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[REVIEW]

What Are Head Cavities? — A History of Studies on Vertebrate Head Segmentation

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Motivated by the discovery of segmental epithelial coeloms, or "head cavities," in elasmobranch embryos toward the end of the 19th century, the debate over the presence of mesodermal segments in the vertebrate head became a central problem in comparative embryology. The classical segmental view assumed only one type of metamerism in the vertebrate head, in which each metamere was thought to contain one head somite and one pharyngeal arch, innervated by a set of cranial nerves serially homologous to dorsal and ventral roots of spinal nerves. The non-segmental view, on the other hand, rejected the somite-like properties of head cavities. A series of small mesodermal cysts in early *Torpedo* embryos, which were thought to represent true somite homologs, provided a third possible view on the nature of the vertebrate head. Recent molecular developmental data have shed new light on the vertebrate head problem, explaining that head mesoderm evolved, not by the modification of rostral somites of an amphioxus-like ancestor, but through the polarization of unspecified paraxial mesoderm into head mesoderm anteriorly and trunk somites posteriorly.

Key words: embryo, evolution, head cavities, head segmentation, mesoderm, vertebrates

INTRODUCTION

The study of vertebrate morphology started with the question of body segmentation centered on the composition of the head; namely, whether the vertebrate head is composed of vertebra-like segments (reviewed by Veit, 1947; Wedin, 1949b; Kuratani, 2003). In comparative embryology, segmentation was expected primarily in the head mesoderm, or more precisely, mesodermal coelomic cavities (reviewed by Adachi and Kuratani, 2012; Onai et al., 2014). Even if the segments were absent in the adult vertebrate head, vestigial segments were expected to arise in the embryo as a recapitulated signature of the ancestral morphological pattern (Huxley, 1858).

To understand the long history of vertebrate head segmentation, one must note two important backgrounds. One is "the Vertebral Theory", which was initially proposed by Goethe and Oken (Goethe, 1790; Oken, 1807). They and many contemporary anatomists regarded the vertebrate skull as a modification of several vertebrae, and their somewhat idealistic notion has profoundly affected the study of vertebrate head segmentation in the centuries that followed (Owen, 1848; Goodrich, 1930; Holland et al., 2008). The other, which has been referred to as "elasmobranch worship", is the belief that elasmobranch embryos show the most general vertebrate body plan, and is characterized by a tendency to use shark and skate embryos as representative of the basic and/or ancestral morphological patterns in vertebrates (Gee, 1996; see also Gillis and Shubin, 2009). This trend was originally introduced by Gegenbaur (Gegenbaur, 1871, 1872), and later enhanced by the studies of Balfour, Marshall, and van Wijhe, who described head cavities in elasmobranch embryos.

Head cavities, or epithelial mesodermal coeloms in the head, typically found in the elasmobranch pharyngula (Fig. 1A), are structures thought to represent serial homologs of somites. Based on this assumption, the vertebrate head was suggested by some authors to consist of units equivalent to somite-derivatives, as we see in the reproduction of the famous scheme by Goodrich (1930; Fig. 1B). However, there also exist counter opinions to this view, and the debate continues today (Holland et al., 2008; Kuratani, 2008; Northcutt, 2008). Herein, we review historical studies regarding vertebrate head segmentation, particularly focusing on several biologists (Balfour, Marshall, Götte, van Wijhe and Platt) who performed epoch-making discoveries contributing to this debate, and highlight unresolved issues concerning the elasmobranch head and recent molecular works that have addressed this intricate problem.

Balfour

Francis Balfour, a British comparative embryologist, was the first to report on the mesodermal coeloms in the vertebrate embryonic head. He studied the development of

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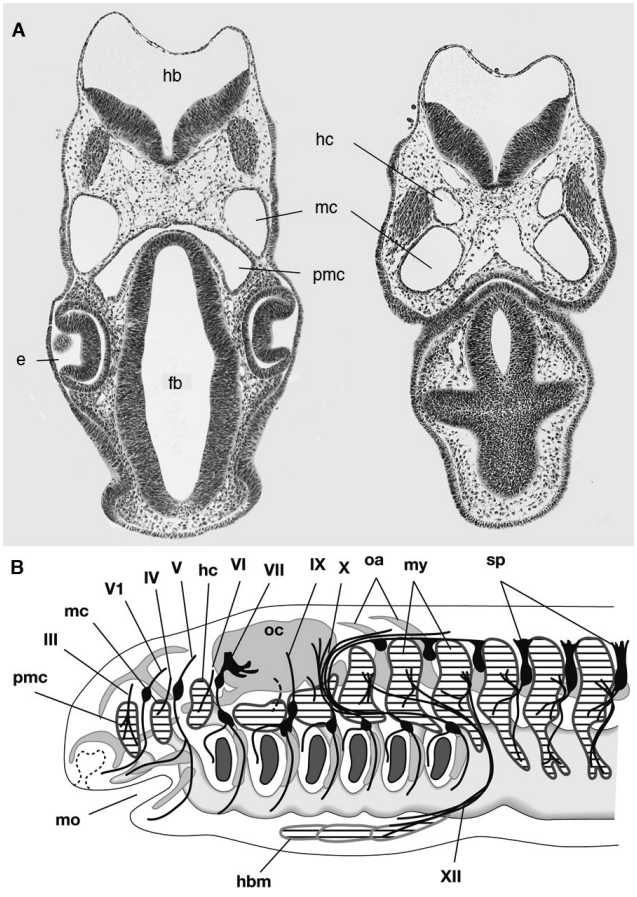


Fig. 1. Head cavities and head segmentation of vertebrates. **(A)** Histological observation of head cavities in *Scyliorhinus* pharyngula. Transverse sections at two levels. Note that the premandibular cavities are connected at the midline. e, eye; fb, forebrain; hb, hindbrain; hc, hyoid cavity; mc, mandibular cavity; pmc, premandibular cavity. **(B)** Head segmental scheme by Goodrich (1930). Preotic mesodermal segments (pmc, mc, hc) are shown as rostral continuation of postotic somitic segments (my). Two segments below the otic capsule (oc) are obliterated in this interpretation. Redrawn from Goodrich (1930).

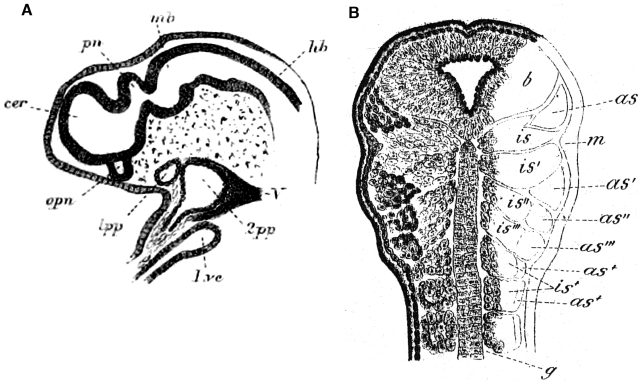


Fig. 2. Discovery of mesodermal segments in vertebrate embryos. **(A)** The first description of head cavities in shark embryos by Balfour in a paper published in 1878, as well as in a monograph published the same year. Parasagittal histological section. Premandibular and mandibular cavities are labeled as 1pp, 2pp, respectively. The first pharyngeal pouch is labeled as 1vc. Balfour initially called these the "preoral" and "postoral" segments. The hyoid cavity is not shown. From Balfour (1878). **(B)** Head segments in a frog embryo described by Götte. Labeled "is" and "as" are the medial and lateral parts of the head segments, respectively. In the rostral part of this illustration the lateral elements (as, as', as'', and as''') appear to correspond to neural crest-derived ectomesenchyme and the medial (is, is', is'', and is''') to the mesodermal components. In the posterior part, however, the lateral (is†) and medial (as†) divisions appear to show dermomyotomes and sclerotomes. From Götte (1875).

sharks and skates, and his research was published in separate papers in multiple volumes of the *Journal of Anatomy and Physiology* from 1876 to 1878. According to Balfour, the early pharyngula (Balfour's stage F) of a shark develops three pairs of coeloms in the head, along the anteroposterior axis (Balfour, 1874, 1876, 1877, 1878; Fig. 2A). He observed that these cavities were formed of two epithelial layers that arose by delamination of mesoderm, similar to the coelomic cavity and somites in the trunk. Therefore, he regarded these cavities in the head as a rostral continuation of the mesodermal coelom in the trunk (including somites). Head cavities were compared, not only to somites (paraxial mesodermal elements), but also to lateral plate-derived coelom in the trunk.

The three pairs of head cavities are apparently separated from each other by pharyngeal pouches, thereby exhibiting metamerical arrangement (Fig. 2A). The rostralmost head cavity, or the premandibular cavity, is located adjacent to the eye, and Balfour thought it gave rise to all the extrinsic eye muscles (Balfour did not trace the later development of premandibular cavity, nor observe that the posterior two cavities differentiate into eye muscles). Regardless, presence of the head cavities led Balfour to the idea of head segmentation, which first arose in early mesodermal patterning, not in cartilaginous anlage of vertebrae-like structures as discussed by Huxley (1858).

In Balfour's scheme of head segmentation, all the cranial nerves were arranged anteroposteriorly, not distinguishing branchiomeric and eye muscle nerves. The latter groups of nerves (cranial nerves III, IV, and VI) were all thought to belong to one single segment, without exception. This was consistent with his belief that all the extrinsic eye muscles were derived from one head cavity. For other cranial nerves, Balfour thought that each nerve should be assigned to a single pharyngeal arch, representing a modified spinal nerve. Thus, the vertebrate head was thought to consist of metameres (head segments) that contained one pharyngeal arch, a somite-homolog and its derivatives, as well as a spinal nerve homolog. For him, the somitic metamerism (somitomerism) coincided perfectly with the metamerism of the pharyngeal arches, explaining why he designated the head cavities as premandibular, mandibular, and hyoid cavities, corresponding to the pharyngeal arches. The discovery of the head cavities and embryological schematization of the vertebrate head by Balfour triggered the second phase of controversies regarding head segmentation of vertebrates.

Marshall and Götte

In general, it is still acknowledged that the head cavities serve as the source of extrinsic eye muscles, although this has not been experimentally demonstrated to date (Platt, 1890, 1891a, b; Johnson, 1913; Fraser, 1915; Neal, 1918; Wedin, 1953a, b; Bodemer, 1957). Nevertheless, there are

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numerous papers that described the histological development of these muscles from the head cavities (reviewed by Neal, 1918a). There are six extrinsic eye muscles (two obliquus and four rectus muscles) in jawed vertebrates, innervated by three cranial nerves (cranial nerves III, IV, and VI).

In the shark, all three head cavities are believed to differentiate into extrinsic eye muscles. Namely, the premandibular cavity gives rise to inferior oblique, superior rectus, internal rectus, and inferior rectus muscles innervated by the oculomotor nerve (cranial nerve III); the mandibular cavity differentiates into the superior oblique muscle innervated by the trochlear nerve (cranial nerve IV); and the hyoid cavity gives rise to the lateral rectus muscle innervated by the abducens nerve (cranial nerve VI). Marshall (Marshall, 1881; Marshall and Spencer, 1881) was the first to recognize the metameric relationships between the head cavities and the cranial nerves that innervate their derivatives, which he compared to the relationship between myotomes and spinal nerves in the trunk. Pharyngeal arches, on the other hand, were thought by Marshall to represent another type of metamerism unrelated to the somite-associated metamerism. He observed that the pharyngeal arches were divided via protrusion of pharyngeal pouches, which was different from the manner of head cavity development. In this regard, he first recognized the independent formation of head cavities from pharyngeal arches.

Since Balfour, a number of comparative embryologists attempted to find mesodermal coeloms in the vertebrate embryonic head to schematize the morphological plan of the head. This led to Goodrich's famous segmental scheme in the early 20th century (Goodrich, 1930; Fig. 1B). The idea of a simple metamerical head inevitably urged morphologists to compare the embryonic morphotype of vertebrates with that of the amphioxus whose "somites" extend to the rostral tip of the body.

Balfour was not the first to refer to the segmental units in the vertebrate head, although he first discovered the head cavities. Before Balfour, a German embryologist, Götte (1874–1875), discovered four pairs of segments in the head of a frog embryo (Fig. 2B). According to Götte, the frog embryo has two pairs of segments in front of the otic vesicle (preotic region) and two posterior to the vesicle, and these segments are further divided into lateral and medial components. If the latter is true, the two postotic segments should represent true somites that will differentiate into occipital cartilage. Then, to which of the three segments in the shark embryo will the remaining two segments in the frog correspond? In Götte's illustrations, the lateral and medial components in the rostral part of the head appear to correspond to neural crest- and mesodermal mesenchymal cell masses, respectively (Fig. 2B). Götte states, for example, that the first lateral segment ('as' in Fig. 2B) give rise to jaw muscles and nerves, whereas the first medial segment ('is' in Fig. 2B) differentiates into eye muscles and the nasal septum. However, more posteriorly, the same lateral/medial distinction corresponds to dermomyotome/sclerotome subdivition (Fig. 2B). Thus, it is not easy to evaluate Götte's statements.

Similarly, Stöhr (1881) reported the development of the occipital cartilage from mesodermal segments in the frog embryo; however, the developmental stage was too late to observe head cavity-like structures. Sewertzoff (1895) reported head cavities in a younger embryo of the frog *Pelobates*; however, they are not clear enough to evaluate homology of these structures with those of elasmobranch embryos. This description rather sounds like an interpretation of the amphibian embryonic head according to the scheme established in elasmobranchs. Thus, in the study of head segmentation, amphibians never became a primary animal group for research.

Ahlborn (1883, 1884) also studied non-elasmobranch embryos. He selected *Petromyzon* and *Bombina*, and found more head segments than did Götte. This discovery led him to conclude that paraxial mesodermal segments are independent from that of pharyngeal arches (Ahlborn, 1884). To establish homologies of mesodermal segments, Ahlborn assumed three segments in the postotic region, but only one mesodermal cell mass in the preotic region (as we normally see in mouse embryos). The latter mass, according to Götte, represents six (?) segments as found in the shark, which have secondarily fused together. Thus, not only the number of head segments, but also the distinction of mesodermal segments and head cavities were previously confused. Nevertheless, as far as typical head cavities are concerned, many gnathostome embryos, even those of amniotes, generally develop head cavities (Fig. 3; Fraser, 1915; Wedin, 1949a; Gilbert, 1952, 1953, 1954, 1957; Jacob et al., 1984; Wachtler et al., 1984; Wachtler and Jacob, 1986; Kuratani et al., 2000; Kundrát et al., 2009; Adachi and Kuratani, 2012), although full sets (three pairs) of cavities are only seen in the cartilaginous fishes (Balfour, 1878; van Wijhe, 1882; Dean, 1906; Goodrich, 1918; Kuratani and Horigome, 2000; Adachi and Kuratani, 2012).

Thus, elasmobranch embryology played a leading role in the research of head segmentation from its very beginning in the latter part of the 19th century to its conclusion in the early 20th century. This was primarily because of the basal phylogenetic position of elasmobranch fishes conjectured at the time, as well as the fact that elasmobranch embryos yielded very clear histological images (Gegenbaur, 1871, 1872). Simultaneously, it was obvious that elasmobranch-centered embryology may have imposed a bias on the interpretation of data obtained from other animal groups that may have different patterns of development (Koltzoff, 1901). No doubt, that tendency would have underestimated evolvability of vertebrate developmental program. In a similar context on a different scientific background, Hall (1998) has drawn attention to the fact that "model animals" in modern biology tend to have shorter generation periods, which may affect embryonic developmental patterns. It is conceivable that such a bias have shifted developmental process towards disappearance of head cavities in the model animals.

Van Wijhe

The head cavity interpreted by Balfour arises in a single pharyngeal arch, to represent a serial homolog of somites in the trunk. Thus, according to this scheme, the vertebrate body has only one metamerical pattern that somites and pharyngeal arches follow. Marshall, on the other hand, compared the head cavities only to somites (not to abdominal coelom), and noticed properties of head cavities somewhat

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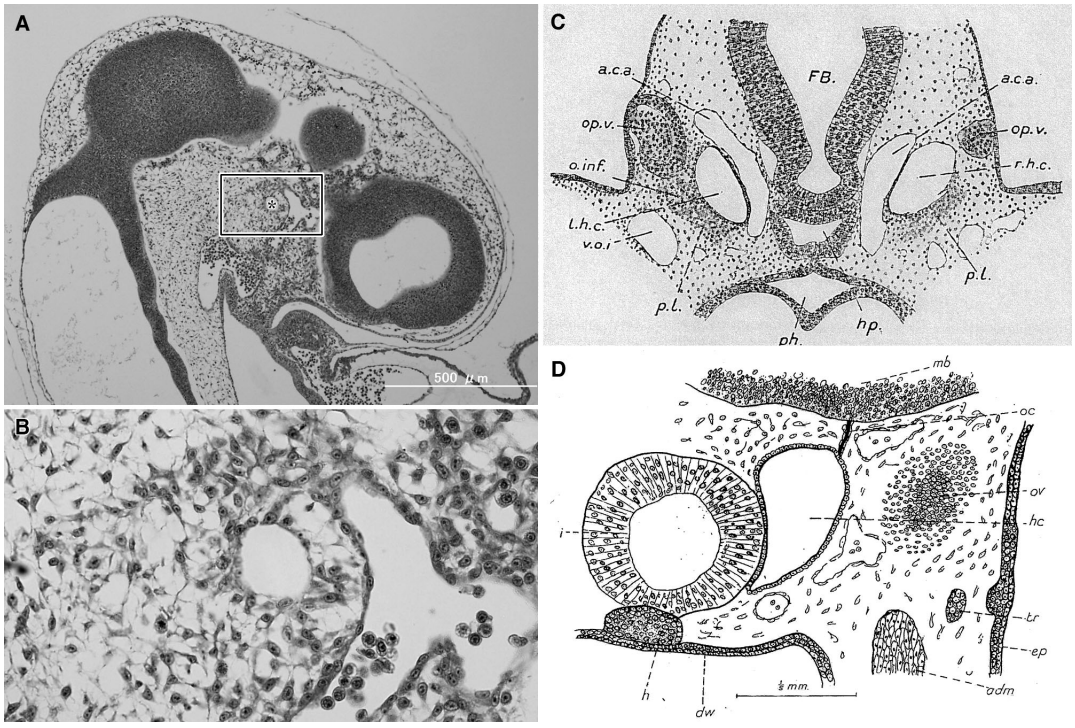


Fig. 3. Head cavities in amniote and bony fish embryos. **(A)** Premandibular cavity (asterisk) of the chicken embryo. **(B)** Magnified view of the box in **(A)**. The premandibular cavity is in the middle of the panel. Note the histological difference between the epithelia of the head cavity and the artery shown in the right part of the panel. **(C)** Premandibular cavity (r.h.c. and l.h.c.) of the embryo of a marsupial species, *Trichosurus vulpecula*. From Fraser (1915). **(D)** Premandibular cavity of a pharyngula of *Amia*, at the stage prior to differentiation. Note the topographical relationship with the cranial nerve III (oc). From de Beer (1924).

independent from pharyngeal arches. To reconcile these different interpretations, it was necessary to introduce the distinction of mesoderm (paraxial and lateral partitioning), and it was van Wijhe (1882) who first did that. Based on the achievement of Balfour and Marshall, van Wijhe divided the head mesoderm into the paraxial part that lies along the side of the notochord and neural tube, and the lateral part that extends laterally and ventrally into the pharyngeal arches.

Also using embryos of the elasmobranchs *Scyllium* (currently *Scyliorhinus*), *Galeus*, and *Pristiurus*, van Wijhe re-defined the term head cavities (Kopfhöhle) to include only the dorsally swollen portion of the cavity that occupies the paraxial position (Fig. 4), which becomes apparent in slightly older embryos than those observed by Balfour. These dorsal portions correspond to what is generally recognized as head cavities today. The premandibular cavity solely retains its original definition due to the lack of pharyngeal arch mesoderm. Now the epithelial components in head mesoderm consist of paraxial head cavities and lateral pharyngeal arch mesoderm, which forms an epithelial tube (Fig. 4: top).

In the trunk, the paraxial (somites) and lateral (coelomic wall) regions of the mesoderm roughly correspond to the distinction between somatic and visceral parts of the body. Somites give rise to skeletal muscles and axial skeletons, whereas the lateral mesoderm wraps the digestive tract and differentiates into smooth muscles. Thus, the somatic/visceral distinction arises partly through mesodermal specification into paraxial and lateral compartments. Van Wijhe saw a similar distinction in the head mesoderm and distinguished between the paraxial (head cavities) and lateral (pharyngeal arch) portions in the head mesoderm (Fig. 4). For van Wijhe, therefore, the pharyngeal arch muscles were visceral in their position and function (to move the pharynx as the foregut). Thus, the extrinsic eye muscles arising from the paraxial head cavities should be analogous to skeletal muscles in the trunk.

Since Gegenbaur (1871), the cranial nerves have been defined as peripheral nerves exiting from the skull, in contrast to the spinal nerves, which arise from the vertebral column. However, in terms of their function and distribution, there are at least two distinct groups among the cranial nerves. One contains nerves (cranial nerves III, IV, and VI) that lack sensory ganglia and innervate the extrinsic eye muscles, were likened by van Wijhe to the ventral roots of spinal nerves. The other group, the branchiomotor nerves (cranial nerves V, VII, IX, and X), contains those nerves that innervate pharyngeal arches and their derivatives. These nerves are accompanied by sensory ganglia and therefore resemble dorsal roots of spinal nerves. Thus, van Wijhe assumed a segmental unit of cranial nerves that consists of one ventral root and one dorsal root, together representing a serial homolog of one spinal nerve. For van Wijhe, therefore, one metamere (segment) of the head contains one head cavity (head somite) and one pharyngeal arch, innervated by a spinal nerve homolog whose dorsal and ventral roots are separated from each other. Like Balfour, van Wijhe also believed there was only one type of segment in the vertebrate head, although he anatomically divided paraxial and lateral parts. Whether the vertebrate head is segmented into somites and pharyngeal arches or not, van Wijhe's scheme

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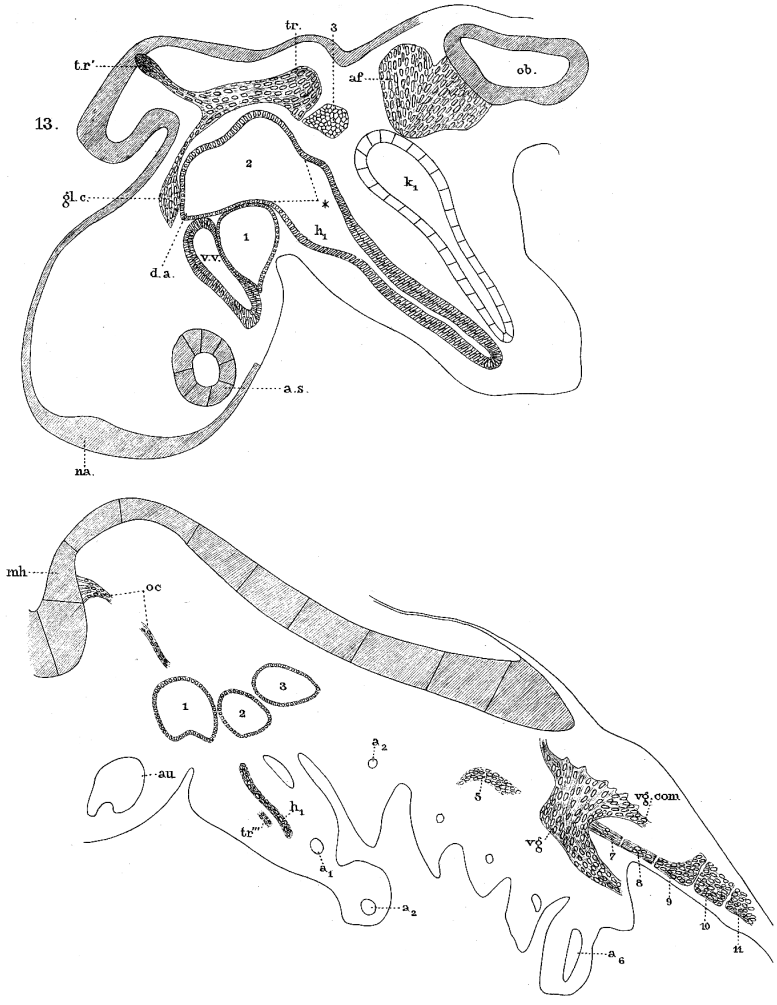


Fig. 4. Head cavities by van Wijhe (1882). Top. Stage K (pharyngula) embryo of *Galeus canis*. A parasagittal section. van Wijhe called only the dorsal (paraxial) swollen part of the mesodermal coelom the head cavities. Premandibular cavity is labeled '1', the mandibular cavity '2', the first pharyngeal pouch 'k1'. The mesodermal cyst labeled 'vv' indicates a muscle precursor associated with the premandibular cavity. This appears to correspond to Platt's vesicle. Note that the mandibular cavity continues ventrally to an epithelial tube (mandibular arch mesoderm) that runs along the dorsoventral axis of the mandibular arch. Bottom. A stage L *Scyllium canicula* embryo. Head cavities (1–3) are tandemly arranged along the anteroposterior axis. From Fig. 2 of van Wijhe (1882).

Somites	Cephalic somitic muscles	Ventral nerve root	Segments	Head cavities	Visceral (arch) muscles	Dorsal nerve roots
1	Extrinsic eye muscles innervated by Cn III (mm. rect. sup, int, inf, et obl. inf.)	Oculomotor (III)	1	Premandibular cavity	?	Ophthalmic nerve of the trigeminus
2	m. obl. sup.	Trochlear (IV)	2	Mandbular cavity	Pharygeal and gill arches	Maxilloman dibular nerve of the trigeminus
3	m. rect. ext (lat).	Abducens (VI)	3	Hyoid cavity		Acustico-facialis
4	-	-	4			
5	-	-	5	3rd somite		Glosso-pharyngeus
6	Rudimentary	?	6	4th somite		Vagus
7	Hypobranchial muscular system derived from occipital somites	Hypoglossal (XII)	7	5th somite		
8			8	6th somite		
9			9	Undifferentiated from pericardium		

Fig. 5. Head segmentation by van Wijhe (1882). Modified from Veit (1947).

contains some concepts that are still accepted today.

Van Wijhe's idea of head segmentation is schematized in Figure 5. This conception was so influential that it eventually served as a basis for Goodrich's scheme (Fig. 1B). Van Wijhe's work was similar to Marshall's in that he saw a continuity of paraxial mesodermal segments from head to trunk, but did not question whether there were two different types of head segmentation. To that end, van Wijhe can be viewed as a typical segmentalist.

Segmentalists are those researchers who assume somite-equivalent mesodermal segments in the vertebrate head. This idea stems from the vertebral theory advocated by Goethe (1790) and Oken (1807). Non-segmentalists, on the other hand, typically reject somite-like segments in the head mesoderm. There is, however, a spectrum of various views between the extremes of segmentalists and non-segmentalists. The idea of dual metamerism by Ahlborn (1884) (head somites and pharyngeal arches repeating independently) cannot easily be categorized as belonging to either of the two views. Nonetheless, van Wijhe's approach, which emphasized the histological clarity of elasmobranch embryos and contributed to the trend of "elasmobranch worship," together with the strong influence from Gegenbaur's anatomical version of head segmentation, raised the standards of precision and accuracy for morphological description, as well as consistency of schematization.

Platt's vesicle and number of segments

Using the elasmobranch species *Pristiurus* and *Scyllium*, van Wijhe postulated nine segments in the head, being serially homologous with those in the trunk. Of the nine, the head cavities belonged to the rostral three segments. This scheme was meant to represent a commonly shared ground plan for the vertebrate head; the number of head segments was not thought to change across species. However, rostral to the premandibular cavity, another head cavity was added.

The new cavity was discovered by Julia Barlow Platt, an American embryologist studying abroad in Germany. Today, she is most often remembered as the first scientist to advocate for the neural crest origin of the cranium (Platt, 1893). However, at the time she was better known as the discoverer of the head cavity, often called Platt's vesicle (also known as the "anterior cavity;" van Wijhe, 1882; Platt, 1890, 1891a, b; Zimmermann, 1891; Hoffmann, 1894; Neal, 1918) that developed rostral to the premandibular cavity (Fig. 6). Due to its position, this vesicle was regarded as representing the rostralmost segment of the vertebrate head (Lamb, 1902; Dohrn, 1904; Neal, 1918; de Beer, 1922; Jarvik, 1980; reviewed by Goodrich, 1930; Veit, 1947; Wedin, 1949b).

Platt found this mesodermal coelom in embryos of the shark *Acanthias*, but no similar mesodermal elements were

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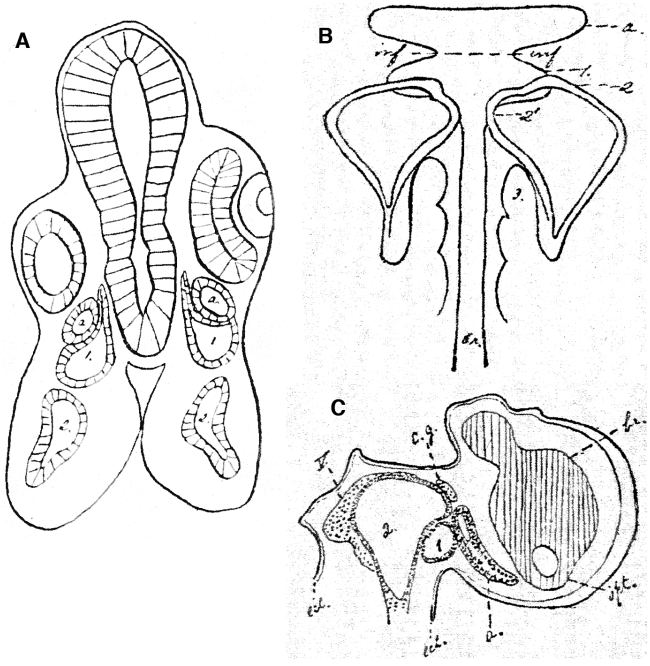


Fig. 6. Platt's vesicle. **(A)** Transverse section of *Acanthias* embryo to show the anterior cavity of Platt (a) attached on the lateral aspect of the premandibular cavity (1). Mandibular cavity is labeled "2." van Wijhe also observed a Platt's vesicle-like structure in *Galeus* embryo, which he thought to be a part of the premandibular cavity. From Platt (1890). **(B, C)** Description of *Acanthias* embryo performed by Platt in Wiedersheim's laboratory, supervised by Keibel. Graphic reconstruction viewed from the dorsal aspect **(B)** and parasagittal section **(C)**. In **(B)**, the prechordal plate is divided into anterior and posterior portions, of which the posterior part will become the premandibular cavity. In **(C)**, the anterior (a), premandibular (1), and mandibular (2) cavities are shown. From Platt (1891b).

unambiguously recognizable in other species, such as *Scyllium*. Van Wijhe also observed a few small mesodermal cysts associated with the premandibular cavity of *Galeus* (see Fig. 4: top). If he had allowed for the possibility that the cysts represented an independent entity, it might have been van Wijhe who first identified the rostralmost head cavity. However, he eventually concluded that these vesicles only represented a portion of the premandibular cavity (Fig. 4; van Wijhe, 1882). Based on histological observations, it was readily seen that the position of Platt's vesicle coincided with that of the inferior oblique muscle, and the vesicle was generally regarded as the anlage of that muscle, which normally arises from the premandibular cavity. This was a major reason why van Wijhe identified the anterior cavity as a portion of the premandibular cavity, an idea that was also embraced by Jefferies (1986). Goodrich also invoked a similar explanation (Goodrich, 1930).

The number of segments was one of the central issues in the debate regarding head segmentation. Indeed, Platt's vesicle raised controversies as to the number of segments incorporated in the vertebrate head. From a certain point of view, the controversy can be seen as a recapitulation of the classical debate on transcendental morphology, during which Goethe, Oken, and Geoffroy St. Hilaire argued regarding the number of vertebrae contained in the skull (reviewed by de Beer, 1937). In comparative morphology during the late 19th century, embryologists often advocated various numbers of head somites based on embryos of various (often non-elasmobranch) vertebrate species. A constant number was expected, of course, for head mesodermal segments, since the problem of head segmentation was still influenced by an idealistic morphology in pursuit of a single archetype for all vertebrate species. For example, both van Wijhe and Balfour recognized three pairs of segments in front of the inner ear, and the complete set of head cavities were only found in cartilaginous fish. In other taxa, posterior cavities were thought to disappear frequently.

Other than *Acanthias*, there are a few elasmobranch species, such as *Galeus* and *Squalus*, which develop Platt's vesicles (Zimmermann, 1891; Hoffmann, 1894, 1896). In addition, the vesicle has also been assumed to occur in the embryos of some osteichthyans called "Ganoids," such as, *Amia*, *Lepidosteus*, *Polypterus*, and *Acipenser*, in the form of the "adhesive organ" (see Neal, 1898; Reighard and Phelps, 1908; reviewed by Neal and Rand, 1946 and Wedin, 1949b; but also see Beer, 1924 and Veit, 1924 for objections). In *Squalus* embryos, there is another small vesicle even rostral to Platt's vesicle, called Chiarugi's vesicle (Holmgren, 1940; Lindahl, 1944; Jarvik, 1980; Horder et al., 1993). The latter is even rarer than Platt's vesicle, although topographically it may more closely resemble the adhesive organ in terms of its position.

Based on segmentalist theory, the idea of three head segments in the preotic region was a problem, because there is apparently no visceral arch associated with the premandibular cavity. In other words, the presence of the premandibular arch was a prerequisite for segmentalists to be consistent, and there was some circumstantial evidence to support this concept. For example, the trigeminal nerve is a composite cranial nerve that arises as two separate portions, one innervating the mandibular arch, and the other innervating the premandibular domain. Huxley's idea that the prechordal portion of the neurocranium (trabecula) represents the vestigial premandibular arch skeleton was also consistent. The discovery of Platt's vesicle, of course made the situation even more complex, which led Sewertzoff (1911) to assume two premandibular arches. Similarly, Jarvik and his colleague Bjerring accepted the existence of another pair of head somites that they called the "terminal somite," which was assumed rostral to the premandibular somites (Fig. 7; Jarvik, 1980; Bjerring, 1977, 2014).

As seen above, it was not easy to postulate a common developmental and segmental plan for the vertebrate head, even within the limited group of elasmobranchs. The actual developmental patterns of vertebrates were found to be more complicated and less consistent than was expected. The situation in the late 19th century was summarized as critical questions by Sewertzoff (1898a):

1. Can head cavities be homologized among different species?
2. If they are not always homologous, which pattern is more ancestral—more or fewer head cavities?

Head cavities and somites

Before the discovery of head cavities, several comparative embryologists had already suggested that postotic somites contribute to the formation of the occiput, the cau-

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dalmost component of the neurocranium (Rathke, 1839; Vogt, 1842; Remak, 1850). Thus, in gnathostomes, the head partially contains some vertebral elements at least in the posterior portion (Jackson and Clark, 1876; Stöhr, 1881; Froriep, 1882, 1883, 1905a, b, 1917; Sewertzoff, 1895; Goodrich, 1910; reviewed by Goodrich, 1930; de Beer, 1937). This fact largely encouraged segmentalists and they thought the assimilation of postotic somites to the skull as strong evidence for the vertebrate head segmentation. The assimilation, however, represents a secondary modification in development found only in the lineage of jawed vertebrates. Furthermore, the anterior portion of the skeletal components, such as the parachordal cartilage, is derived from unsegmented preotic and postotic mesoderm and develops in a manner hardly similar to the occipital skeleton (Rathke, 1839; Huxley, 1858, 1864). In addition, several researchers observed a discontinuity between the head cavities and true somites (see Kastschenko, 1888; Rabl, 1889; Kupffer, 1893; Froriep, 1917; Kuratani, 1997, 2003, 2008; Adachi and Kuratani, 2012). These researchers, including the authors, could collectively be called non-segmentalists in a strict sense. Their arguments can be summarized as follows:

1. Morphologically there is an obvious discontinuity between the preotic and postotic mesodermal components.
2. The shape of each head cavity varies, whereas somites all look similar and regular.
3. Head cavities are not always well distinguished from the pharyngeal mesoderm that is not paraxial.
4. Head cavities do not undergo typical compartmentalization into sclerotomes and dermomyotomes (Rabl, 1889).
5. Head cavities do not always differentiate into the same sets of structures, unlike somites.

Thus, the vertebrate mesoderm shows a conspicuous difference between the preotic and postotic regions (Fig. 8). Simply put, non-segmentalists emphasized this difference to refute the idea of head segmentation. Even today, the problem about continuity or discontinuity between the head and trunk mesoderm has not been settled, as seen in the debate concerning the presence or absence of rostral somite-like structures in the apparently unsegmented vertebrate preotic mesoderm. The debate over cephalic somitomeres is also recognized as a similar argument (reviewed by Jacobson, 1988, 1993).

What are head cavities?

If the head cavities found in elasmobranchs represent typical head cavities, their commonality would be summa-

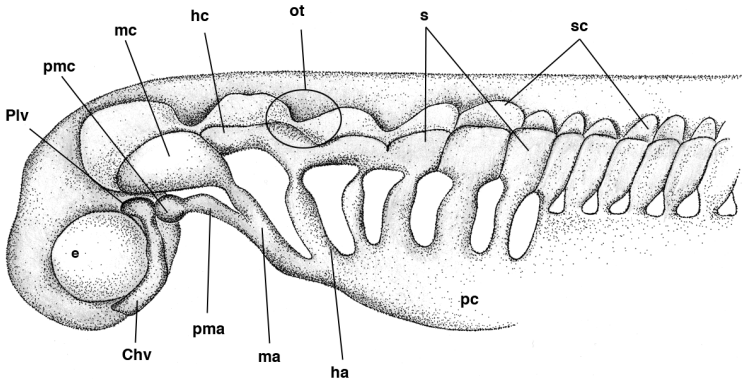


Fig. 7. Schematic illustration of head cavities in the elasmobranch embryos by Jarvik (1980). This figure shows an idealized mesodermal pattern of elasmobranch embryos. Based on van Wijhe (1882) and Goodrich (1930), head cavities are defined as a paraxial swollen part of the head mesodermal coelom. Premandibular (pmc), mandibular (mc) and hyoid (hc) cavities are commonly found in cartilaginous fishes. For Balfour (1878), on the other hand, each head cavity contained the entire head mesodermal moieties delineated by pharyngeal pouches, extending the whole dorsoventral axis. Thus, Balfour's mandibular and hyoid cavities are shown in this figure as, 'mc + ma' and 'hc + ha', respectively. All the reported mesodermal elements are shown in one figure. Both Chiarugi's vesicle (Chv) and Platt's vesicle (Plv) are drawn as portions of the rostralmost segment called the terminal mesoderm. Note that coelomic tubes in pharyngeal arches leads to pericardium (pc) ventrally. Redrawn from Jarvik (1980).

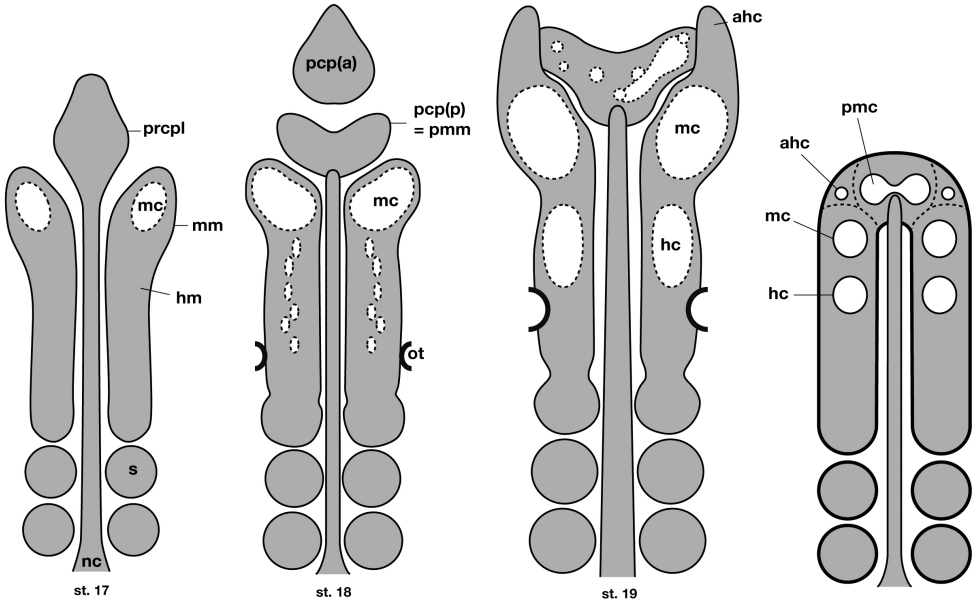


Fig. 8. Development and homologies of head cavities. **(A–C)** Developmental sequence of head cavities in *Scyliorhinus torazame*. Head cavities are formed either by delamination of solid mesoderm or fusion of small cysts appearing in the mesoderm. **(D)** Schematic model of the vertebrate head mesoderm with positions of head cavity development. Note that the head cavities are formed along the inversed U-shaped domain within the paraxial mesoderm, with prechordal plate-derived premandibular cavity (phc) as the most rostral element, and a pair of anterior cavities lateral to the latter (ahc). Redrawn from Adachi and Kuratani (2012).

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rized as below:

1. Head cavities arise as mesodermal epithelial coeloms in the head mesenchyme, occupying paraxial positions in the preotic region of the embryonic head. Their epithelia are multi-layered, unlike blood vessel endothelium.
2. Head cavities are likely to differentiate into mesodermal derivatives including extrinsic eye muscles, and maintain close association with cranial nerves III, IV, and VI, even before the muscles differentiate.
3. Unlike initially believed, head cavities arise not by the process of enterocoely, but by coalescence of small mesodermal cysts developing irregularly in the head mesenchyme (Fig. 8; reviewed by Adachi and Kuratani, 2012).
4. The mandibular cavity appears first, followed by the hyoid cavity, and then the premandibular cavity (Fig. 8).
5. The premandibular cavity arises from the prechordal plate after the latter becomes an obvious mesenchyme (Fig. 8; the premandibular mesoderm of the lamprey also arises from the modification of the prechordal plate - Kuratani et al., 1999).
6. The complete set of head cavities consisting of three pairs of cavities only appears in cartilaginous fishes.

In consideration of the above respects, we have to revisit the head mesoderm of jawless vertebrates, lamprey and hagfish. Historically, some embryologists reported the existence of head cavities in the lamprey embryonic head (see Kupffer, 1894; Koltzoff, 1901; Neal, 1918; Edgeworth, 1935; Damas, 1944; reviewed by Adachi and Kuratani, 2012). However, these observations could be strongly biased due to the elasmobranch Worship, and misrepresented as being analogous to observations in shark embryos.

The mandibular 'arch' mesoderm does appear as a protrusion of the archenteron in the lamprey, which was once explained as the mandibular cavity of this animal (Balfour, 1881; Koltzoff, 1901). However, this mesoderm does not lie in the paraxial position, but resides within the pharyngeal arch, likely representing the pharyngeal arch mesoderm of jawed vertebrate embryos then a head somite (Kuratani et al., 1999). Similarly, it has to be stressed that development of the extrinsic eye muscles has never been reported in the cyclostome embryos by modern methods (see Koltzoff, 1901). Thus, the head cavities of cyclostomes reported in classical studies do not seem to represent a true head cavity as seen in elasmobranchs.

Until now, no head cavities (by definition of van Wijhe) have been reported from cyclostomes. Although SEM-based modern observations, like those by Horigome et al. (1999), cannot conclude the absence of head cavities in cyclostome embryos (Horder et al., 2010), other histological observations failed to identify any head cavities, or mesodermal cysts in the cyclostome head mesoderm (Kuratani et al., 1999; Adachi and Kuratani, 2012; Oisi et al., 2013; Suzuki et al., 2016; Adachi and Kuratani, unpublished data): we propose that head cavities are most likely a gnathostome synapomorphy rather than an ancestral trait for all the vertebrates (as to the distribution of head cavities across vertebrates, see Gilbert, 1952).

What is Platt's vesicle?

The premandibular mesoderm arises from the anteromedial prechordal plate or a part of the preoral gut, which is located slightly rostral to the oropharyngeal membrane, as well as Rathke's pouch. The premandibular mesoderm gives rise to the premandibular cavity as a pair of coeloms, which are often connected at the midline (like a dumbbell-shaped balloon) with the rostral tip of the notochord (Figs. 1, 8). This morphological pattern indicates that this coelomic pair likely represents the rostralmost component of the vertebrate mesoderm (de Beer, 1924; Adelmann, 1926, 1927; Gilbert, 1952; Jacob et al., 1984; Wachtler et al., 1984; Wachtler and Jacob, 1986; Horigome et al., 1999; Kuratani et al., 1999, 2000; Kundrát et al., 2009). This idea leads to the conclusion that the orbital cartilage (acrochordal cartilage, a mesodermal neurocranial portion formed around the rostral tip of the notochord) that occupies a similar position is derived from the premandibular coelom, as speculated by several authors (Bertmar, 1959; Bjerring, 1967; Jollie, 1977). Simultaneously, however, this hypothesis proposes a serious morphological problem in regards to the rostralmost position assumed for Platt's vesicles, which are obviously paired.

In that regard, Wedin (1949b) reported that Platt's vesicle arises as paired elements from the beginning and occupy rather lateral positions normally occupied by a rostral part of the mandibular cavity in other gnathostome species (de Beer, 1924; Kuratani et al., 2000; Adachi and Kuratani, 2012). In other words, regardless of the number and identities of head cavities, the space occupied by the epithelial coelom remains constant and never changes in the embryonic head (Fig. 8D). Thus, the boundaries between head cavities are variable to some extent, unlike those between somites or their derivatives in the trunk.

From the above, it can be seen that the ventrolateral and rostral part of the vertebrate embryonic head, the position of the future inferior oblique muscle, is always occupied by certain head cavities, in some cases by the rostrolateral process of the mandibular cavity (as in sturgeon; Kuratani et al., 2000). In this case, Platt's vesicle can be regarded as a part of the mandibular cavity, which was secondarily detached from the major part of the latter. In other cases, the same position is occupied by the lateral portion of the premandibular cavity (Fig. 8).

Conceivably, the above speculation is tightly linked to the developmental mode of head cavities. Namely, the head cavities do not arise as primordial segments that directly grow as head cavities, but rather as numerous small vesicles or cysts that will secondarily become fused together locally to form larger cavities (Adachi and Kuratani, 2012; Fig. 8). Thus, it is highly probable that Platt's vesicle, as well as Chiarugi's vesicle, represent irregularly segmented portions of either mandibular or premandibular cavities that tend to arise in certain animal species. After all, these cavities do not represent the rostralmost cavities, but accessorial structures originated from mesodermal components that are caudal, not rostral, to the premandibular cavity. This conclusion is quite similar to that initially drawn by Platt herself (Platt, 1891a, b) and Wedin (1949b).

Why then do gnathostome embryos sometimes develop head cavities and sometimes not? Wedin (1949b) first put

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forth a hypothesis that the head cavities were acquired as an adaptation to enlarged eyes, because limited mesodermal materials can be supplied spatially to form extrinsic eye muscles surrounding the eyeball. It is true that the rostral process of the mandibular cavity or Platt's vesicle, when present, appears to correspond to the position where the inferior oblique muscle develops among those innervated by the oculomotor nerve (Holmgren, 1940). Nevertheless, it is also true that amniote embryos, whose embryonic eyes are comparatively larger than those of elasmobranchs, tend to have head cavities to a far less degree. Regardless, head cavities appear to imply the existence of very flexible and adaptive properties of the head mesoderm in vertebrates (see Horder et al., 1993). It is also possible that Wedin's interpretation is correct (elasmobranch head cavities as 'local adaptations' for enlarged eyes), and many crown gnathostomes have secondarily lost the coelomic configurations as the head mesoderm has acquired abbreviated patterning developmental programs for the extrinsic eye muscles. Then, the presence and absence of head cavities would be regarded as an extreme example of developmental system drift (DSD: True and Haag, 2001; see also Remane, 1956, for DSD in various modes of coelom formation in enteropneust larvae).

Mesodermal segmentation and evolution

In the comparative embryology of head mesoderm in the late 19th to early 20th centuries, few studies have described all developmental stages using three-dimensional images. In most papers, head cavities were described as in earlier works (Balfour, 1876, 1878; Marshall, 1881; van Wijhe, 1882; Neal, 1898). Wedin (1949b) in the mid-20th century dealt with staged embryos of several different species (*Torpedo*, *Etmopterus*, and *Petromyzon*) and showed sequential regionalization of head mesoderm (Fig. 9). According to Wedin, most vertebrate species develop head cavities in some form, but he did not believe they were all homologous. Nor did he regard head cavities as the signature of somite-like segmentation. In that sense, he belonged to non-segmentalists.

For Wedin, trunk (postotic) somites were homologous among all the vertebrate species and the "head mesoderm" rostral to the typical somites should be comparable. Namely, the vertebrate head mesoderm as a whole is homologous among species for the following reasons:

1. The topographical relationship between the first pharyngeal pouch and the head mesoderm is identical in all species (Fig. 9C and D).
2. Morphological pattern and shape of the head mesoderm is similar in all species (also see Kuratani et al., 1999; Adachi and Kuratani, 2012).
3. Connection between the head mesoderm and somites is comparable in all species (Fig. 9F–H).

He also attempted to homologize the vertebrate head mesoderm with amphioxus rostral coeloms, in order to reveal the basic (ancestral) morphological pattern of the mesoderm. In the embryonic amphioxus, the anterior gut diverticulum (AGD) was formed from the rostral endoderm by enterocoely, and this diverticulum was equated with the lamprey mandibular mesoderm, which also develops as an enterocoel (Fig. 9A–C and E). The lamprey mandibular

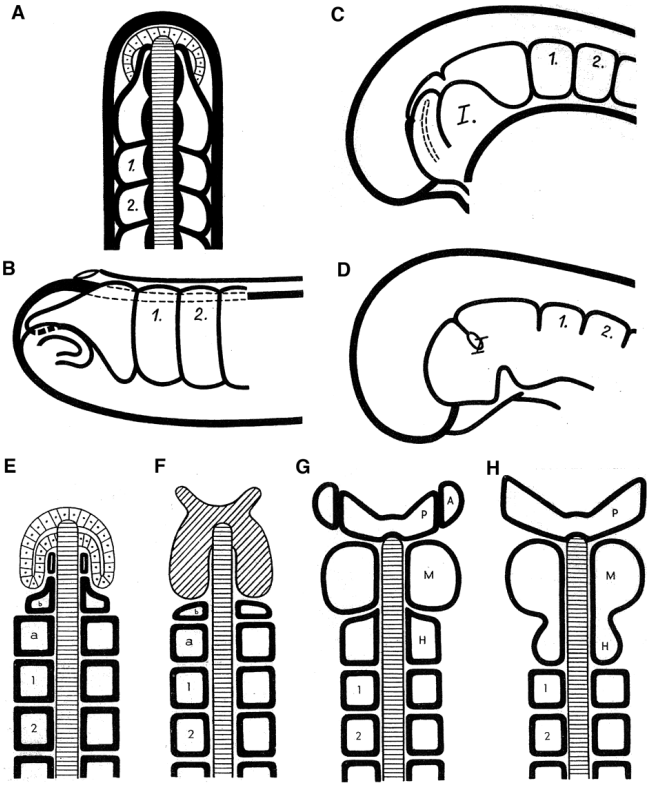


Fig. 9. Comparison of embryonic head mesoderm by Wedin (1949b). In all the panels, numbered segments represent comparable somites; note the numbering of somites in amphioxus. **(A, B)** Dorsal **(A)** and left lateral **(B)** views of an amphioxus embryo (9-somite stage; after Hatschek, 1881). The anterior pole of the endoderm protrudes a pair of enterocoels called the anterior gut diverticulum (AGD). **(C)** Early pharyngula of *Petromyzon* (8–10 somite stage). The only enterocoel developing in vertebrates is the one rostral to the first pharyngeal pouch (I) in the lamprey embryo, which is thought by Wedin to correspond to the AGD. At this stage, the premandibular mesoderm has not developed from the prechordal plate. **(D)** Early pharyngula of *Etmopterus* (9-somite stage). This scheme resembles the actual lamprey embryo at the early pharyngular stage. **(E)** An 8–10-somite stage embryo of *Petromyzon*. The inversed U-shaped coelom (usually identified as the mandibular mesoderm) is explained as the AGD homolog. **(F)** A 20-somite stage embryo of *Petromyzon*. **(G)** *Etmopterus* embryo (40-somite stage). The preotic head mesoderm consists of four pairs of head cavities (A, anterior cavity; P, premandibular cavity; M, mandibular cavity; H, hyoid cavity). The anterior cavity was explained by Wedin to be a part of the mandibular cavity. **(H)** 5-mm embryo of *Torpedo*. This embryo does not show an independent anterior cavity and resembles the pattern of lamprey head mesoderm as described by Kuratani et al. (1999). From Wedin (1949b).

mesoderm was fused with more medially located mesenchyme at the later stage (Fig. 9E and F). This homology, however, has not been supported by other morphologists, including Kuratani et al. (1999). However, Wedin explained that the presence or absence of AGD distinguishes the cyclostome + amphioxus group and gnathostomes. Otherwise, the head mesoderm is very similar between cyclostomes and gnathostomes.

According to Wedin, the entire vertebrate head mesoderm should be found in the rostralmost somite-like segment in the amphioxus that arises caudal to the AGD (Fig. 7B,

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rostral to the somite labeled '1'). The shape of this somite tapers rostrally and resembles that of the head mesoderm (Fig. 9B). Thus, Wedin did not assume any segments within the whole head mesoderm of gnathostomes (Wedin, 1949b). This leads to the homology of the second amphioxus somite and the first postotic somite in vertebrates. The homology by Wedin, however, is rather confusing. In the Japanese lamprey *Lethenteron japonicum*, the actual morphology of the embryonic mesoderm more closely resembles that of elasmobranchs (Kuratani et al., 1999). Furthermore, accepting Wedin's homologies results in inconsistent positions of the otic vesicles and prechordal plate (or its derivative, the premandibular mesoderm). Thus, the head mesoderm is more likely comparable only among vertebrates. The problem associated with Wedin's comparison reflected the inaccuracy associated with histological observations of lamprey embryos (see Kuratani et al., 1999).

Torpedo enigma

There were some comparative embryologists who stressed the importance of small mesodermal vesicles or cysts that appear prior to the head cavities. They rejected segmental entities in the head cavities, but believed that these vesicles truly represent serial homologs of somites (Sewertzoff, 1895; Froriep, 1902a). Anton Dohrn, for example, reported as many as 12–15 vesicles in *Torpedo marmorata* (Dohrn, 1890b), and he found that they represent precursors of head cavities (Fig. 10A). Therefore, a single head cavity cannot be compared directly to a single somite. Killian (1891) also reported the appearance of small cysts (17 or 18) in *Torpedo ocellata*, but he never observed the coalescence of these cysts to form head cavities (Fig. 10D).

Dohrn was one of the few scientists to publish a detailed illustration deserving of modern scrutiny (Dohrn, 1890). Dohrn's Figure 7 in Plate I shows that numerous cysts are developing in a pattern somewhat similar to the head mesenchyme prior to the appearance of head cavities in *Scyliorhinus* (Adachi and Kuratani, 2012; Fig. 10A). This figure was inaccurately reproduced, and ironically, those copies often better reflected Dohrn's argument than did the originals (Killian, 1891; Rabl, 1892; Fig. 10B and C). Posteriorly in Dohrn's Figure 7, paraxial mesodermal components are shown along the notochord, as well as pharyngeal pouches ventrally. The rostralmost one represents the future first pouch. Dorsal to the pouch, the mesoderm does not appear to be segmented like somites (Fig. 10A). The most rostral mesodermal segment that resembles a somite appears dorsal and posterior to the second pouch, which is postotic (namely, trunk) in position (the otic vesicle will develop dorsal to the second pharyngeal arch, slightly rostral to the second pouch). As such, the latter mesoderm appears to be a real somite, and Dohrn's figure does not show any preotic mesodermal segments. Overall, the mesodermal configuration in the *Torpedo* shown in Dohrn's paper does not seem very different from that in *Scyliorhinus* or even chicken embryos, nor does it support the argument of Dohrn himself.

Although Dohrn's interpretation often changed in each paper, and his theories were known to be frequently inconsistent (Rabl, 1892), it is quite possible that *Torpedo* uniquely develops multiple cysts in the head mesoderm, as evidenced by similar observations of different authors. Froriep (1902a) also observed *Torpedo*, and if his sketches are correct, this animal has three or five pairs of rostral (preotic) mesodermal cysts that Dohrn failed to observe. The youngest embryo (corresponding to a late neurula?) described by Froriep possesses a tandem array of small vesicles (unlike the small cysts that appear prior to the formation of the head cavities) lateral to the notochord, which were termed as "n, o, p, q..." in an anterior to posterior direction (Fig. 10E–I). Apparently, Froriep believed that these cysts were coextensive as the notochord (similar to Gegenbaur, who attempted to find segmental patterns only at the notochordal level). According to Froriep, these cysts gradually disappear in an anterior to posterior direction, and by the stage slightly later than the embryo described by Dohrn, the rostralmost segment corresponds to "p," which is located rostral to the second pharyngeal pouch, namely in the preotic domain.

At a glance, the above comparison suggests that even in the same species (genus), different interpretations tend to be drawn from different observations. Nevertheless, because Froriep and another morphologist, Sewertzoff, independently reported a similar preotic somite in *Torpedo*, we are compelled to reconsider the possibility of a preotic (non-head cavity) somite in *Torpedo* embryos. Sewertzoff (1898b) reported such a vesicle dorsal to the first pharyngeal pouch in *T. ocellata* and *T. marmorata*, apparently supporting the observation of Froriep. The paper by Sewertzoff (1898a) represented the most detailed and accurate description of the *Torpedo* embryonic head, showing the somite-like segment that was called "o" by Froriep later. However, a couple of cysts posterior to that segment resemble precursors of the future hyoid cavity. In addition, an irregular coelom that appears more rostrally corresponds to the precursor of the mandibular cavity, which was also described by Froriep.

Regarding the uniquely numerous mesodermal vesicles in *Torpedo*, Sewertzoff explained that this animal would have had a long bodied ancestor, in which the trunk had been reduced anteroposteriorly (Sewertzoff, 1898a); however, this should have involved the unusual homeotic shift of mesodermal segments as well. In the latter explanation, the position of otic vesicle, or head/trunk junction, is fixed along the anteroposterior axis, and only the number of somites is assumed to have changed. Furthermore, Sewertzoff believed the number of head cavities was also conserved in *Torpedo* evolution, in which the third and fourth vesicles were thought to form the hyoid cavity (Sewertzoff, 1898a). Thus, according to Sewertzoff, the head of *Pristiurus* terminates posteriorly with the ninth head somite, that of *Acanthias* with the tenth, and *Torpedo* head has as many as 13 head somites. In addition, Sewertzoff explained that these animals have different numbers of occipital somites in the posterior part of the head (three in *Pristiurus*, four in *Acanthias*, and two in *Torpedo*).

The morphological significance of early mesodermal cysts in *Torpedo* still remains enigmatic, similar to the "cephalic somitomeres" advocated by Meier (1979) and his colleagues (reviewed by Jacobson, 1988, 1993) toward the end of the 20th century. Curiously, the assumed number of cephalic somitomeres also exceeded that of head cavities,

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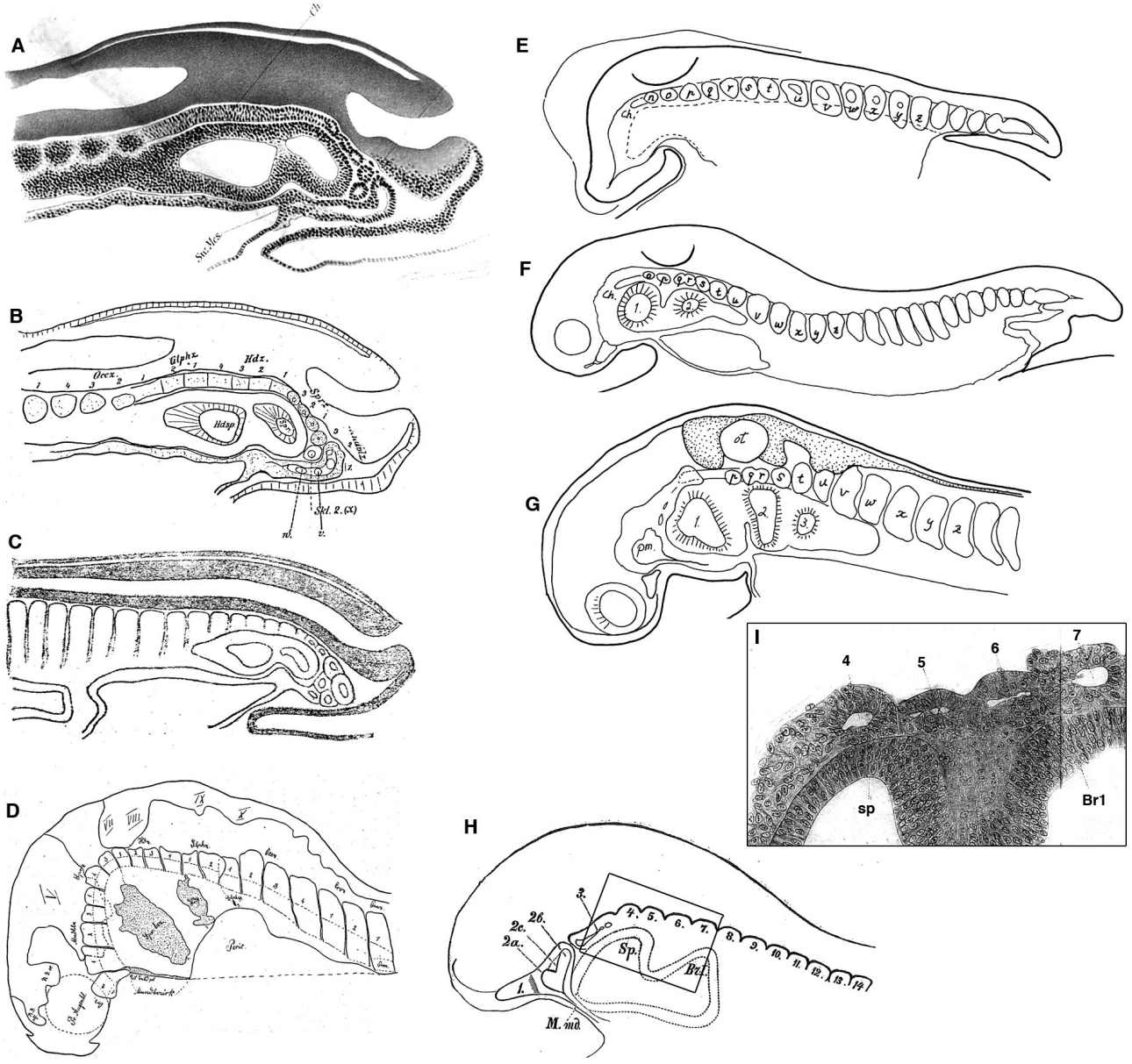


Fig. 10. Early mesodermal development in *Torpedo*. **(A)** Parasagittal section of an early pharyngula of *Torpedo marmorata* shown in Fig. 7 of Plate I in Dohrn (1890). The prechordal plate is clearly depicted at the forebrain level. Posteriorly, the mandibular mesoderm with a coelomic tube is connected to the pericardiac mesoderm. Dorsal to the pharynx, somites, notochord, and small mesodermal cysts are seen along the anteroposterior axis. From Dohrn (1890). **(B)** Reconstruction of the head of the same embryo in **(A)**. This illustration was made by Killian (1891) based on seven figures that appeared in Dohrn (1890). Small mesodermal cysts are illustrated along the entire axis. Many of the cysts probably represent precursors of head cavities, not somite homologs. From Killian (1891). **(C)** Another reproduction of the Dohrn's figure of *Torpedo marmorata* illustrated by Rabl. Somitomeric segmentation in this drawing is obviously emphasized (compare with **(A)**), but it conveys Dohrn's idea more clearly. From Rabl (1892). **(D)** *Torpedo* embryo described by Killian (1891). Somite-like segments are arranged along the entire anteroposterior axis. Neural crest-derived ectomesenchyme is also drawn. This paper assumed the largest number of head somites, but illustrations are not very trustworthy. From Killian (1891). **(E–G)** Developmental sequence of the head mesoderm in *Torpedo ocellata* by Froriep (1902). Redrawn from Froriep (1902). **(H)** Development of *Torpedo* by Sewertzoff. This embryo is approximately at the 2.7-mm stage *Torpedo* illustrated by Froriep (G). From Sewertzoff (1898b). **(I)** Histology of the square in H. The mesodermal cyst numbered 4 and posterior ones appear to be serial homologs of somites. H and I from Sewertzoff (1898b).

as do the small cysts in *Torpedo*. A possible explanation for this is that, in the absence of somite segmenting signaling (Jouve et al., 2002), the paraxial mesoderm of the head retains the capacity for autonomous epithelialization and segmentation, as has recently been shown by Dias et al. (2014), and such an ability might be particularly conspicuous in early *Torpedo* embryos. Therefore, these small cysts may not necessarily represent serial homologs of somites. This species may still have a lot to tell us about the mesodermal segmentation of the vertebrate head.

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Gene expression

The significant progress of molecular biology in the last few decades has enabled us to approach to the problem of vertebrate head segmentation by comparing the vertebrate head and trunk at the level of gene expression and signaling network. These approaches provide a wide variety of comparative criteria, which highlights the fundamental similarities and differences between head and trunk mesodermal coeloms. Fortunately, a considerable amount of molecular data has been accumulated for the developing mesoderm of the vertebrate head and trunk. Notable is the systematic survey of developmental gene expression in the chicken mesoderm conducted by Dietrich and her group (Mootoosamy and Dietrich, 2002; Bothe and Dietrich, 2006; Bothe et al., 2007). They classified mesoderm-related genes into categories in terms of their developmental functions. The first group of genes is known as segmentation clock genes and related genes (for roles and expression patterns of *Notch 1*, *Dll1*, *Lfrg*, and *EphA4*, see Peel and Akam, 2003; Tautz, 2004; Dequéant and Pourquié, 2008; Krol et al., 2011 and also reviews by Bothe and Dietrich, 2006; Pourquie, 2011). Expression of these genes is primarily associated with somites, whereas in the head mesoderm, only two oscillating gene expressions have been reported (Jouve et al., 2002; but also see Bothe and Dietrich, 2006). The second group of genes is associated with muscle differentiation, which is also expressed differently between the head mesoderm and somites (Mootoosamy and Dietrich, 2002; Noden and Trainor, 2005; Bothe and Dietrich, 2006; Noden and Francis-West, 2006; Bothe et al., 2007; Grifone and Kelly, 2007; Bryson-Richardson and Currie, 2008; Buckingham and Vincent, 2009). Characteristic expression in head mesoderm is known for *Pitx2*, which functions in extrinsic eye muscle differentiation, and *Tbx1* and *Isl1*, which play roles in differentiation of pharyngeal arch muscles (see Nathan et al., 2008). The differentiation of these head muscles is not accompanied by *Pax3* expression (Buckingham and Vincent, 2009; Rios and Marcelle, 2009). The latter two groups of gene expression coincide with the distinction between somatic (paraxial mesoderm-derived) and visceral (arch mesoderm-derived) portions in traditional morphology (see van Wijhe, 1882). Indeed this distinction corresponds to the innervation by different groups of cranial nerves (see above).

In experimental embryology, it is hypothesized that embryonic head mesoderm (in avian embryos) only consists of paraxial mesoderm, whose lateral portion is specified as the source of pharyngeal arch mesoderm (Noden, 1988; Noden and Francis-West, 2006; as for the discussion about this issue, see Sambasivan et al., 2011; Adachi et al., 2012). However, at pharyngula stages, vertebrate embryos show clear distinction between the paraxial (dorsal) and lateral (ventral or pharyngeal arch) portions in the head mesoderm that are not only anatomically regionalized, but are also molecularly characterized by *Pitx2* and *Tbx1* expression, respectively. Curiously, expression of these genes partially overlap in early stages (*Tbx1* expression appears slightly later), which are only secondarily excluded from each other as the morphological partitioning of these mesodermal components become apparent (Adachi et al., 2012). Thus, it appears that early head mesoderm of gnathostomes first arises as a paraxial mesoderm, in which lateral mesodermal portion becomes specified secondarily through development. In this respect, trunk mesoderm is specified and regionalized into paraxial and lateral parts from the beginning, which is in striking contrast with head mesoderm. Moreover, although the muscle differentiation gene, *Myf5*, is equally expressed in the paraxial mesoderm throughout the body axis, timing of expression is earlier in somites than in the head mesoderm. There is also a conspicuous difference in the expression of *Pax3* and *Pax7*, which are only expressed in the trunk somites. Again, the discontinuity between the head and trunk mesoderm is clear in the myogenic program.

In the study of head cavities, molecular evidence leads to curious insights. Classically, as noted by Balfour and van Wijhe, head cavities were thought to represent ancestral somitomeric features of the head mesoderm, which tends to be ambiguous in derived lineages of vertebrates like amniotes. Therefore, if the head cavities reflect the ancestral property of segmented mesoderm, the cavities are expected to exhibit a gene expression profile more similar to somites than the unsegmented head mesoderm of amniotes. However, gene expression patterns of *Pax3*, *Pax7*, *Pitx2*, and *Tbx1* in the shark head cavities do not show any similarity to somites, but show patterns that are very similar to those in amniote and lamprey head mesoderm, suggesting that coelom formation in the shark head mesoderm *per se* does not reflect somite-like developmental properties (Adachi et al., 2012). Whether or not the head cavities or any forms of mesodermal segments appear in some animal lineages, therefore, the head and trunk mesoderm is well specified from each other in vertebrates, showing an overt discontinuity between these two regions. Namely, head cavities do not represent vestigial somites in the head.

Even more interesting is the fact that, in the amphioxus, there is no head/trunk differentiation in the mesodermal gene expression profile (see citations in Adachi et al., 2012). In other words, both the head-specific and trunk-specific genes are expressed in “somites” in this animal, possibly implying that the head mesoderm is not a specialized trunk mesoderm, but trunk mesoderm could be differentiated from the common, undifferentiated state of mesoderm (Onai et al., 2015a, b). In the amphioxus, what appears to be trunk mesoderm has not yet been specified as such. In the history of morphology, there has been an unrecognized and unstated prejudice to regard the trunk as the default stage, from which the head would have been established through its modification and specification. However, recent molecular developmental biology rejects this idea (Adachi et al., 2012; Onai et al., 2015a). Curiously, the scenario of anteroposterior polarization of the mesoderm giving rise to the head and trunk coincides well with the comparison of the neural elements in the neural tube between amphioxus and vertebrates (Fritzsch and Northcutt, 1993).

Are there segments in the head?

This review dealt with the head cavities first recognized in the elasmobranch embryos, and discussed the origin of the vertebrate head, which apparently is not segmented as is the trunk. From the data at hand, it appears likely that the head cavities do not reflect somite-like segmentation in the

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hypothetical ancestor. However, that may not entirely rule out the possibility of head segmentation per se. We still have many enigmatic embryological phenomena remaining to be solved, like the small mesodermal vesicles arising in the early embryos of *Torpedo*. Thus, the mesodermal component of the vertebrate head may still possess somite-like segmental signatures in a form we have not seen yet. Nevertheless, as has been noted above, there are ways to tackle this problem with recent molecular and cellular methodologies. Moreover, segmentation or metamerism is no longer a central issue in developing a better understanding of the origins of the vertebrate head. There are accumulating data to show the anteroposterior polarization of the common mesodermal precursor resulted in the simultaneous acquisition of the head and trunk mesoderm. Now the more fundamental questions arise. Namely, what is the origin of mesodermal coeloms along the anteroposterior axis? If it was in the ancestor that resembled dipleurula larvae, where do we find the homologs of three pairs of coeloms; namely, protocoel, mesocoel, and metacoel? Do we still see these three coeloms in our own bodies?

Regarding above questions, among the head cavities, the premandibular cavity was often suggested to be homologous to the anterior gut diverticulum in the amphioxus (van Wijhe, 1901), and further to the protocoel (anterior coelom) of tricoelomate dipleurula larvae (Goodrich, 1917; Neal and Rand, 1946; Kuratani et al., 1999; Holland and Holland, 2010). To support this, it would be worth mentioning that premandibular cavities of *Torpedo* (!) have been known to grow epithelial canals that open to the exterior (Goodrich, 1917; de Beer, 1955), resembling the coelomic morphology in dipleurula larvae (as for its relevance to the anterior gut diverticulum and mouth formation in amphioxus, see Kaji et al., 2016). Also, recent molecular developmental analyses have shown a similarity of gene expression profiles of prechordal plate (source of the premandibular cavity) in vertebrates and the hemichordate stomochord, a derivative of the protocoel in tornaria larvae (Gerhart et al., 2005). This scenario is relevant to the origin of mesodermal coeloms and not necessarily supports the somite-like segmental property of the head cavity. Further molecular developmental studies will be needed to evaluate the homology of the premandibular cavity/mesoderm, as well as those of other head cavities.

The history of head segmentation started as a transcendental morphological concept, in search for the idealistic pattern called the ‘archetype’ to explain the wide variety of shapes of all the vertebrate species. Evolutionary developmental studies today compel us to abandon the archetype, and to approach the question of segmentation from a wider evolutionary perspective along the phylogenetic tree, asking new questions about the true origins of mesodermal coeloms and mechanisms of axial specification at molecular developmental levels. Many more riddles remain to be solved.

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