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"A new lachrymal gland with an excretory duct in red and fallow deer" by Johann Jacob Harder (1694): English translation and historical perspective

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Summary

The Harderian gland is an enigmatic orbital gland that has been described for many tetrapods, although a consistent definition of this structure has remained elusive. In particular, an unambiguous distinction between the Harderian gland and the nictitans gland, which may both occur in the anterior aspect of the orbit of mammals, remains problematic. These glands were first distinguished in 1694 by Johann Jacob Harder, a Swiss physician and anatomist. To facilitate a renewed examination of the anatomical and developmental relationships of the anterior orbital glands, we review the historical context of Harder's discovery, and provide Harder's original Latin text as well as an English translation.

Introduction

The Harderian gland is a prominent, but enigmatic orbital gland, typically situated deep behind the eyeball. Harderian glands have been described for most terrestrial vertebrate groups, although the homology of the various anterior orbital glands, both among mammals and between the different tetrapod taxa, has remained problematic (Sakai, 1981, 1989, 1992; Chieffi-Baccari et al., 1992; Payne, 1994; Buzzell, 1996; Rehorek et al., 2007). An unusually diverse array of functions have been ascribed to this gland, ranging from ordinary orbital lubrication to pheromone production, extraretinal photoreception and thermoregulation; the Harderian gland has also been implicated in the regional immune response of the upper respiratory tract in some taxa, and it may play a role in the

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vomeronasal sense in others (for reviews and references, see Webb et al., 1992; Payne, 1994; Hillenius and Rehorek, 2005; Rehorek et al., 2006). According to Payne (1994), the Harderian gland is "arguably one of the last remaining large organs of widespread distribution among vertebrates to which we cannot confidently ascribe a confirmed function."

Likewise, the evolutionary history of this gland remains poorly understood, in no small part because of the lingering uncertainties about the homology of these glands among the different tetrapods. In a companion paper we describe the organogenesis of the Harderian gland in deer (Rehorek et al., 2007). That study reveals that the Harderian and nictitans glands of cervids in fact originate from a common inception point, and represent two lobes of a single, heterogeneously developed anterior orbital gland. A future paper will address the issues concerning the homology of the anterior orbital glands of tetrapods. For this purpose, however, it is necessary to revisit the original description of the gland by the Swiss physician and anatomist Johann Jacob Harder, published in 1694. Harder's paper is cited frequently even by recent authors (e.g., Paule, 1957; Sakai, 1989; Olcese, 1992; Payne, 1994), but the only other English translation from the original Latin (Rastogi, 1994) is not widely available. With the publication of Freer and Cunningham's (1996) translation of Wharton's *Adenographia* (1656), and an earlier translation (Steno and Gotfredsen, 1951) of Steno's *De Glandulis Oculorum* (1662), both of which figure prominently in Harder's work, it is appropriate to make available a similar translation of Harder's short, but seminal paper, together with a brief examination of its historical context.

Historical background

By the middle of the 17th Century, when the "Scientific Revolution" at last began to gather momentum, glands became the focus of considerable attention, as they were one of the first organs whose physiological function, long mysterious, suddenly became relatively clear. Until that time, glands had been merely regarded as peculiar clumps of tissue: both the Latin and Greek words for gland derive from the word for "acorn," which they were thought to resemble (Cunningham, 1996). Ancient authors categorized the glands variably by size, shape or texture, and ascribed various vague functions to them: many (e.g., lymph glands) were thought merely to provide support for blood vessels where these divide, and only some (including, for example, the brain) were considered to have some role in the production of fluids. However, during the 1650s and 1660s knowledge of glands rapidly improved as their functions as secretory structures suddenly became clear. Johann Georg Wirsung's discovery of the pancreatic duct, in 1642, is usually cited as the first sign of progress (e.g., Foster, 1901; Cunningham, 1996), but it was Francis Glisson's (1654) realization of the liver's role in the production of bile, and the publication of Thomas Wharton's *Adenographia* (1656), the first comprehensive treatise of the glandular system as a whole, that especially drew attention to these structures. Wharton, building on Glisson's interpretation of the liver as an excretory organ, as well as his own discovery of the duct of the submaxillary gland, redefined the concept of a gland and proposed that glands serve to produce fluids "for nutrition, excretion, and restoration." Physiologically, however, both Glisson and Wharton still retained strongly traditional, Galenic views: they conceived that glandular secretions were produced by "similar attraction" from a "*succus nerveus*," a mysterious fluid supposedly contained within the nerves, and essentially little more than an updated incarnation of Galen's ancient concept of "animal spirits" (Foster, 1901; Brown, 1981; Cunningham, 1996). For example, although Wharton had implicated two orbital glands in the release of tears, he retained the Galenic perspective that the brain was the true source of the tear fluids. Wharton considered the orbital glands themselves too small to be capable of producing such copious fluids: instead, he saw their role as merely to separate the "superfluous fluids" from the "*succus nerveus*" delivered by the brain to the glands via their nerves.

Within just a few years, however, such obscurantist views were rendered untenable and obsolete. Konrad Victor Schneider's (1660–1662) massive, five-volume *De Catarrhis* compiled overwhelming evidence demonstrating that catarrhal secretions do not emanate from the brain but locally from the various mucosae; for example, he pointed out that abnormal mucosal discharges are typically caused by local irritation or inflammation of the specific mucous membranes. In the same manner, Schneider deduced that tear fluids are produced locally as well, although he ascribed that function to the orbital conjunctiva rather than specific tear glands (Marx, 1874). Meanwhile, Franciscus (de le Boë) Sylvius (1660) had pointed out the structural differences between "conglobate" (smooth, i.e., lymphatic) glands and "conglomerate" (compound) glands, which distinction led Sylvius' student Nicolaus Steno (1662), who