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Review

What is the molluscan osphradium? A reconsideration of homology

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ABSTRACT

The relationships among the living classes of molluscs have remained contentious, in part because of a lack of consistent morphological characters that unequivocally unite clusters of taxa within this extremely disparate phylum. The osphradium, a chemosensory organ on or near the gills, is a putative potential synapomorphy of Mollusca. Although the osphradium regularly appears on illustrations of hypothetical unifying molluscan bauplans, the homology of these putative sensory structures has been debated in most classes. Considered examination of the evidence for homology based on development, ultrastructure, neural architecture, and function, demonstrates a lack of support for inferred homology among the varied structures described as 'osphradia'. Neuroanatomical features are increasingly recognized as important for resolving deep phylogenetic divergences. The construction of morphological character sets for phylogenetic inference is dependent on robust determination of homology. Naming a structure does not underwrite its relationship to any other sensory organ. A fundamental assumption that one clade is 'primitive' may have biased the interpretation of anatomical results by early, and even some contemporary researchers, leaving the equality among important characters in doubt. Although these various sensory structures are no doubt real anatomical features, we question the assumption that there is a single molluscan osphradium and propose that at least two distinct classes of epithelial sensory structures have been identified as the molluscan osphradium. The complex suite of characters that describe the many varied sense organs in the mantle cavities of molluscs, may yet provide a foundation for neurophylogenetic insights to molluscan evolution.

Contents

1. Introduction 14
2. The molluscan osphradium 15
3. Evidence for and against homology 16
   3.1. Innervation and neural architecture 16
   3.2. Position 16
   3.3. Function 17
   3.4. Morphology – shape and form 18
   3.5. Development 18
   3.6. Ultrastructure 19
4. Discussion 19
   Acknowledgments 20
   References 20

1. Introduction

Sensory structures in animals represent a crucial interface between organism and environment; the nervous system as a whole represents a pipeline linking morphology, physiology, and ultimately behavior. Sensory structures are therefore subject to adaptive or selective pressure at several levels. There is also a

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clear case that neural structures are energetically expensive and therefore there is strong pressure for organisms to retain useful structures that provide a net benefit (Niven and Laughlin, 2008). But convergences among sensory features occur at deep and shallow phylogenetic levels, such as the eye structures among many phyla including cephalopod molluscs and vertebrate chordates.

The molluscan osphradium is a sensory structure found in the mantle cavity of most living molluscs, broadly characterized as a pigmented patch of epithelium on or adjacent to the ctenidia (gills). There are few anatomical features that can readily be compared directly between different classes of molluscs, so a potential uniquely molluscan sense organ should be of great interest to molluscan phylogeny. Inter-relationships among major molluscan clades remains contentious (Sigwart and Lindberg, 2015) and different data- and taxon sets produce well-resolved yet mutually contradictory topologies (Smith et al., 2011; Stöger et al., 2013; Zapata et al., 2014). Variable structures identified as 'osphradia' have been reported in six of the eight living classes of molluscs.

There appears to be little questioning that these characteristic mantle cavity features are homologous where they are seen in closely-related species and clades (Haszprunar, 1987a; Salvini-Plawen, 1972; Sigwart et al., 2014). Yet homology of the 'osphradium' between and even within some classes has been long questioned (Haller, 1882a; Lankester and Bourne, 1883; Pelseneer, 1899; Yonge, 1947; Bayne et al., 1976; Kraemer, 1979). Arguments for or against osphradial homology are typically based on comparisons of position, morphology, neuro-wiring, development, and function (e.g., Haszprunar, 1987a) – classic approaches to determining homology (see Hall, 1994 and references therein). While many early workers (Lankester, 1883; Nicholson and Lydekker, 1889; Pelseneer, 1906) were reluctant to include the osphradium as a feature of the molluscan ancestor or archetype (Lindberg and Ghiselin, 2003), more recent authors in the 20th century (Yonge, 1947; Morton, 1958; Seed, 1983; Salvini-Plawen, 1981; Haszprunar, 1987a) argued for the homology of osphradia between molluscan classes. If correct, this would identify the osphradium as a symplesiomorphy within the Mollusca.

The debate on how homologies can be inferred is complex and continues to the present (Patterson, 1982; Roth, 1984; Mindell and Meyer, 2001; McCune and Schimenti, 2012). Early researchers' reluctance to consider the osphradium as a unified homologous and ancestral feature was due to the confusing patterns they saw in its variation and distribution among the Mollusca. That is, it was a reflection of genuine doubt of similarity rather than archaic views of what constitutes a homologous structure.

Most textbook descriptions of phylum Mollusca include mention of the osphradium as a pigmented chemosensory epithelium patch in the mantle cavity, though many authors note the anatomical variability or lack of evidence regarding function (e.g., Brusca and Brusca, 2003). These repeated claims are not supported by primary evidence, neither in terms of implied common ancestry, nor indeed empirical evidence of function. Here we revisit the characters and arguments for homology of the molluscan osphradium by reviewing six lines of evidence useful in determining homology: innervation and neural architecture, position, function, shape and form, development, and ultrastructure. We find the epithet 'osphradium' to be only a generalized term for sensory epithelium in the mantle cavity. The homology of structures under this name does not stand up to close scrutiny.

2. The molluscan osphradium

The osphradium was first described by Lacaze-Duthiers (1872) as 'organe special' in the hygrophilians *Lymnaea* and *Physa*. Spengel (1881) expanded taxonomic coverage when he surveyed similar pigmented patches on the mantle epithelium in other gastropod groups, several bivalves, and chitons. In the first paragraph of his article Spengel (1881) committed to an hypothesis that these pigment patches represented olfactory sense organs. He constructed an argument that comparative neural architecture among molluscs was indicative of the common ancestry of Mollusca, and the olfactory sense organs were one aspect of that thesis. Spengel (1881) primary challenge was to create a comparative context to accommodate streptoneury in gastropods and its arising asymmetry; the organization of sense organs is one line of evidence in that investigation. Several subsequent authors referred to these pigment patches as 'Spengel's organ' and the term 'osphradium' was later coined by Lankester (1883) using a term from the Greek for 'strong scent'.

The molluscan osphradium is the most ubiquitous and well-studied of the mantle cavity sense organs (Spengel, 1881; Yonge, 1947; Kohn, 1961; Haszprunar, 1985a; Lindberg and Ponder, 2001). However, this prominence is largely based on their occurrence in the Gastropoda. Of the 280 papers recorded in Web of Science®, 79.3% are based on studies of gastropods. Thus, our knowledge of the molluscan osphradium is strongly biased by a single clade – the Gastropoda and there is always the danger of considering what is common to also be primitive (Wiley, 1981). However, we are fortunate to have an excellent comparative survey of the molluscan osphradium across the whole phylum afforded by the work of Haszprunar (1985a,b, 1987a,b).

The definition of the osphradium has been flexible. Even the original descriptive work of Spengel (1881) incorporated enlarged but unpigmented epithelia in the vicinity of the gills as part of the general patterns of sensory features. When present, the osphradium position in the mantle cavity can be highly variable. In Gastropoda they are located on the ventral surface of the pallial cavity in basal patellogastropods, but are positioned on the dorsal surface of the cavity in other gastropods (Ponder and Lindberg, 1997). In the vermiform aplacophoran molluscs (two classes, Caudofoveata and Solenogastres), the putative osphradium is not even located in the mantle cavity but rather outside of it on the posterior edge of the dorsal surface of the animal (Salvini-Plawen, 1972). Only in the bivalves are the osphradia relatively conservative in their morphology and position throughout the group (Haszprunar, 1987a), as a pair of pigmented or unpigmented epithelium at the base of the ctenidia on or near the visceral ganglia. In chitons, the order Chitonida has putative osphradia on either side of the anus (adanal sensory stripes), though there is uncertainty about the homology of polyplacophoran gills and other molluscan ctenidia (Spengel, 1881). The more plesiomorphic clade of chitons (Lepidopleurida) possesses a different pigmented sensory organ in the anterior mantle cavity which has been rejected as an osphradium based on differences in position and ultrastructure (Sigwart et al., 2014). (Yet the lepidopleuran Schwabe organ is not particularly more different in structure or innervation to 'real' osphradia than all the other various structures referred to by that name.) In cephalopods, only *Nautilus* has an osphradium and in fact has two different putative types: the 'inner or medial osphradium' a fused paired structure on the surface on the body median behind the anus, and the 'outer osphradium' pair at the posterior base of the gills (Willey, 1902). Osphradia are entirely absent in two classes, Scaphopoda and Monoplacophora, and are also absent from several large subclasses – coleoid cephalopods, some heterobranch gastropods, and lepidopleuran polyplacophorans. For a feature considered to be plesiomorphic for the phylum, there is no osphradia in two living clades that are often considered to be two of the earliest-derived clades among molluscs with Cambrian origins: monoplacophorans and basal polyplacophorans.