NOTE ADDED IN APRIL 2017

Chapter 6 has been kept in the book for historical reasons. In the 1980s and 1990s, somitomeres were all the rage. I described them as seven immature somites occurring in the head cranial to the occipital somites. I said they were incompletely separated from one another, and do not form sclerotomes or dermomyotomes. This, and my further discussion of their fate was based largely on Noden (1) and the references cited therein. After *Essentials of Gross Anatomy* was published, Noden reversed his position and cast doubt on the existence of somitomeres, asserting that the paraxial mesoderm cranial to the occipital somites is unsegmented (2, 3). All authoritative researchers now agree with this assessment (4 - 10). The unsegmented paraxial mesoderm anterior to occipital somites is simply referred to as cranial paraxial mesoderm (CPM). Furthermore, no clear morphological boundary separates the CPM from the splanchnic lateral plate mesoderm (9 - 11). A separation of the two is clearly detectible only by the fact that they express different genes (9).

What does the unsegmented CPM do? From the early 1980s until recent times, it was believed that CPM is the source of all striated muscle in the head. The current view of experts about the source of branchiomeric muscles is complex. The mesodermal core of a branchial arch is composed dorsally of CPM cells and ventrally of splanchnic lateral plate cells (12, 6, 13). Regarding the first arch, the major masticatory muscles (masseter, temporalis, pterygoids) come mainly from the CPM component of mesodermal core. On the other hand, certain first arch muscles (e.g., mylohyoid and anterior digastric) are entirely derived from lateral plate (12, 14, 7, 11). All muscles of the second arch are probably derived from the lateral plate contribution to branchial mesoderm (12, 7), as are all the muscles associated with more caudal arches (i.e., those muscles innervated by CN IX, X, and XI). Surprisingly, so is a part of the splenius (15, 9). As if this complexity were not enough, it turns out that the most ventral part of the mesodermal core of the first and second arches give rise to a substantial portion of the heart (12, 14, 6, 13, 7, 16, 15), which evens receives some contribution from the CPM that migrated into the first branchial arch (4, 12, 14, 6, 7). Indeed, the modern view is that the mesodermal core of the branchial arches is part of a cardio-craniofacial developmental field (12, 11, 17).

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CHAPTER 6

Segmental Patterns in the Head and Upper Neck

A considerable portion of Chapter 2 was devoted to a discussion of how the body wall of the trunk, and particularly its innervation, has a fundamentally segmental nature derived from the role played by somites in its development. The history of comparative anatomy and embryology is replete with attempts to find a similar segmentation underlying the structure of the head and upper neck linked to the development of the branchial (gill) arches. Some lovely stories have been created to "homologize" various cranial nerves with either dorsal or ventral roots of spinal nerves, and then pairing off each such cranial "ventral root" with a cranial "dorsal root" to make a segmental nerve whose two "roots" have simply failed to join. Intimately tied to these stories was the belief that in the cranial region the lateral plate mesoderm did the very unusual thing of differentiating into voluntary skeletal muscle. Skeletal muscles so derived were referred to as *special* visceral motor structures. The motoneurons innervating them were called special visceral motoneurons. The axons of special visceral motoneurons were supposed to do the very peculiar thing of exiting the CNS via cranial "dorsal roots." Noden[22] has reminded us that this story, although based on a large body of descriptive evidence, was supplemented by a considerable amount of conceptual bias. Unfortunately, though the tales that can be told are elegant, the evidence that Noden has gathered force us now to view the issue rather differently. Read on if you are interested in this new view on head and upper neck segmentation. If you want only a description of the anatomy of a fully developed human, skip to Chapter 7.

SEGMENTATION OF THE PARAXIAL MESODERM CRANIAL TO THE 1ST CERVICAL SOMITE

It will be recalled that embryonic spinal cord lies dorsal to the notochord and is flanked by the paraxial mesoderm, which soon breaks up into somites (see Figs. 2-1, 2-2). But the notochord and paraxial mesoderm also extend cranially into the region where the brain is forming. They reach as far as the site where the pituitary gland arises from the diencephalon. The paraxial mesoderm immediately cranial to the spinal cord breaks up into somites, which number four on either side of the caudal part of the medulla (Fig. 6-1). These are called **occipital somites**. Further cranial still, one can distinguish within the paraxial mesoderm a linear array of seven rudimentary somites called **somitomeres**. Unlike genuine somites, the somitomeres do not separate completely from one another, nor do they develop recognizable dermomyotomes and sclerotomes.

The somitomeres and the four occipital somites constitute the 11 paraxial mesoderm "blocks" of the head. Like their counterparts in the neck and trunk, each contributes to the skeleton surrounding the neural tube, i.e., in the head, most of the of the braincase.[23] Each of the 11 paraxial blocks also gives rise to striated voluntary muscle. You will recall that one spinal nerve ventral root is destined to innervate the muscles to which its neighboring dermomyotome contributes. A similar, but less certainly determined,

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[22]Noden, DM: The embryonic origins of avian cephalic and cervical muscles and associated connective tissues. Am J Anat 168: 257-276, 1983.

[23] The skeleton of the face, and some parts of the braincase, have an origin unlike any bone we have heretofore considered. They are derived from neural crest cells that leave their usual site alongside the developing neural tube.

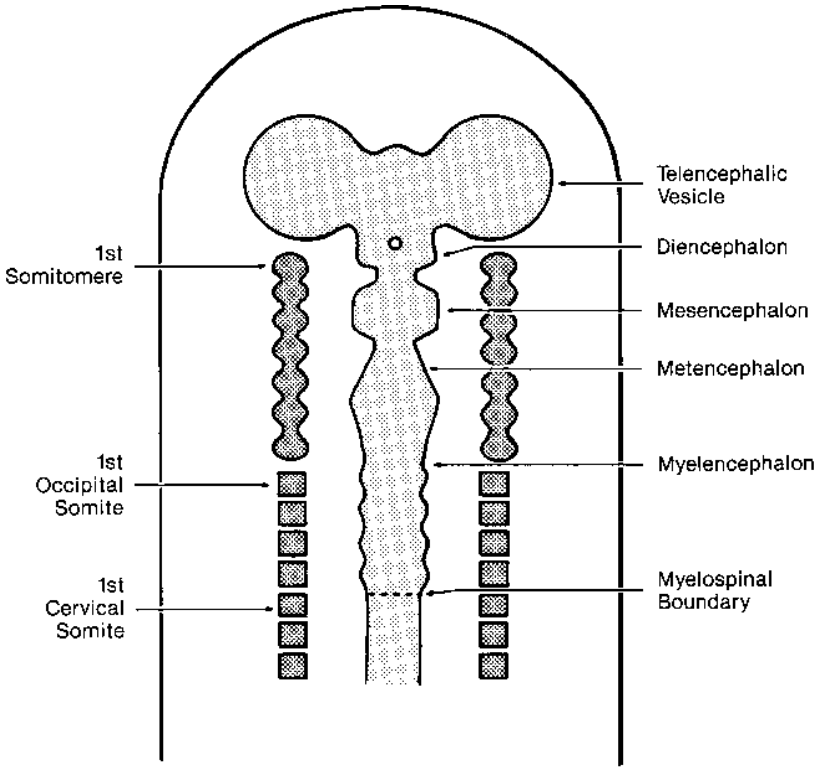

Figure 6–1. A schematic coronal section through the cranial end of an embryo illustrating the somitomeres and somites of the head in relation to the developing brain.

pattern exists in the head, where each somite or somitomere seems to have a cranial nerve destined to innervate its descendant muscles. Table 6-1 presents a scheme of this pattern.

TABLE 6-1
(Modified from Noden[1])

Source of Voluntary Striated Muscle	Cranial Nerve Supplying Motor Innervation to the Muscles
Prechordal mesoderm and	
Somitomeres 1 & 2	Oculomotor (III)
Somitomere 3	Trochlear (IV)
Somitomere 4	Trigeminal (V)
Somitomere 5	Abducens (VI)
Somitomere 6	Facial (VII)
Somitomere 7	Glossopharyngeal (IX)
Occipital somite 1	Vagus (X)
Occipital somite 2	Vagus (its recurrent laryngeal branch)
Occipital somite 3	Hypoglossal (XII)
Occipital somite 4	Hypoglossal

Four cranial nerves have been excluded from Table 6-1. Three of them are purely sensory[24]: olfactory (I), optic (II) and stato-acoustic (VIII). The other is the spinal accessory (XI), which indeed does carry somatic motor axons. These axons innervate certain muscle fibers in the sternocleidomastoid and trapezius that are probably derived from the last three occipital somites. The motoneurons for the spinal accessory nerve lie in the ventral horn of the cervical spinal cord, possibly having migrated there from the embryonic brain.

[24] Except that the optic and stato-acoustic nerves do actually carry nonmotor efferent fibers.

THE BRANCHIAL ARCHES--ANOTHER KIND OF SEGMENTATION

Like the paraxial mesoderm and notochord, the gut tube extends as far cranially as the site of origin of the neurohypophysis. Whereas in the trunk the gut tube is separated from the ectoderm by lateral plate mesoderm (within which is the coelom), in the head and upper neck the lateral plate mesoderm is either nonexistent or very diminished. If it exists, its only contribution is to the endothelial lining of the vasculature. Where lateral plate ought to be is a space that is invaded by neural crest cells, which are said to form an **ectomesenchyme**. This ectomesenchyme becomes partially segmented by the development of laterally directed evaginations of the cranial foregut (pharynx) toward corresponding invaginations of the ectoderm (Fig. 6-2). The evaginations of the foregut are called **pharyngeal pouches**, and they number four on each side. The corresponding invaginations of the ectoderm are called **branchial clefts**. Where ectoderm and endoderm meet, they form the **branchial septa** (closing plates of the pharyngeal pouches). The four pharyngeal pouches and branchial clefts divide the ectomesenchyme that lies lateral to the pharynx into five blocks called **branchial arches**. They are numbered 1, 2, 3, 4, and 6 because a rudimentary (5th) arch, between the last two major arches, can sometimes be seen. The ectomesenchyme ventral to the pharynx is not segmented.

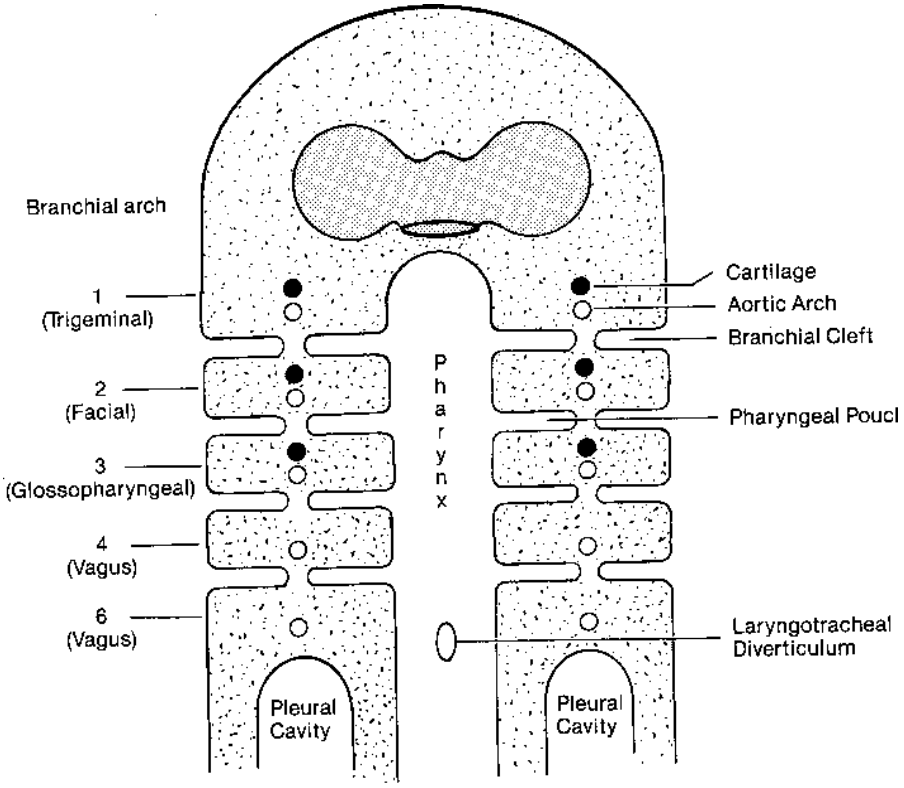

Figure 6–2. A schematic coronal section through the cranial end of an embryo (ventral to the level shown in Fig. 6–1) illustrating the development of pharyngeal pouches, branchial clefts, and branchial arches filled with ectomesenchyme.

Ectomesenchyme will eventually differentiate into all the connective tissue, dermis, tendon, smooth muscle, and skeleton of the face and uppermost neck. The cells of the first branchial arch will contribute to the incus, malleus, sphenomandibular ligament, mandible, and maxilla. Ectomesenchyme of the 2nd branchial arch contributes to the stapes, styloid process of the skull, stylohyoid ligament, and the lesser horn and upper part of the body of the hyoid bone. Ectomesenchyme of the 3rd branchial arch contributes to the greater horns and lower part of the body the hyoid bone. It is unclear whether or not the

ectomesenchyme of the 4th and 6th arches form any skeletal elements (some authors believe that it contributes to the laryngeal cartilages).

The creation of branchial arches seems to be a phenomenon that occurs independently of the segmentation of the paraxial mesoderm; the number of arches varies between vertebrates, whereas the number of somitomeres does not. Nonetheless, there is a relationship between somitomeres and branchial arches created by the migration of some somitomere cells into the ectomesenchyme of the arches. It turns out that the cells from the 4th (trigeminal) somitomere migrate into the first branchial arch where they become muscles associated with the skeletal elements derived from the ectomesenchyme of this arch. Cells from somitomere 6 (facial) migrate into the 2nd branchial arch, and cells from somitomere 7 (glossopharyngeal) enter the 3rd branchial arch. The caudal two arches receive a cellular input from the 1st and most of the 2nd occipital somites (the two vagal somites). The remaining two occipital somites send most of their cells ventral to the pharynx into the tongue region.

CRANIAL NERVES WITH DORSAL ROOTS

So far, we have considered cranial nerves as if most were entirely homologous to the ventral roots of spinal nerves that innervate striated voluntary muscle. However, the four cranial nerves associated with somitomeres that send cells into branchial arches are also characterized by sensory ganglia that can be homologized to dorsal root ganglia. Thus, the trigeminal, facial, glossopharyngeal, and vagus nerves are more completely comparable to spinal nerves than are the others.

CRANIAL NERVES WITH GENERAL VISCERAL MOTOR AXONS

Some cranial nerves, like some spinal ventral roots, carry preganglionic general visceral motor axons. Just as there was no rhyme or reason to the pattern of spinal ventral roots that did so, so there is no way to predict which cranial nerves have autonomic fibers. One must simply memorize that the oculomotor, facial, glossopharyngeal, and vagus do. All such preganglionic autonomic axons belong to the parasympathetic system, thus are concerned with energy intake and conservation. In the case of the oculomotor, facial, and glossopharyngeal nerves, the preganglionic parasympathetic axons will synapse on postganglionic cells that are located in named dissectible ganglia. The vagal preganglionic parasympathetic axons go to postganglionic cells distributed in the walls of the organs to be innervated.

SPECIAL SENSATIONS

Olfaction, vision, taste, hearing, and equilibrium are very special sensations because they have no counterpart in the trunk. Olfaction and vision are so special that each has its own uniquely structured cranial nerve unrelated to any segmental scheme of the head. Taste is said to be a **special *visceral* sensation**. Of the four cranial nerves associated with branchial arches (V, VII, IX, and X) and consequently having sensory components, only the facial, glossopharyngeal, and vagus carry taste fibers. Hearing and equilibrium are referred to as **special *somatic* sensations**. In lower vertebrates, special somatic sensory axons run with the facial, glossopharyngeal, and vagus nerves. In mammals, however, such fibers are associated only with the facial nerve and form a separate bundle called cranial nerve VIII, or the stato-acoustic nerve.