly received better material from Hans Bluntschli. Strahl [8] was the first to describe the prominent haemophagous organ found at the centre of the placental disk and to characterize the presence there of crystals of haematoidin, a breakdown product of haemoglobin. He noted that in addition to the placental disk there was a more diffuse placenta and later used it to illustrate his terminology (see below).

5. The villous placenta of the nine-banded armadillo

Since human placenta is villous, with an intervillous space, it is familiar to students of medicine. Therefore it is often not recognized that this is an unusual placental form. Apart from higher primates, it occurs only in armadillos and anteaters. There the intervillous space is established in unique fashion by villi branching into pre-existing blood spaces in the uterine wall. This was first described by Strahl [24–27] for the nine-banded armadillo (*Dasypus novemcinctus*) and Fernandez [28] for the Southern long-nosed armadillo (*D. hybridus*).

The armadillo membranes are familiar to many scientists through the recent work of Enders [29,30], but there was much interest in the embryology of armadillos a century ago. Then as now the focus was on obligate twinning and discussion was fuelled by the work of Fernandez in Argentina (e.g. [31]) and Newman and Patterson in Texas [32]. An entertaining account of how this research depended on a regular supply of gravid armadillos is given by Garcia [33].

6. The mesoplacenta

In addition to armadillos, Strahl obtained and described some South American rodents. In Azara's agouti (*Dasyprocta azarae*), he showed that the term placenta maintained only a tenuous connection to the uterine wall through a structure he called the mesoplacenta (*Mesoplacentarium*) [34]. This would later be described in greater detail by his pupil Hellmut Becher [35]. One of Strahl's particular interests was involution of the uterus post partum [6], which was the starting point for his classification of placentation [36]. Many hystricognath rodents engage in post partum mating and Strahl [34] noticed that detachment of the mesoplacenta would result in little tissue damage and facilitate the early establishment of a new placenta. Analogous conditions were later found in relatives of the agouti such as the guinea pig (*Cavia porcellus*) [37]. The necrosis in the mesoplacenta observed by Strahl [34] would later be re-interpreted as an apoptotic process [38].

7. Placentation in primates

When Hill [39] reviewed placentation in primates little was known about the placentae of great apes and, indeed, this still is the case [40]. Hill [39] was, however, familiar with the work of Emil Selenka [41,42], who had collected gravid uteri of gibbons and orangutans during an expedition to the Dutch East Indies. When Selenka died in 1902, his legacy was passed to a trio of authors that included the embryologists Hubrecht and Strahl. This resulted in an important publication by Strahl on the placenta of the gibbon (*Hylobates* sp.) and orangutan (*Pongo* sp.) [43]. Because later work has been mainly on delivered placentae, the papers of Selenka [41,42] and Strahl [43] remain our best documentation that interstitial implantation with the formation of a decidua capsularis occurs in all the great apes. The accompanying histology is disappointing and focuses on the structure of the villous trees and fibrin deposition. No attempt was made to characterize the placental bed. Knowledge of trophoblast invasion in the great apes has emerged only recently and data on the orangutan is still needed [40].

In contrast to other primates, lemurs and lorises have epitheliochorial placentation. Once again some of the earliest descriptions of placentae from lower primates were those of Strahl. His paper on a member of Galagidae, the Northern greater galago (*Otolemur garnettii*) [44] was well in advance of the better known study of *Galago demidoff* by Gérard [45]. He showed that it had