

An Episode in the Ancestry of Vertebrates: From Mitrate to Crown-Group Craniate

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Human beings have a natural interest in their origins. We are vertebrates, within the craniates, within the chordates. Fossils indicate how the chordates separated, in early Palaeozoic times or before, from their latest common ancestor with the echinoderms. The most primitive known fossil chordates retained a calcitic skeleton of echinoderm type (calcichordates) and some of these, the mitrates, were like giant calcite-plated tunicate tadpoles, consisting of a head and a tail with no trunk region. Some mitrates are themselves craniates in the broad sense and represent the ancestral group (stem group) from which extant craniates descended. In this paper, we describe such a stem-craniate mitrate, and reconstruct, from the shared characteristics of the extant craniates supplemented by evidence from fossils, the latest common ancestor of extant craniates which we call “animal x” (In most respects animal x would resemble a hagfish, but its larva would filter-feed like a lamprey larva.) We then list the changes involved in transforming a mitrate into animal x and describe the probable changes in development in early embryos that converted a mitrate into animal x. During this transition, our ancestors took to swimming forwards rather than crawling rearwards, lost the calcitic skeleton, and acquired the trunk region, the notochordal region to the head, kidneys, and neural-crest cartilage. An important developmental mechanism involved was forward extension of the notochord, caused by anteriorly directed convergent extension movements.

KEY WORDS: chordates, echinoderms, calcichordates, mitrates, evolution of craniates, convergent extension

This paper aims to reconstruct how the latest common ancestor of extant craniates arose from the fossils known

as mitrates. More concretely, we aim to show how an animal somewhat resembling a hagfish arose from one much like a giant calcite-plated tunicate tadpole.

Human beings, like cows and codfishes, are gnathostomes (jawed vertebrates). The gnathostomes plus lampreys constitute the vertebrates.¹ The vertebrates plus hagfishes constitute the craniates. And the craniates, in turn, are part of the chordates (craniates plus acraniates plus tunicates). Moreover, it has long been supposed, mainly on embryological grounds, that the chordates as a group are closely related to the echinoderms (the starfishes and their allies).^{2,3} Evidence from fossils now confirms and elaborates this close relationship.

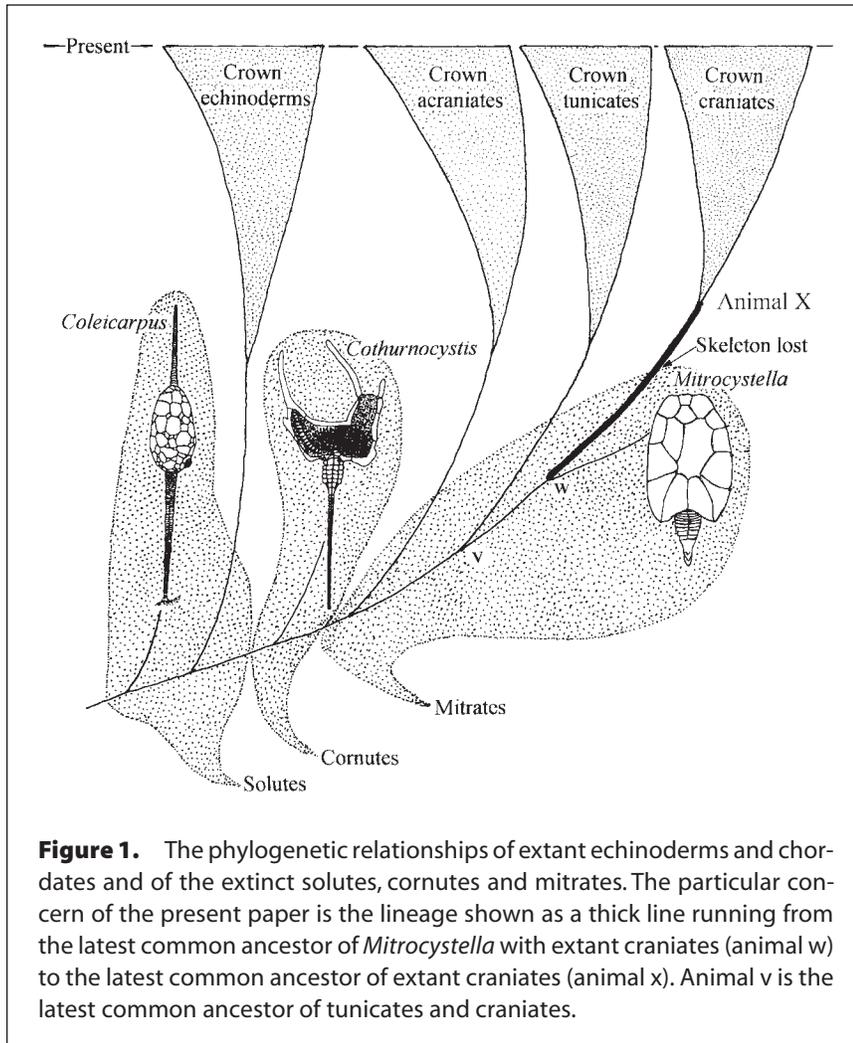
Modern echinoderms all have a strikingly radial anatomy, primitively with five rays, and a skeleton of calcium carbonate in which each plate is a single crystal of calcite in the arrangement of its atoms. For more than a century, however, ancient marine fossils have been known with a calcitic skeleton of just this type but no trace of a radial anatomy.^{4,5}

These fossils, called by the general name of carpoids,⁶ are found in rocks of Cambrian to Pennsylvanian age (about 570 to 300 million years old). The carpoids are very informative fossils whose skeletons often allow the soft parts to be reconstructed.

There are several major traditional groups of carpoids, mostly first recognized in the early 20th century.^{6,7} Of particular importance here are the solutes, the cornutes and the mitrates (Fig. 1).

The solutes, ranging in age from Middle Cambrian to Devonian (540 to 380 million years old), consist of a head with a tail at one end and a feeding arm at the other. All parts are calcite-plated. The head lay with one surface on the sea bottom. The flexible feeding arm contained a water vascular system with tube feet — a system that is also present in the arms of extant echinoderms. Some solutes had a gill slit at posterior left in the head. Most known solutes are probably chordates in the wide sense, meaning that they are probably more closely related to extant chordates than to any-

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thing else still extant. One solute, however, *Coleicarpus sprinklei* from the Middle Cambrian of Utah,^{3,8} is probably neither an echinoderm nor a chordate, but belongs to the common stem group from which echinoderms and chordates descended. *Coleicarpus* was fixed to the sea bottom by the end of its tail but in almost all other solutes the tail was probably locomotory, serving to pull the head rearwards across the sea floor. The latest common ancestor of echinoderms and chordates would have been a solute.⁹ The solutes, as a group, were ancestral to cornutes.

The cornutes, known from Middle Cambrian to late Ordovician (540 to 440 million years old), had a head and a tail.^{10,11} They derived from the solutes by loss of the feeding arm. The head always had several gill slits on the left side only and sometimes was grossly asymmetrical in outline, as in the bizarre *Cothur-*

nocystis elizae from the Upper Ordovician of Scotland. The tail of cornutes, however, was bilaterally symmetrical. The presence of gill slits on the left side only is strikingly reminiscent of larval amphioxus, among present-day chordates, in which all the gill slits are left gill slits. This transitory state in amphioxus can be seen as a recapitulation of the ancestral cornute condition. The tail of cornutes such as *Cothurnocystis* is adapted for pulling the head rearwards across the sea floor, waving from side to side and pushing the down-turned tip into the bottom mud as a punt pole.¹² Since *Cothurnocystis* had no feeding arm, but in its large pharynx had several gill slits rather than the single one present in solutes, it probably fed by a mucous filter inside the pharynx, as does larval amphioxus.^{13,14} The cornutes as a group were ancestral to the mitrates.

The mitrates, known from Lower Ordovician to Pennsylvanian (505 to 300

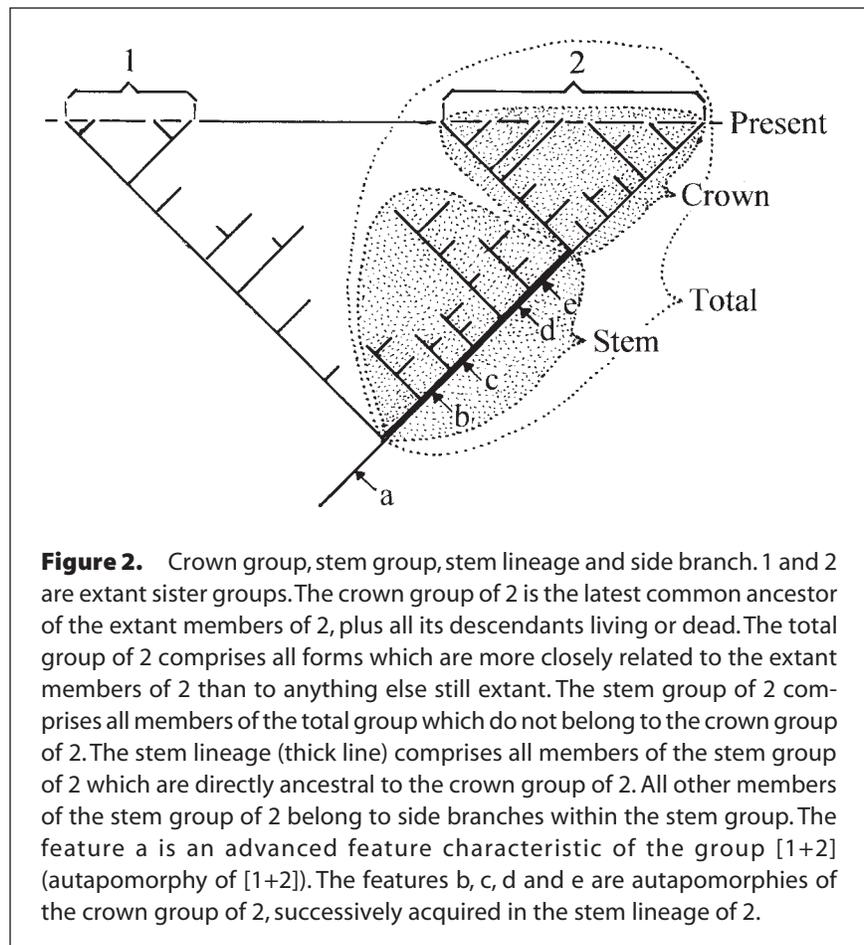
million years old), resembled cornutes in having a head, a tail and no feeding arm. The head was almost bilaterally symmetrical in outline (as was also true of some particularly mitrate-like cornutes)¹⁵ but still retained strong left-right asymmetry in its internal structure. In the cornutes, as already mentioned, there were left gill slits only, and these would have opened from the single, left cornute pharynx. In mitrates, however, there are indications of a right pharynx, additional to the left pharynx which already existed in cornutes. The right pharynx of mitrates pouted out of the left pharynx in the course of ontogeny. This change is repeated in the metamorphosis of amphioxus, when the first right gill slits appear, suddenly and simultaneously, to join the left gill slits already present. There are no external gill slits in mitrates but there was a pair of atrial openings at posterior left and right in the head. These represent the outlets of the left and right atria — small chambers external to the gill slits. Such slits are observed to be present in two known mitrates¹⁶⁻¹⁸ and presumably existed in all of them. Mitrates almost certainly pulled themselves rearwards across the sea floor by pushing the tail into the bottom sediment ventrally and forwards under the head. This supposition was based, until recently, solely on functional morphology but has now been confirmed by finding a mitrate dead at the end of its own locomotion trace, as will be described elsewhere. All known mitrates can be assigned to the extant subphyla of chordates, being most closely related either to modern acraniates such as amphioxus, or to the tunicates or to the craniates.^{10,19} The latest common ancestor of living chordates would be a mitrate. It follows that the calcitic skeleton of mitrates has been lost three times — once in the origin of the acraniates (amphioxus and allies), once in the origin of the tunicates (sea squirts) and once in the origin of the extant craniates. In basic layout and in many anatomical details, the mitrates are similar to the tadpole larva of modern tunicates. They also resemble the somatico-visceral animal postulated as an ancestor of the vertebrates by Romer (1972).²⁰

The carpooids, calcichordates, solutes, cornutes and mitrates are all groups of traditional type, defined by the presence of recognizable characteristics without direct reference to phylogeny.

Present-day systematics, however, is not content with such traditional groups. Rather, it follows a cladistic approach which seeks to place organisms in relation to their phylogeny.³ So far as extant organisms are concerned, cladistics thus aims to recognize none but strictly monophyletic groups, meaning those which include all the descendants, and only the descendants, of a single extinct stem species. It also aims to arrange such monophyletic groups into pairs of sister groups, each of which is more closely related to its sister group than to anything else still extant.²¹ ("Is more closely related to..." means: "shares a more recent common ancestor with...") Each pair of sister groups forms a more inclusive monophyletic group, which will have its own sister group, and so forth.

In applying cladistics to fossils, every monophyletic group with extant members can be delimited in two obvious ways — a broader and a narrower. The broader delimitation includes all forms, whether living or dead, which are more closely related to the extant members of the group than to anything else still extant. This is called the total group. The narrower delimitation includes the latest common ancestor of the living members of the group, and all descendants of that ancestor, whether living or dead. This can be called the crown group. And if the crown group is subtracted from the total group, what remains is the stem group which by definition is extinct.²¹⁻²⁴ Through the stem group runs the stem lineage. This is the exact series of ancestors and descendants which leads to the crown group from the latest common ancestor with the sister group. In this stem lineage, the advanced characteristics special to the crown group were acquired (Fig. 2).

The name of an extant group, in our usage, applies to all the members of the total group. Thus, to take a contentious example, the dinosaurs belong to the total group of the birds, being more



closely related to birds than to anything else still extant. In our usage, therefore, the dinosaurs *are* birds.

The particular aim of this paper is to reconstruct the evolutionary changes by which craniate mitrates gave rise to the latest common ancestor of extant craniates (the first member of the craniate crown group) and to suggest their developmental causes. Most of these changes occurred after the mitrate calcitic skeleton had been lost and before bone had been acquired. They have thus left no fossil record and what we write is speculative. However, we start from a known beginning and end with an animal which, though hypothetical, can be reconstructed by cladistic argument.

We do not here defend the calcichordate theory of the origin of chordates but simply assume it to be correct.^{10,18,3,24-26} There are also contrary views.^{27,28} Gee gives a non-partisan overview.²⁹

One of the most important changes in passing from the mitrates to the latest common ancestor of extant craniates

was craniate tail-head overlap.³ By it the anterior part of the mitrate tail pushed forward over the posterior part of the mitrate head, giving rise to the notochordal head and the trunk of extant craniates. We shall suggest how rather simple changes in the early development of the animal forms intervening between a stem-craniate mitrate and animal x could account for the new parts and rearrangements. A modified set of cell movements in ontogeny, associated with the process known as convergent extension, was probably the basic cause of tail-head overlap and thus explains the origin of the new notochordal part of the head and the relocation into the trunk of animal x of parts, such as non-pharyngeal gut, gonad and heart, that had been in the mitrate head.

In embryos of extant chordates, convergent extension is a movement of cells within the notochordal plate, and within the neural plate, toward the midline and along the midline, thus narrowing these tissues and extend-

ing them along the midline. In a mitrate, as in a tunicate tadpole, this extension would be solely posterior in direction, causing the notochord and spinal nerve of the tail to protrude entirely rearwards. In animal x, on the other hand, as in modern craniates, there would be a dead point part way along the notochord and neural plates. Anterior to the dead point, cells would converge on the midline then move anteriorly. Posterior to the dead point they would converge on the midline then move posteriorly. The dead point thus marked the junction between the new trunk and the new tail.

As to timing, the earliest known vertebrates with bony skeletons are from the Upper Cambrian, about 520 million years ago.³⁰ These would be descendants of animal x, which must, therefore, have been older. The earliest known mitrates, on the other hand, are from the base of the Ordovician, about 505 million years ago. (The 15-million-year discrepancy in age is unimportant, because in the lower Ordovician the mitrates are already diverse and must therefore have existed earlier.) The events here discussed thus probably occurred sometime in the Cambrian, perhaps some 550 million years ago.

THE ANATOMY OF A MITRATE

As a representative mitrate we take the Lower Ordovician *Mitrocystella incipiens* (Barrande) from the Middle Ordovician of the Czech Republic and France (about 460 million years old). Details of its anatomy, mentioned below, suggest that *Mitrocystella* was a craniate in the broad sense and represents the stem group from which crown-group craniates evolved.^{31,19,24}

Mitrocystella consisted of a head and a tail (Fig. 3). The head was massive and externally almost bilaterally symmetrical with a flat dorsal face and a convex ventral face. The tail was bilaterally symmetrical and divided into fore tail, mid tail and hind tail. The skeleton both of tail and head was made of calcitic plates each of which, as in echinoderms, had the molecular structure of a single calcite crystal.

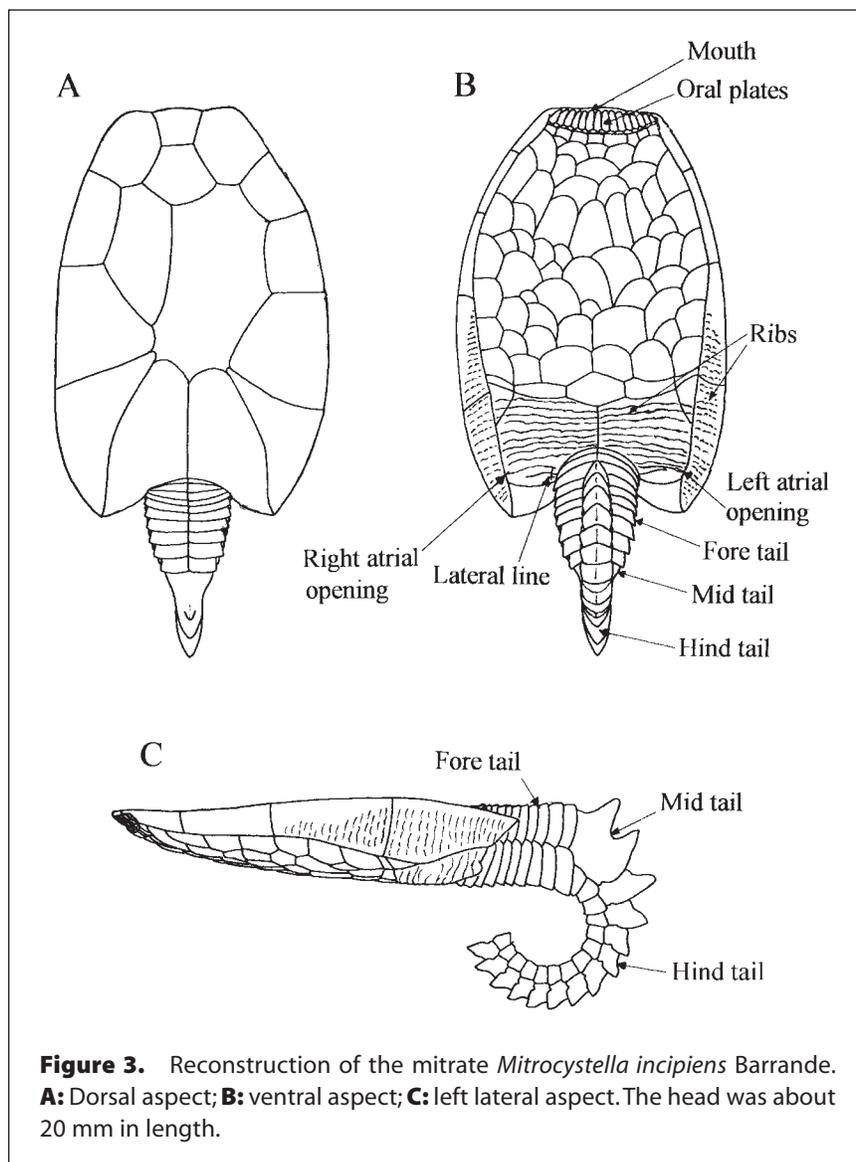


Figure 3. Reconstruction of the mitrate *Mitrocystella incipiens* Barrande. **A:** Dorsal aspect; **B:** ventral aspect; **C:** left lateral aspect. The head was about 20 mm in length.

The openings of the head in *Mitrocystella* consisted of a large mouth anteriorly, a pair of atrial openings between the dorsal and ventral skeleton posteriorly, and a lateral line in the form of a groove on the right postero-ventral plate of the head. The mouth had a rigid upper lip and a flexible lower lip guarded by a series of spike-shaped oral plates.

The following chambers of the head can be reconstructed in mitrates on the basis of the internal sculpture of the head skeleton and many interconnected comparative arguments which will not be given here (Fig. 4).

1) The **buccal cavity** lay just inside the mouth. It was presumably lined with ectoderm as in extant chordates.

2) The **left pharynx** extended from the buccal cavity to near the posterior left corner of the head.

3) The **right pharynx** extended from the left pharynx to near the posterior right corner of the head. The two pharynges were not symmetrical, therefore, particularly anteriorly, where it is likely that the buccal cavity opened mainly, or perhaps only, into the left pharynx. The right boundary of the left pharynx was marked by a strong ridge in the dorsal skeleton, corresponding to a groove in the natural mould (Fig. 5), which ran from anterior right to posterior left (oblique ridge and oblique groove). This ridge is weaker in its anterior portion, as if,

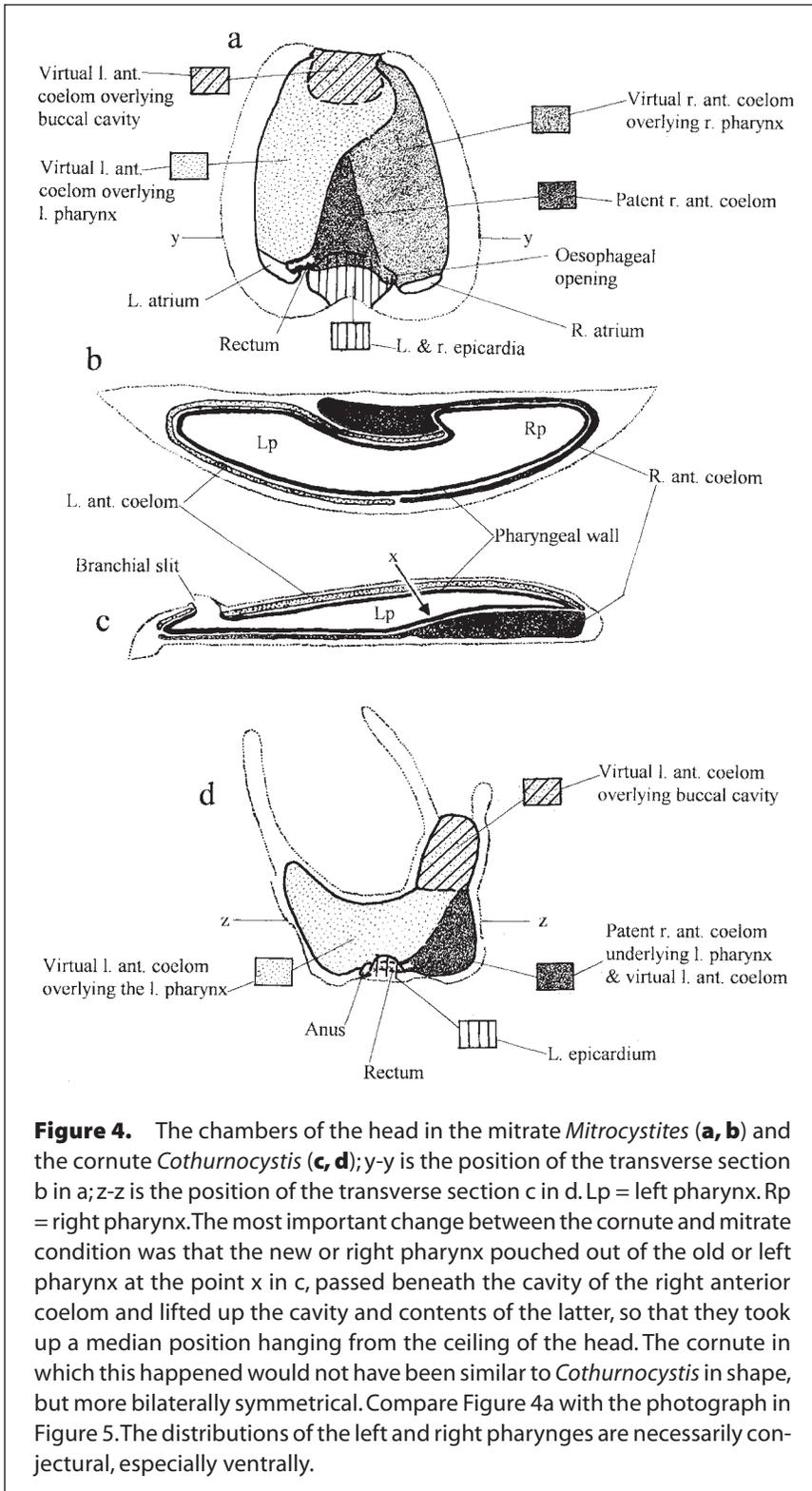


Figure 4. The chambers of the head in the mitrate *Mitrocystites* (a, b) and the cornute *Cothurnocystis* (c, d); y-y is the position of the transverse section b in a; z-z is the position of the transverse section c in d. Lp = left pharynx. Rp = right pharynx. The most important change between the cornute and mitrate condition was that the new or right pharynx pouched out of the old or left pharynx at the point x in c, passed beneath the cavity of the right anterior coelom and lifted up the cavity and contents of the latter, so that they took up a median position hanging from the ceiling of the head. The cornute in which this happened would not have been similar to *Cothurnocystis* in shape, but more bilaterally symmetrical. Compare Figure 4a with the photograph in Figure 5. The distributions of the left and right pharynges are necessarily conjectural, especially ventrally.

in ontogeny, the right pharynx arose later than, and pouched out of, the left pharynx, partly erasing the anterior part of the oblique ridge when it did so. A comparable asymmetry occurs in living am-

phioxus, in that the left pharynx similarly precedes the right pharynx in ontogeny.

4) The **left and right atria** were situated behind the left and right pharynges, between them and the left

and right atrial openings. There would be gill slits in the anterior walls of the atria, by which water would pass from the adjacent pharynx into the atrium. The rectum and gonoduct opened into the left atrium, as in a tunicate tadpole.

- 5) The **left and right epicardia** formed a single chamber "the posterior coelom" just in front of the tail. They would be homologous with the chambers called left and right epicardia in extant tunicates. The latter pouch out of the left and right pharynges, respectively, in the course of ontogeny and this was presumably true in mitrates also.
- 6) The **left and right anterior coeloms** are deduced to have existed mainly from comparative arguments. The left anterior coelom would have been wrapped around the buccal cavity and left pharynx and would have been entirely virtual (with no patent cavity). The right anterior coelom would have had a virtual part, wrapped around the right pharynx, and a patent part hanging from the ceiling of the head and occupying a triangular area between the left and right pharynges. This patent cavity would have contained the non-pharyngeal gut, the gonad and probably the heart.

The cornutes differed from mitrates in having left gill slits, left pharynx and left epicardium only, but no right equivalents.¹⁰ Moreover, the cavity of the right anterior coelom, with the contained viscera, lay at posterior right on the floor of the head in cornutes, rather than being suspended from the ceiling of the head near the mid line as in mitrates. The differences can be explained if, in the origin of the mitrates from the cornutes, the new right pharynx pouched out of the left or primary pharynx and extended to right posterior, under the cavity and contents of the right anterior coelom, which it lifted up and squashed into a median position, hanging from the ceiling of the head. Right gill slits developed at the posterior end of the new right pharynx and atria developed outside the gill slits, both on right and left.

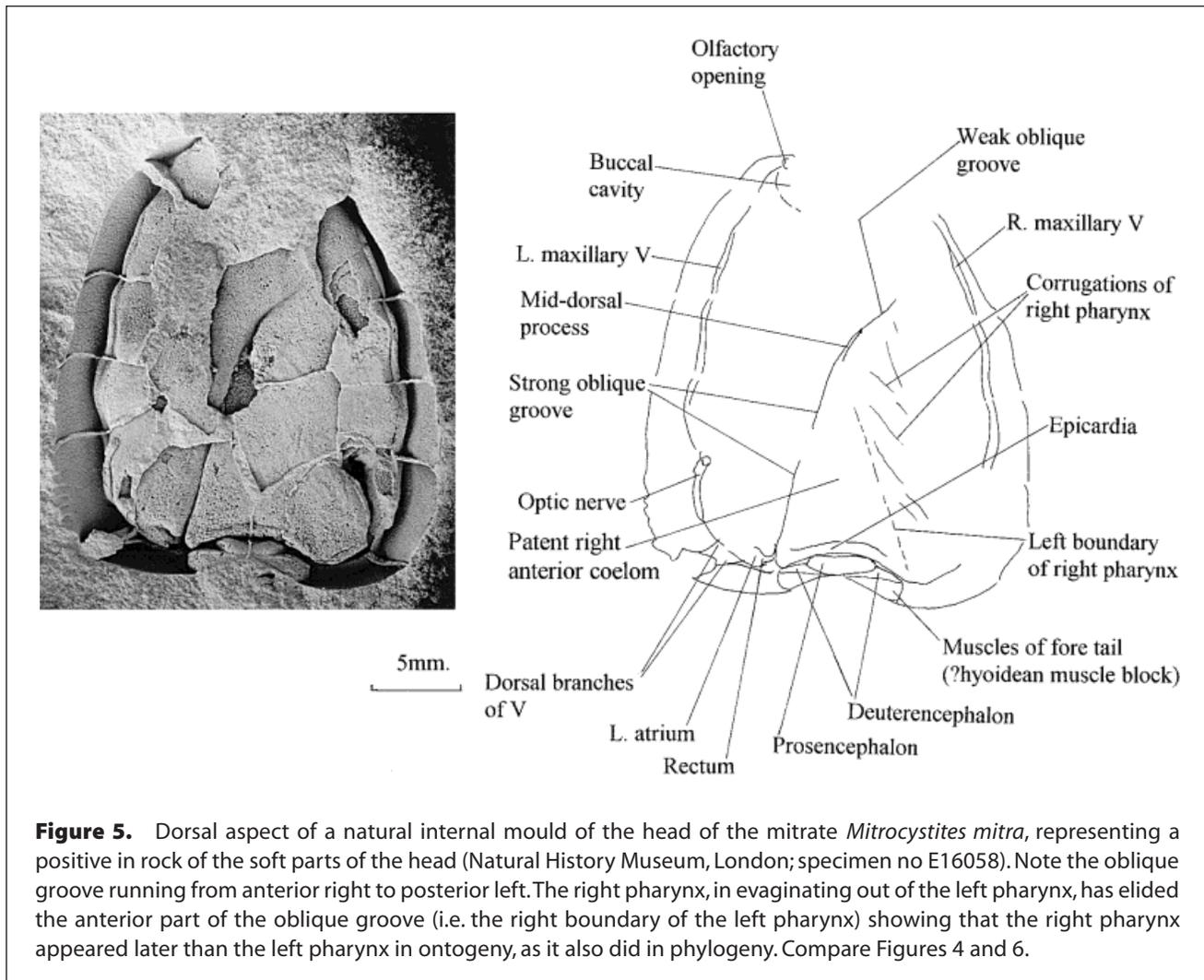


Figure 5. Dorsal aspect of a natural internal mould of the head of the mitrate *Mitrocystites mitra*, representing a positive in rock of the soft parts of the head (Natural History Museum, London; specimen no E16058). Note the oblique groove running from anterior right to posterior left. The right pharynx, in evaginating out of the left pharynx, has elided the anterior part of the oblique groove (i.e. the right boundary of the left pharynx) showing that the right pharynx appeared later than the left pharynx in ontogeny, as it also did in phylogeny. Compare Figures 4 and 6.

In the origin of the mitrates there were also considerable changes in the tail.

The classical vertebrate head somites (pre-mandibular, mandibular, hyoidean etc.) can be recognized in mitrates (Fig. 6).^{31,10} Once again, left-right asymmetries are important. As already mentioned, the buccal cavity of mitrates would have been enveloped entirely or almost entirely by the left anterior coelom of the head. This coelom would therefore have carried the velar mouth which would penetrate the posterior wall of the buccal cavity. In the larva of amphioxus, the larval mouth, which becomes the velar mouth of the adult, first appears on the left side of the animal, perforating the ventral part of the left mandibular somite. This asymmetry, because it appears early in ontogeny, may well represent the phylogenetically primitive situation. This suggests that

the left anterior coelom of mitrates could be homologous with the left mandibular somite of amphioxus (and therefore of the craniates). In that case, the right anterior coelom of mitrates would be homologous with the right mandibular somite of craniates and amphioxus. This is a reasonable result, since the mandibular somites of craniates are supplied by the trigeminal nerves and these are represented in mitrates by nerves passing the mouth region and to the ventral wall of the head.

As to the left and right pre-mandibular somites, they were probably represented in mitrates by a structure called the crescentic organ which lay in *Mitrocystella* at the posterior end of the head, in a median position, just anterior to the forebrain and dorsal to the bases of the optic nerves.^{31,10} This implies that the pre-mandibular somites in mitrates were pos-

terior to the mandibular somites. The hyoidean somites, if the previous arguments are correct, would be represented by the first pair of muscle blocks in the fore tail, which would be located just behind the disc-shaped brain. The hyoidean somites and branchial somites in mitrates, despite their names, would not be situated in gill bars since, as in a tunicate tadpole, all the gill bars and gill slits were in the head, whereas all the muscle blocks were in the tail. The relationship to gill bars arose only later within the crown-group craniates, probably in the stem lineage of the vertebrates.

The left and right atria of mitrates and tunicates are probably homologous with the otic vesicles of extant craniates, for several reasons.

- 1) Atria and otic vesicles both arise as ectodermal invaginations.

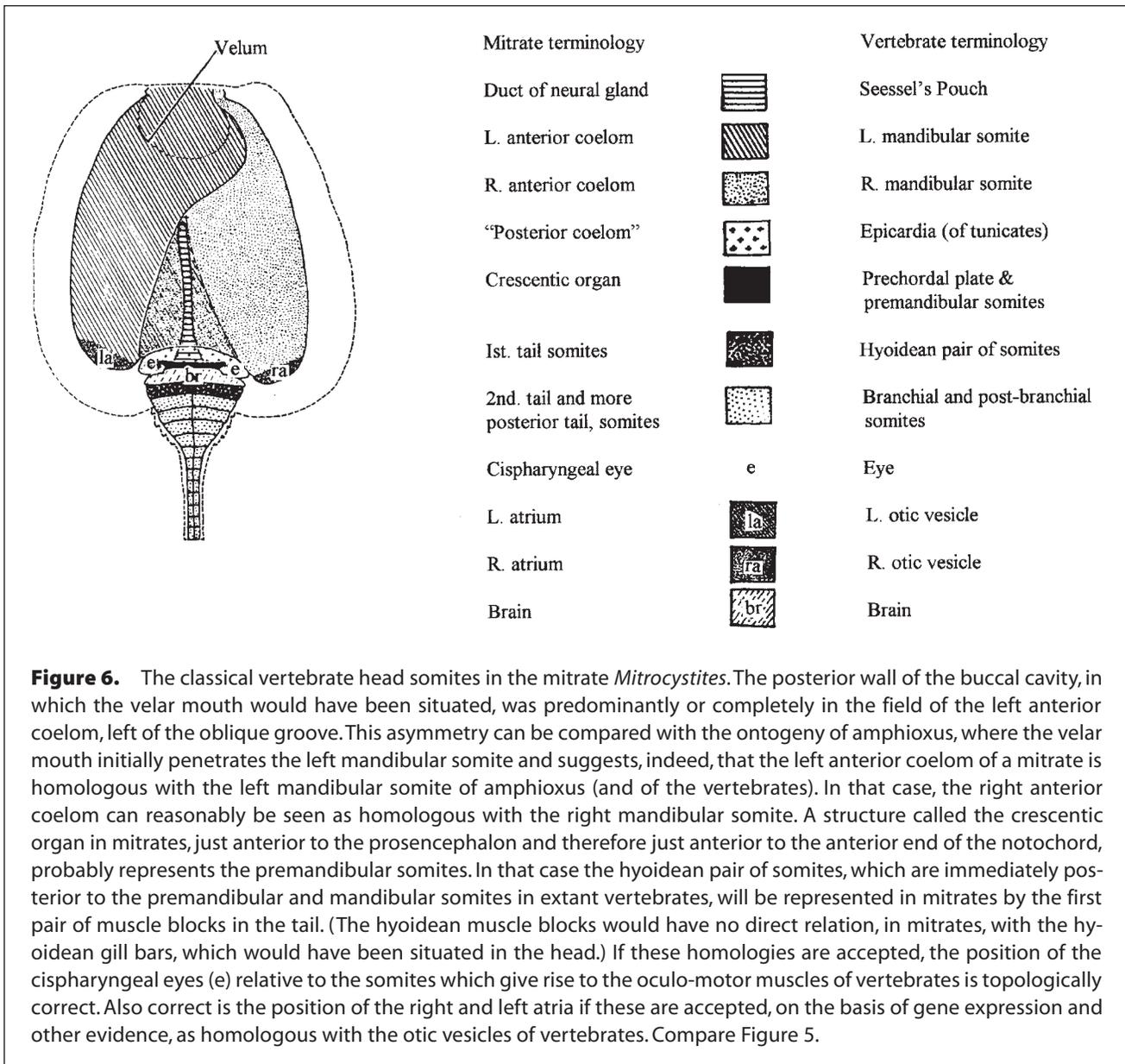


Figure 6. The classical vertebrate head somites in the mitrate *Mitrocystites*. The posterior wall of the buccal cavity, in which the velar mouth would have been situated, was predominantly or completely in the field of the left anterior coelom, left of the oblique groove. This asymmetry can be compared with the ontogeny of amphioxus, where the velar mouth initially penetrates the left mandibular somite and suggests, indeed, that the left anterior coelom of a mitrate is homologous with the left mandibular somite of amphioxus (and of the vertebrates). In that case, the right anterior coelom can reasonably be seen as homologous with the right mandibular somite. A structure called the crescentic organ in mitrates, just anterior to the prosencephalon and therefore just anterior to the anterior end of the notochord, probably represents the premandibular somites. In that case the hyoidean pair of somites, which are immediately posterior to the premandibular and mandibular somites in extant vertebrates, will be represented in mitrates by the first pair of muscle blocks in the tail. (The hyoidean muscle blocks would have no direct relation, in mitrates, with the hyoidean gill bars, which would have been situated in the head.) If these homologies are accepted, the position of the cispharyngeal eyes (e) relative to the somites which give rise to the oculo-motor muscles of vertebrates is topologically correct. Also correct is the position of the right and left atria if these are accepted, on the basis of gene expression and other evidence, as homologous with the otic vesicles of vertebrates. Compare Figure 5.

- 2) The atria, when they first arise in tunicate tadpoles, are at approximately the same transverse level, relative to the anterior end of the notochord and the anterior end of the tail muscles, as the otic vesicles of craniates. In lampreys and gnathostomes the otic vesicles arise in ontogeny lateral and just posterior to the hyoidean somites.^{32,10} In passing from mitrates to extant craniates the topological relations of these capsules (=atria) with the hyoidean (=1st tail) somites would thus remain almost unchanged.
- 3) The atria of tunicates contain cupular organs which seem to function as simple organs of hearing, homologous with neuromasts.³³
- 4) There were auditory ganglia in the atria of mitrates, supplied by auditory nerves. In the Lower Ordovician mitrate *Chauvelia*²⁵ there was a direct connection between the left auditory ganglion, in the left atrium, and the neighbouring part of the brain (in the deuterencephalon). The latter corresponds in position to the left acustico-lateralis nucleus in extant vertebrates. (The right antimer of the left auditory ganglion in *Chauvelia* was the lateral-line ganglion, connected with the lateral line which was a groove on the right postero-ventral surface of the head. There was a right auditory ganglion also, in the right atrium, more anterior than the lateral-line ganglion.)
- 5) There is now gene-expression evidence that the atria of tunicates are indeed homologous with the otic vesicles of vertebrates.³⁴

The tail of *Mitrocystella*, as already mentioned, was divided into fore, mid and hind tail. The fore tail probably contained the major locomotory muscles and an anti-compressional notochord which would allow it to bend without shortening. The plates of the fore tail

are arranged in rings which may correspond to muscle blocks in the soft parts. The hind tail of *Mitrocystella* was able to flex ventrally or straighten. It had a segmental skeleton and the internal sculpture gives evidence of spinal ganglia, dorsal nerve cord and notochord.¹⁰ The mid tail had a large dorsal element (the styloid) with an anterior excavation which probably received the posterior part of the locomotory muscles of the fore tail. By it, the fore tail could move the mid and hind tail as a unit.

The nervous system of *Mitrocystella* was extremely complicated and can be reconstructed in detail because many

parts of it are recorded as grooves or canals in the skeleton.¹⁰ The brain was situated where the tail joins the head. It was approximately dish-shaped and consisted of a median slightly inflated prosencephalon and a less inflated more posterior deuterecephalon. An undifferentiated spinal cord presumably connected with the posterior surface of the brain. (The mid and hind brain of an extant craniate would arise by combining the mitrate deuterecephalon with the anterior part of the mitrate spinal cord.)

The cranial nerves for which there is direct evidence in *Mitrocystella*, in the form of grooves or canals in the skeleton, include homologues of the olfactory,

optic, trigeminal and acustico-lateralis systems and a pair of nerves supplying the endostyle. The exceedingly complicated nervous anatomy is summed up in Figure 7 and photographically illustrated in Figure 8.

The calcitic skeleton is a very striking difference between mitrates and extant chordates. This skeleton is in fact absent in all extant chordates, presumably having been lost at least three times – respectively in the stem lineages of the acranites, tunicates and craniates. In the case of the craniates, this loss was presumably completed in the stem lineage of the craniates, before the latest common ancestor of extant craniates (referred to henceforth as animal x). *Mitrocystella* indicates how the loss began (Fig. 9).³¹ The dorsal skeleton in contact with the left and right pharynges always shows irregular cavities developed on the ventral surface of the plates. These cavities extend irregularly from the sutures between the plates in a manner which suggests resorption since it crosses at random any possible growth lines which the plates could have had. Presumably the cavities were filled with connective tissue, probably some form of cartilage. The resorption cannot be post-mortem since it bears a constant relation to the anatomy. It does not affect craniate mitrates less crownward (less closely related to the crown group) than *Mitrocystella* while more crownward mitrates have resorption cavities more extensive than *Mitrocystella*. Interestingly, signs of resorption have not been observed in the tails of any mitrates. (Beißwenger²⁵ spoke of resorption in the tail of the mitrate *Eumitrocystella* but, in our opinion, the alleged resorption cavities do not show the irregularity which would be expected if they had truly arisen by resorption.) We suggest that the connective tissue in the resorption cavities of the head skeleton probably represents the first phylogenetic appearance of neural-crest cartilage. Its observed location, always in association with the right and left pharynges, fits this interpretation since neural crest, in extant craniates, gives rise to cartilage only when it comes in contact with pharyngeal endoderm.³⁵

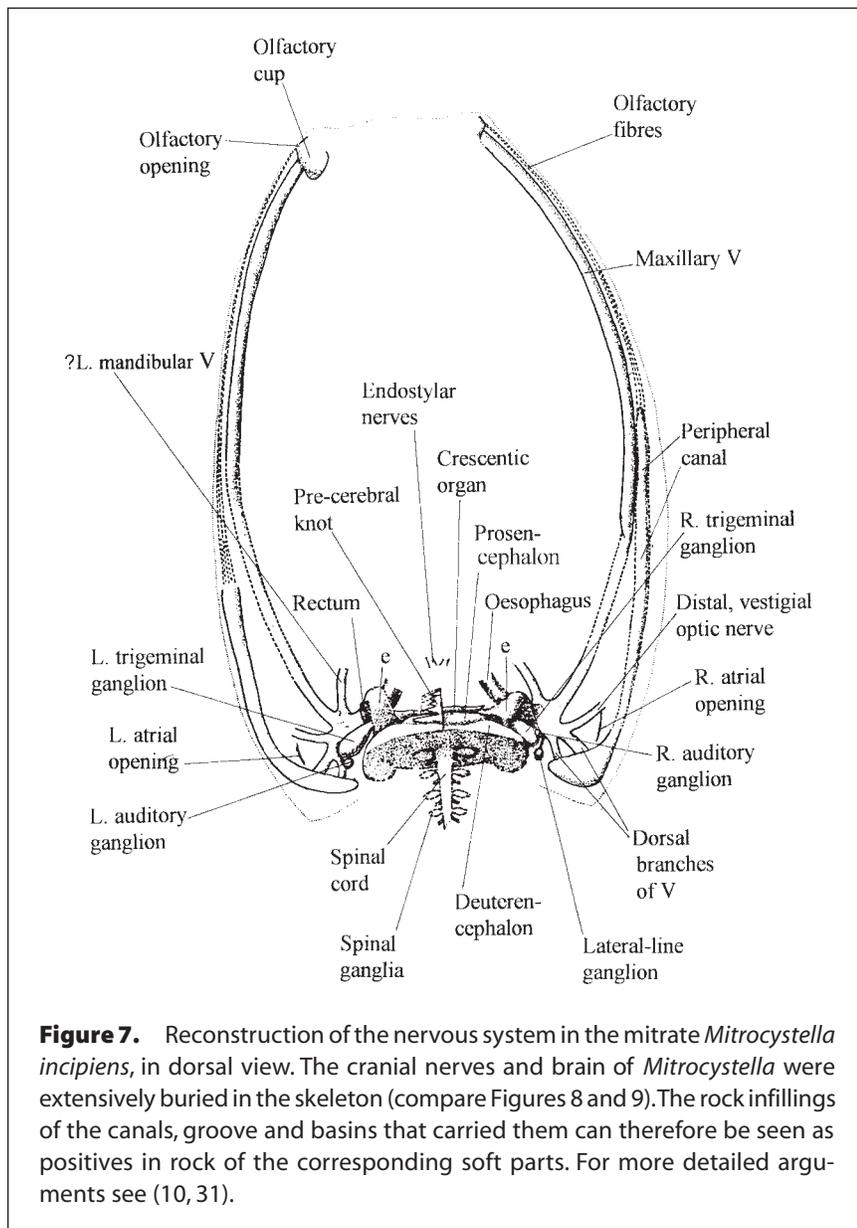


Figure 7. Reconstruction of the nervous system in the mitrate *Mitrocystella incipiens*, in dorsal view. The cranial nerves and brain of *Mitrocystella* were extensively buried in the skeleton (compare Figures 8 and 9). The rock infillings of the canals, groove and basins that carried them can therefore be seen as positives in rock of the corresponding soft parts. For more detailed arguments see (10, 31).

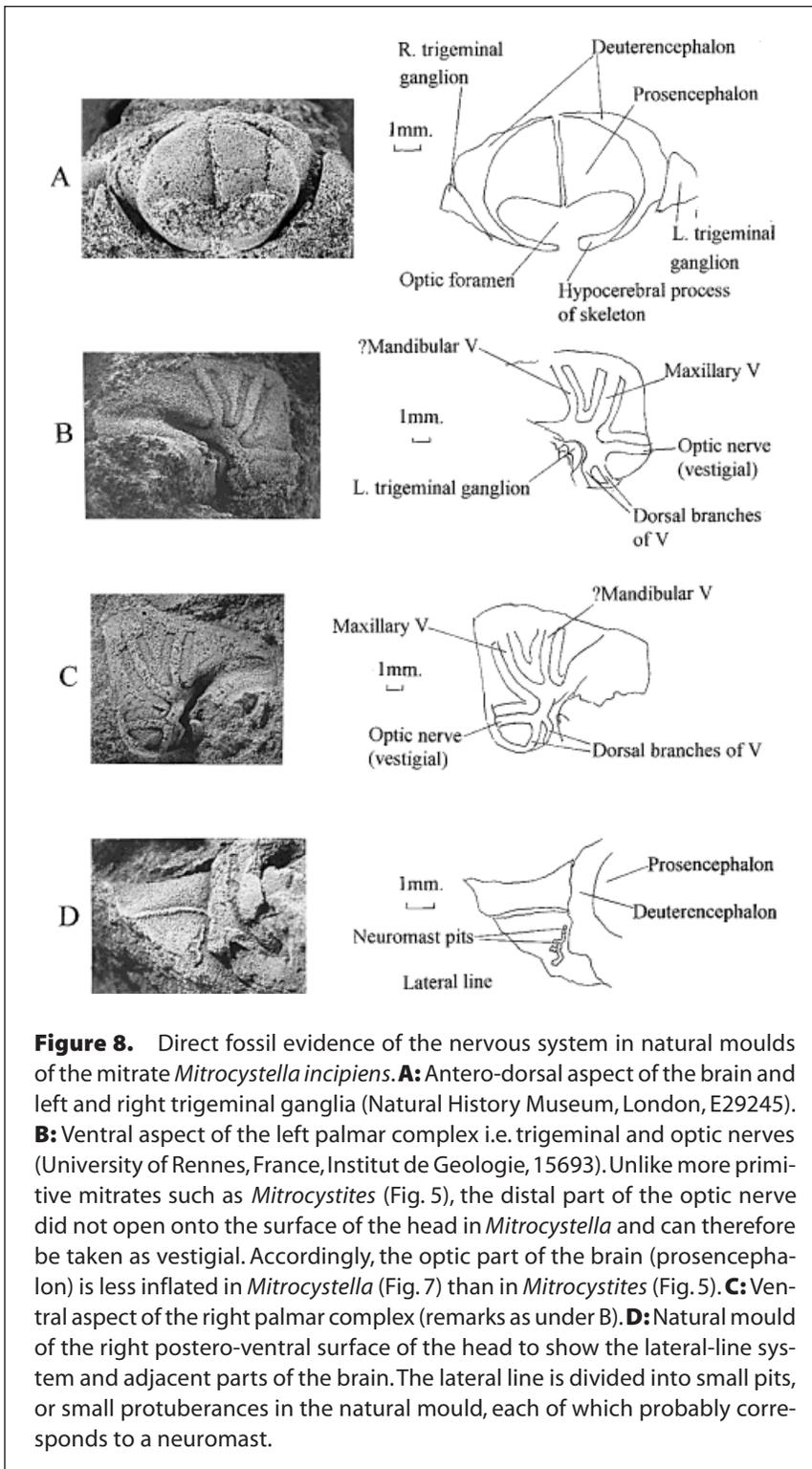


Figure 8. Direct fossil evidence of the nervous system in natural moulds of the mitrate *Mitrocystella incipiens*. **A:** Antero-dorsal aspect of the brain and left and right trigeminal ganglia (Natural History Museum, London, E29245). **B:** Ventral aspect of the left palmar complex i.e. trigeminal and optic nerves (University of Rennes, France, Institut de Geologie, 15693). Unlike more primitive mitrates such as *Mitrocystites* (Fig. 5), the distal part of the optic nerve did not open onto the surface of the head in *Mitrocystella* and can therefore be taken as vestigial. Accordingly, the optic part of the brain (prosencephalon) is less inflated in *Mitrocystella* (Fig. 7) than in *Mitrocystites* (Fig. 5). **C:** Ventral aspect of the right palmar complex (remarks as under B). **D:** Natural mould of the right postero-ventral surface of the head to show the lateral-line system and adjacent parts of the brain. The lateral line is divided into small pits, or small protuberances in the natural mould, each of which probably corresponds to a neuromast.

The locomotion of mitrates can be reconstructed. In *Mitrocystella*, there were ribs on the posterior parts of the ventral surface and sides of the head, each with an anterior steep slope and a posterior gentle slope. Ribs of this shape, as in several extant crabs and bivalves,

would grip the sediment and favor movement towards the gentler slope, suggesting that the animal crawled rearwards, pulled by the tail. In the power stroke of the locomotory cycle the tail would bend ventrally and pull the head rearwards by pushing forwards against

the sediment using a series of transverse bearing surfaces on the hind tail.³⁶ In the return stroke, knife edges in the hind tail would cut through the sediment and allow the tail to be extracted easily from the mud, without the head moving appreciably forwards. Recently, by an extraordinary piece of luck and sharp eyesight, an individual of the German Devonian mitrate *Rhenocystis*, some 390 million years old, has been found dead at the end of its own locomotion trace. As predicted, it was moving rearwards when it died. This extraordinary specimen will be described elsewhere.

As to how mitrates fed, among extant chordates an endostylar pharynx with a mucous filter is found in amphioxus, the tunicates and the larva of lampreys. It would have existed, therefore, in the latest common ancestor of these three groups, which would have been a mitrate. A complicated argument, which will not be repeated here, shows that the head of mitrates contained a filter feeding pharynx of tunicate type with many left-right asymmetries now found in tunicates.^{37,10,31}

The above-mentioned anatomical details which place *Mitrocystella* as a stem-group craniate mitrate include dorsal touch-sensory branches of the trigeminal nerves, the lateral-line system, and resorption of the dorsal skeleton over the left and right pharynges, to be replaced by presumed cartilage of neural crest origin.

THE ANIMAL X - THE LATEST COMMON ANCESTOR OF ALL EXTANT CRANIATES

Figure 10a,b shows the animal x - the latest common ancestor of all extant craniates, as we now reconstruct it. The reconstruction is based on cladistic arguments and assumes that the cladistic interrelationships among extant craniates are [myxinoids (lampreys + gnathostomes)].

The detailed arguments for the reconstruction will not be presented here. Briefly, however, a feature is assigned to x if it is now found in myxinoids (hagfishes), lampreys and gnathostomes (e.g. the trunk region and the perivisceral coelom) or with lower probability, in the myxinoids and lampreys only (e.g. the

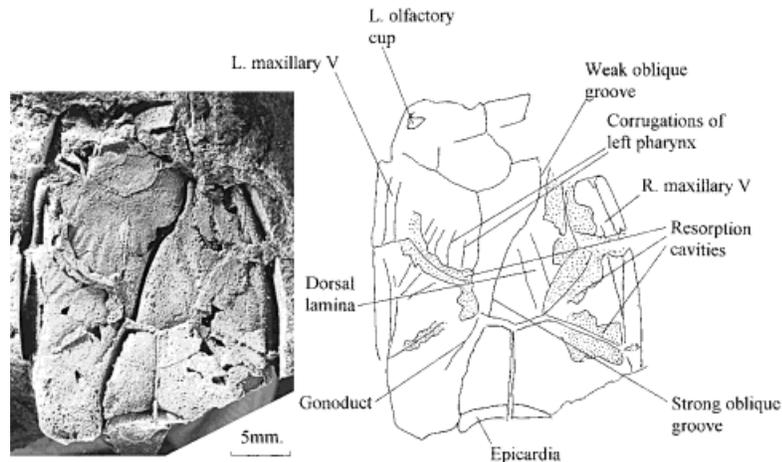


Figure 9. Dorsal aspect of the natural internal mould of the head of the mitrate *Mitrocystella incipiens* (Natural History Museum, London, E28888). Note the signs of resorption of the skeleton spreading out from sutures between the plates. These irregular cavities do not relate to any possible growth lines of the plates and must therefore represent resorption. Their constant relationship to the chambers of the head, always in contact (or almost so) with pharyngeal endoderm, shows that they are not post-mortem, so resorption took place late in the ontogeny of the individual. The connective tissue which probably filled them represents the phylogenetic beginning of the neural-crest cartilage of the head. The corrugations of the left pharynx can be compared with those of the right pharynx of *Mitrocystites* (Fig. 5). The anterior boundaries of the corrugations probably represent the positions of the peripharyngeal ciliary bands of the pharynx.^{10,18,31} The dorsal lamina is a structure represented in the pharynx of extant tunicates which serves to roll up the mucous rope and pass it posteriorly into the esophagus.

tongue apparatus with great muscular body and horny teeth^{10,37}). If found only in extant lampreys and gnathostomes, but not in myxinoids, a feature will not be assigned to x, but regarded as a vertebrate autapomorphy (vertebrates = lampreys + gnathostomes). Moreover, if a feature occurs in only one of the three major groups descended from x, but also in the mitrates, tunicates or acranians, then it too can be assigned to x. An example of this is the endostylar mucous filter in the pharynx. This occurs, among extant craniates, only in the ammocoete larva of lampreys. It is also found in adult tunicates and adult acranians and almost certainly existed in adult mitrates also. It is not found in extant myxinoids or gnathostomes, whether adult or juvenile. This distribution makes it almost certain that the larva of x, like the larva of a lamprey, possessed a filter-feeding endostylar pharynx although the adult

did not. This “ammocoete” larval stage has been lost independently in myxinoids and gnathostomes. The probability that a feature is correctly assigned to x depends not only on its known systematic distribution, but also on the probability that the known occurrences are homologous with each other.

Adult animal x would have been very much like a myxinoid, with an elongated body fringed posteriorly by a caudal fin, supported by cartilaginous fin rays. There would have been an extensive trunk region with a large perivisceral coelom and the anus would open into a median ventral cloaca near the posterior end of the animal. There would also have been an extensive notochordal head region where the notochord was dorsal to the pharynx and to the tongue apparatus. The latter would be activated by a spindle-shaped great muscular body which would have pulled a group of

horny teeth rearwards into the mouth.³⁸ The main muscles of the body would have been the somitic parietal muscles which served to bend the body from side to side in swimming, acting against the non-compressible notochord. In the trunk region, the parietal muscles of left and right side would probably not reach the ventral mid line, the most ventral part of the body wall being formed from oblique muscles as in a myxinoid. The pharynx may well have had one more gill slit on the left than on the right, homologous with the esophago-cutaneous duct of a myxinoid. A pumping velum may have existed anterior to the pharynx. There was probably no alternation, at any stage of ontogeny, between somites and gill slits, this being an autapomorphy of the vertebrates within the craniates. The non-pharyngeal gut most likely had a flexure along its length, convex forward on the right and convex rearward on the left. There would have been a liver with a gall bladder and a bile duct opening into the gut. The gonad would have been unpaired and probably lay right of the non-pharyngeal gut in the perivisceral coelom. Gametes would leave the perivisceral coelom through a pair of gonopores, or a single median gonopore, opening into the cloaca. There would have been a kidney with a functional pronephros opening into the pericardium and an extensive mesonephros, probably with segmentally arranged glomeruli. The mesonephroi would open into a pair of ureters which would debouch separately into the cloaca. There would have been cartilaginous otic capsules, surrounding the ectodermal otic vesicles, which would have been situated near the anterior end of the notochord, just lateral to the hyoidean somite. Non-motile eyes, with optic cups but without lenses, would have existed. There would have been a median olfactory organ. The brain would have included an extensive hind brain region from which the branchial nerves and the intestinal branch of the vagus took origin. There would have been no hypoglossal nerve as such i.e. the somitic nerves supplying the muscles ventral to the pharynx would not join together to pass around the posterior end of the pharyngeal region. The skeleton

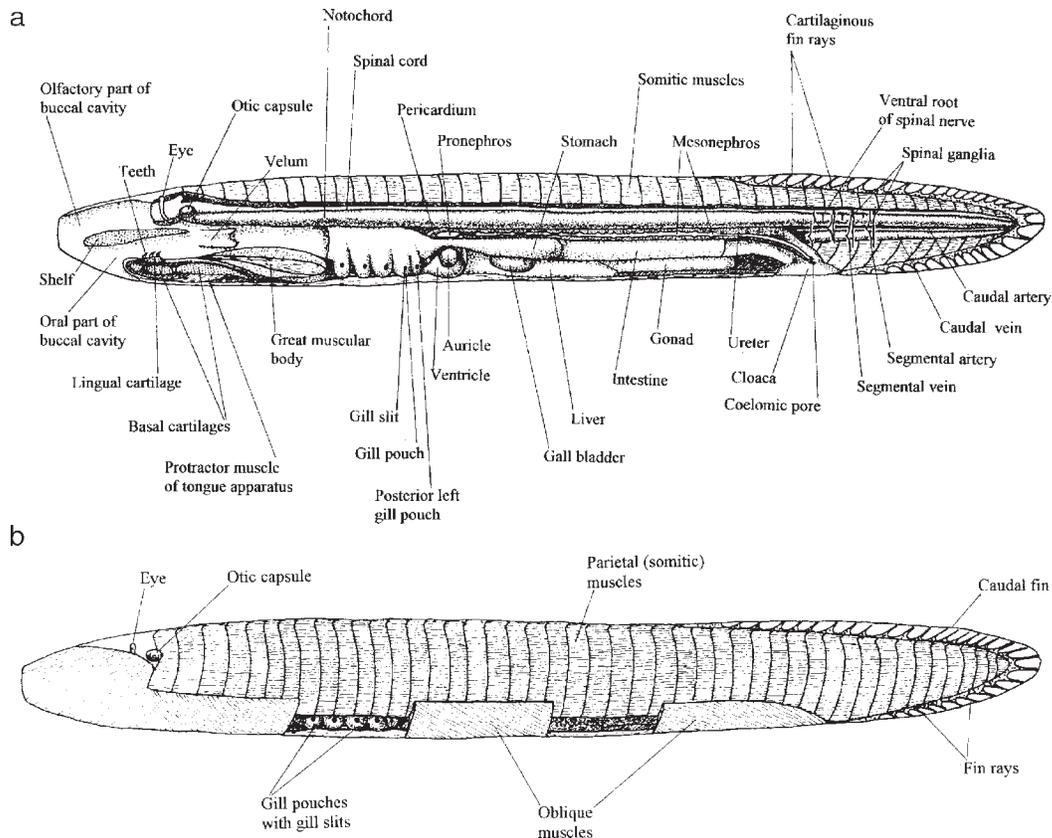


Figure 10. Left lateral reconstruction of the hypothetical animal x, the latest common ancestor of extant craniates. This reconstruction is based on cladistic reasoning assuming that extant chordates are related as: (Acraniata (Tunicata (Myxinoidea (Petromyzonida + Gnathostomata)))) and inserting some information from mitrates. **a:** Internal organs. **b:** Superficial internal anatomy (skin removed). Animal x in most ways resembles a hagfish but would have had an ammocoete-like, filter-feeding larva. The most important difference from the ancestral mitrate was the process of tail-head overlap.

would have included a cartilaginous skull and various other cartilages in the head region, probably all of neural crest origin except the otic capsules. There would also have been cartilaginous fin rays, as already mentioned, in the caudal fin. There would have been no vertebrae and probably no part of the skull was of vertebral origin. Paired cartilaginous otic capsules would have existed, probably with two vertical semicircular canals as in extant myxinoidea. Posteriorly, just anterior to the muscular velum, the buccal cavity was connected with the nasal passage. More anteriorly the cavity and the passage were separated from each other by a horizontal shelf. Animal x probably lived its entire life in the sea and in the adult usually swam forwards, rather than crawling rearwards like a mitrate.

CHANGES IN PASSING FROM A MITRATE TO ANIMAL X

The principal changes in passing from a mitrate such as *Mitrocystella* to animal x would have been as follows.

- 1) The clear mitrate distinction between tail region and head region disappeared, with the origin of the trunk, perivisceral coelom and notochordal head. Concomitant with this, the non-pharyngeal gut and gonad moved rearwards and ventralwards to lie in the perivisceral coelom with the gonad right of the gut. Also, the anus shifted from the left atrium to a posterior median position, opening into a median cloaca. Gametes came to be released, not by ducts entering the left atrium, but by one

or a pair of coelomopores opening into the cloaca (Fig. 11).

- 2) The heart also moved rearwards so as to be posterior to the gill slits, instead of anterior to them.
- 3) The tongue apparatus was developed in the adult for ingesting solid food or blood, and the endostylar mucous filter was abandoned. The endostyle became the thyroid gland. At the same time, a horizontal shelf developed in the buccal cavity, separating the tongue apparatus ventrally from the nasal passage, specialized for olfaction, dorsally. (The old endostylar filter apparatus was retained in the larva of x.)
- 4) Kidneys arose at nephrotomes dorsal to the lateral plate and ventral to the somites, and kidney ducts arose external to the kidney anlagen, con-

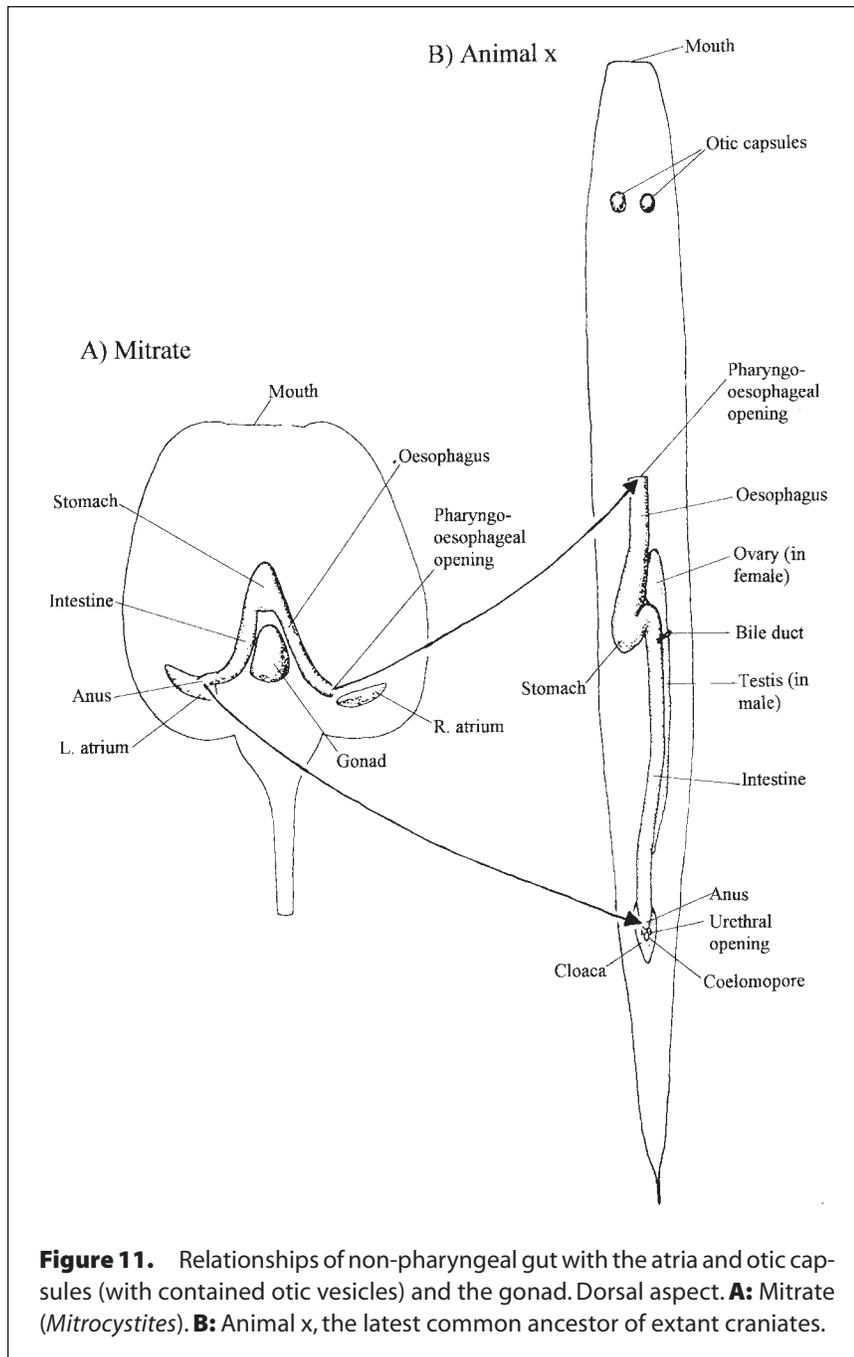


Figure 11. Relationships of non-pharyngeal gut with the atria and otic capsules (with contained otic vesicles) and the gonad. Dorsal aspect. **A:** Mitrate (*Mitrocystites*). **B:** Animal x, the latest common ancestor of extant craniates.

- ducting urine rearwards into the cloaca. The somites, initially dorsal to the nephrotomes in ontogeny as perhaps also in phylogeny, grew ventralwards external to the kidney ducts but did not extend to the ventral mid line.
- 5) Both atria lost their connections with the gill slits, and the left atrium lost its connection with the anus and gonoducts, and so the atria transformed into otic vesicles, specialized for hearing and accelerometry.
 - 6) The mid and hind brain arose by combining elements of the mitrate deuterecephalon with those of the anterior part of the mitrate spinal cord.
 - 7) The calcitic skeleton disappeared completely. In the mitrate head this happened at first by resorption in the adult (Fig. 9), beginning where the dorsal skeleton was in contact, or almost so, with pharyngeal endoderm, so that the old calcitic plates were replaced by connective tissue. This

was the phylogenetic origin of neural-crest cartilage. Presumably, in the course of phylogeny, the resorption started earlier and earlier in ontogeny, until finally no calcite was ever formed in the head. In the mitrate tail it is likely that the calcite skeleton did not disappear by resorption, but simply became thinner and thinner until finally it was never formed.

- 8) The direction and mode of locomotion changed from rearward crawling in the adult, to swimming, predominantly forward. (It is possible that this change was neotenus, if the larvae of mitrates, like those of tunicates, swam forward.)

DEVELOPMENTAL MECHANISMS

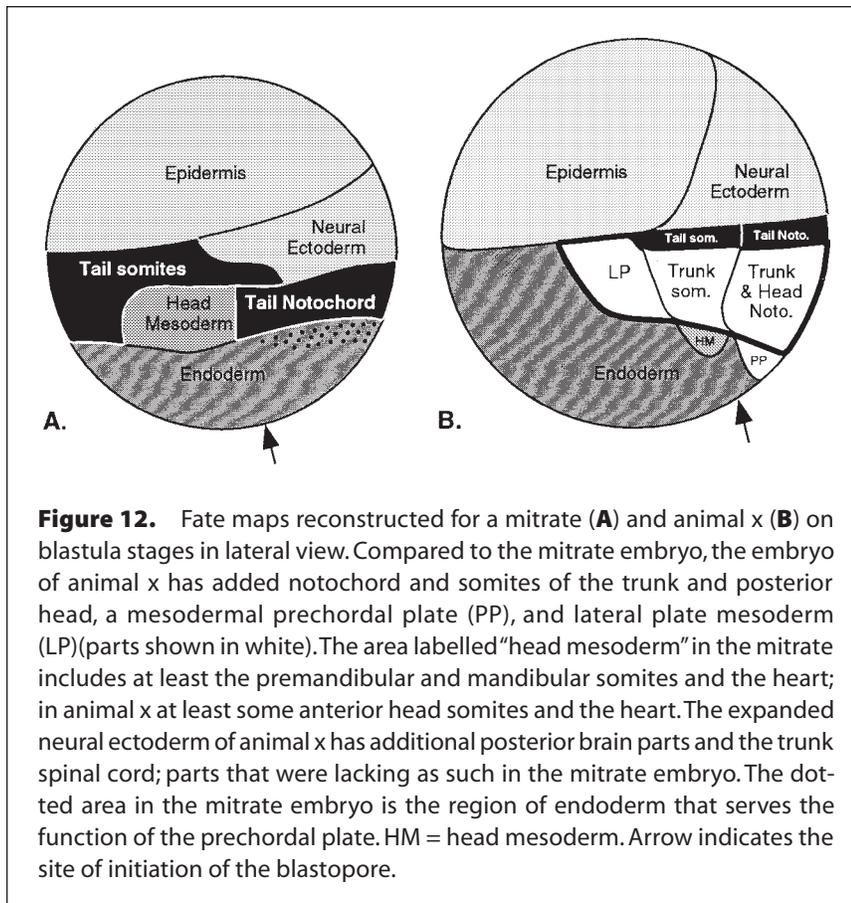
The transitions in adult characters outlined above arose in embryos. We must, therefore, make some guesses about the organization of embryos of mitrates and of animal x, and how a mitrate evolved into animal x.

In all chordates, a group of endodermal cells ("Nieuwkoop's center") induces the dorsal mesoderm, and the dorsal mesoderm ("Spemann's organizer") induces the nervous system.³⁹ The transition from mitrate to animal x required a considerable increase in the amount of dorsal mesoderm induced, followed by induction of parts of the nervous system to form spinal cord of the trunk and additional hind brain. These changes commence in the earliest embryo, well before gastrulation begins. We therefore reconstruct for comparison the fate maps of pregastrula embryos of the mitrate and animal x, guided by fate maps from the most closely similar extant forms (Fig. 12).

The term "dorsal mesoderm" refers to notochord, somites, and head mesoderm including the prechordal plate, if present. "Ventral mesoderm" consists of the lateral plate mesoderm. "Intermediate mesoderm" lies between the dorsal and ventral mesoderm and forms kidneys and gonads in vertebrates.

The Embryo of a Mitrate

Among extant animals, the embryos of ascidians should resemble most closely those of mitrates. Adult mitrates were



similar to the ascidian tadpole in consisting of just a head and a tail. Adult mitrates, though, are much larger than the transient ascidian tadpoles, and their internal development is complete and more complex. It seems likely that the mitrate embryo was larger than the ascidian embryo and had more yolk in its cells, that development took longer, and that the mitrate embryo was more regulative than mosaic. We have reconstructed a fate map for the early gastrula stage of the mitrate embryo (Fig. 12A), modified from the fate map for a similar stage of an ascidian embryo.⁴⁰

On the fate map, the prospective mesoderm (tail notochord and somites, and head mesoderm) forms a band around the equator of the blastula. The band is perpendicular to the future long axis. At gastrulation, this band of mesoderm turns under the blastopore lips (involute), which reverses the anterior-posterior axis of the band, then cells of the prospective tail somites and notochord change neighbors, actively migrate and intercalate in such a way that

they converge toward the midline, crowd together at or near the midline, and thus lengthen the midline, thereby extending the tissue posteriorly. Convergent extension is the morphogenetic mechanism by which an embryo extends its axis and closes its blastopore.⁴¹

Prospective head somites and heart rudiments, which lie in a patch vegetal to the prospective muscles of the tail, involute directly into the head. Endodermal cells move inside the embryo by invagination.

Endodermal cells contiguous to the prospective tail notochord (future endodermal roof of the pharynx) most likely are necessary for induction of the forebrain, a role that similar cells from the A-line endoderm in the ascidian embryo likewise possess, and thus they serve some of the same functions as the prechordal plate of craniates. The ascidian A-line endodermal cells and vertebrate prechordal plates both express genes necessary for brain induction.⁴² These genes are called *Hroth* in ascidians, *Otx* in mice, *zOtx* in zebra fish, *Xotx* in *Xeno-*

pus (frog), *c-otx* in the chick, and all are related to the *orthodenticle(otd)* gene of *Drosophila*. The mitrates must have had an *otd*-related gene. The nerve cord of the tail is induced by tail mesoderm. The neural plate, containing brain and tail nervous system, closes into a tube from posterior to anterior in tunicates. During tail elongation, a strand of endoderm is taken along beneath the notochord in the ascidian embryo, and this likely happened in the mitrate embryo as well.

The mesoderm of mitrate and ascidian embryos consists just of head somites and heart rudiments, and tail somites and notochord, all of which are dorsal mesoderm. No dorsal trunk mesoderm nor intermediate or lateral plate mesoderm are found in these forms, although they occur in all extant craniates. Aside from a probable endodermal strand beneath the notochord in the tail, all of the gut of the mitrate embryo would be in the head.

Neural crest, giving rise to ganglia in the head and tail, was probably present in the mitrates. The evidence for this statement comes from several sources. Firstly, trigeminal ganglia (pyriform bodies) existed in all the mitrates just anterior to the deuterocephalon, and in the acraniate and tunicate mitrates, which had no dorsal branches to the trigeminal nerve, there was probably no placodal contribution to the trigeminal complex, so that the presence of trigeminal ganglia implies the presence of neural crest. Secondly, the presence of spinal ganglia in the hind tails of craniate and acraniate mitrates implies that some neural crest was produced in the embryo. Thirdly, it is often assumed that the small transient larvae of ascidians show no signs of neural crest, but Torrence and Cloney reported sensory nerves in ascidian larvae with the cell bodies extending outside (dorsal of) the spinal cord.⁴³ These cell bodies are likely to be homologous with the spinal ganglia, of neural crest origin, of craniates.

The Embryo of Animal X

Among extant primitive craniates, the embryology of the lamprey has been studied best. This is fortunate, since the embryology of animal x was probably lamprey-like, since lampreys have a mod-

erately small egg and an ammocoete larva—probably in both respects like animal x—not a large yolky egg and no ammocoete larva as in myxinooids.

Weissenberg⁴⁴ constructed a fate map for the embryo of a lamprey (*Lampetra fluviatilis*). Our representation of a fate map on the blastula of animal x is modelled after Weissenberg's map (his figure 13) with some modifications (Fig.12B). We include the tail mesoderm in our map, using the amphibian fate map as a guide to its position.

Forms of mesoderm in the embryo of animal x that the mitrate embryo did not have included prospective notochord and somites of the trunk and posterior head, as well as lateral plate mesoderm. These new regions of mesoderm are positioned vegetal to the tail mesoderm in the pregastrula embryo and involute ahead of the tail mesoderm. As they involute, the prospective head and trunk notochord and somites converge toward the midline and extend themselves anteriorly. The last dorsal mesoderm to involute is that of the tail. As it did in the mitrate embryo, it converges toward the midline and extends itself posteriorly. This contrast between anterior and posterior extension is a critical factor in defining trunk and tail.

The new dorsal and lateral mesoderm of animal x give the appearance of having arisen from endoderm in our map for animal x when compared to the map of the mitrate. However, in the lamprey embryo, these tissues are for a time a part of the roof and walls of the archenteron, then separate as the definitive gut forms.⁴⁴ These new tissues are in an extended dorsal marginal zone that overlaps the gut vegetal cells as a result of increased epiboly that occurs before blastopore formation begins,⁴⁴ and thus originate from the animal hemisphere.

The Transition From the Embryo of a Mitrate to That of Animal X

Comparative embryology suggests some possible mechanisms by which the anterior portion of the notochord comes to occupy the posterior part of the head, while between the tail and the head a trunk is formed containing most of the gut within a perivisceral coelom.

The most-probable scenario for the evolution of animal x from a mitrate was a series of changes in the early embryo.

First, an increased response to the induction of future somites and notochord, possibly accompanied by a more intense inductive signaling from the endoderm, produced an expanded area in the pregastrula embryo that would produce notochord and somites. Most likely, the responding tissue consisted of animal hemisphere cells as we see in amphibian embryos today.^{45,46} Signaling from endoderm to induce dorsal mesoderm commences in cleavage stages and continues to pregastrula stages in extant amphibians. The broader region of future dorsal mesoderm in the embryo of animal x proliferated more cells in the pregastrula embryo than did embryos of the mitrates so epiboly caused this dorsal mesoderm to lap over the endoderm before blastopore formation, as seen in the lamprey embryo.⁴⁴

Second, whereas in mitrates convergent extension acted only posteriorwards

and produced only the tail, the expanded prospective notochord-somite field was divided during and after gastrulation into two portions by different directions of convergent extension, producing in animal x the posterior head and the trunk from anteriorly directed cells, and the tail from posteriorly directed cells (Fig.13). In animal x, the edge of the dorsal mesoderm nearest the forming blastopore would involute first and would later become the anterior part of the dorsal mesoderm that will contribute to anterior head, posterior head and trunk. The last mesoderm to involute would form the tail notochord and somites. The tail mesoderm would be contiguous with the non-involuting ectoderm.

In amphibian embryos, convergent extension movements have been described in the neural plate that coincide with similar movements in the underlying prospective notochord and somite mesoderm.^{47,48} Near the posterior end of the neural (medullary) plate, there is what Jacobson and Gordon⁴⁹ called the

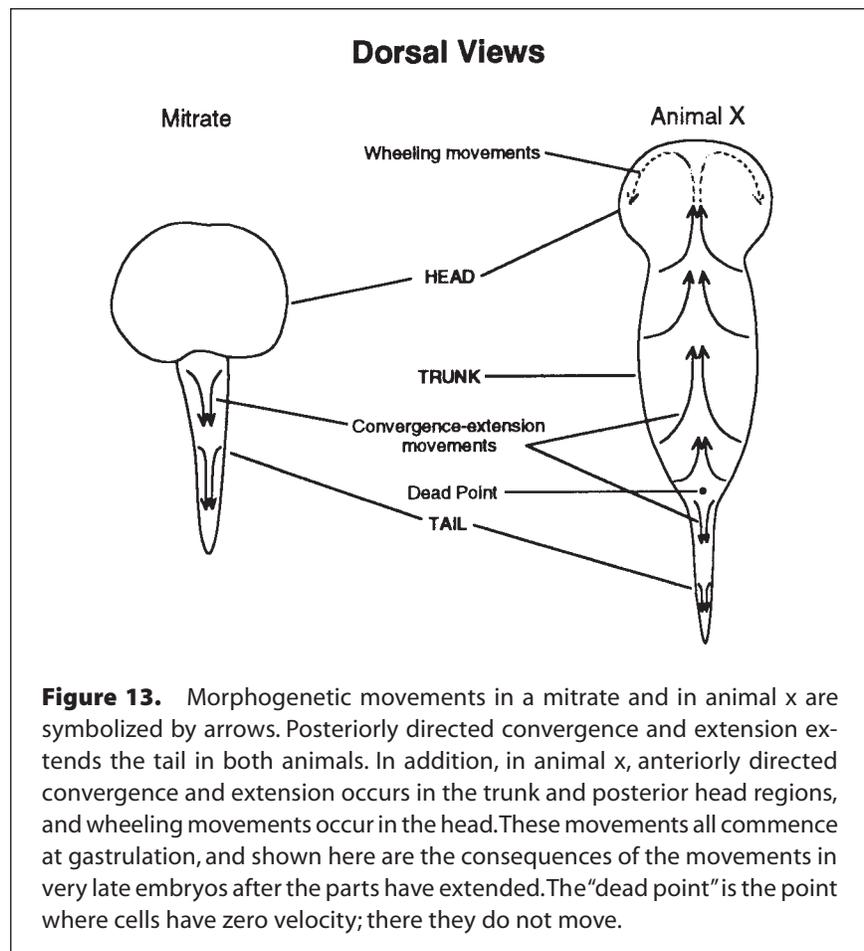


Figure 13. Morphogenetic movements in a mitrate and in animal x are symbolized by arrows. Posteriorly directed convergence and extension extends the tail in both animals. In addition, in animal x, anteriorly directed convergence and extension occurs in the trunk and posterior head regions, and wheeling movements occur in the head. These movements all commence at gastrulation, and shown here are the consequences of the movements in very late embryos after the parts have extended. The "dead point" is the point where cells have zero velocity; there they do not move.

“dead point,” a point that remains in its position (the cells there have zero velocity). Anterior to this position, convergence and extension movements in the neural plate proceed from posterior to anterior, while posterior to the dead point, convergence and extension movements proceed from anterior to posterior. Similar movements occur in the underlying mesoderm. The dead point must have become so positioned during the transition from a mitrate to animal x. Anterior to the dead point is the trunk and head. Posterior to it is the tail.

Third, with the phylogenetic origin of forward convergent extension movements, prospective notochord and somites extended into the posterior head, creating the notochordal part of the head, and causing wheeling movements (Fig. 13) in the more anterior and lateral head tissues. In the embryos of the stem-line animals between mitrates and animal x, wheeling movements caused a repositioning of several organs that had been in the mitrate head. Cells directly in front of the intruding notochord were displaced anteriorly, and the most anterior and the lateral head cells were displaced laterally and then posteriorly like water droplets in a fountain emerging from the anterior end of the notochord. Such wheeling movements are seen anteriorly and laterally during neural plate formation in amphibia,⁵⁰ and underlying mesoderm must make similar movements. Wheeling movements would have thrust premandibular somites anteriorly while displacing posteriorly the mandibular somites and other lateral head tissues, such as those that had formed the atria and heart in mitrates. The atria moved slightly posteriorly in the head and become the otic vesicles of animal x. The heart was displaced from the head into the trunk.

As the trunk elongated, most of the gut became strung out along the length of the new trunk, and the gonad was moved from the head to the trunk. The only endoderm that remained in the head was the pre-oral and the pharyngeal endoderm (which is induced along with the mesoderm in extant vertebrate embryos).⁴⁶ The gut, now lying beneath the trunk somites, might induce lateral plate mesoderm from the ventral portions of

the somites as in amphioxus, and probably also induced the lateral plate to form the coelomic spaces of the trunk. In extant craniate embryos, the lateral plate is induced by ventral endoderm and the induction occurs before and during gastrulation. This early induction of lateral plate may have begun in animal x, but one cannot guess that from a fate map.

Separate genetic mechanisms for the formation of trunk and tail may have emerged as suggested by work of Griffin et al.⁵¹ A zebrafish *brachyury* mutant, *no tail (ntl)*, lacks a tail and notochord, but still has a trunk. Expression of the normal *ntl* gene is regulated by fibroblast growth factor (FGF). Inhibition of FGF receptor-signaling causes complete loss of both tail and trunk. Trunk development, therefore, seems to depend upon an unidentified gene called *no trunk (ntk)* which is regulated by FGF. The trunk and tail thus have separate mechanisms for formation in the zebrafish. The data suggest that in both trunk and tail, FGF affects convergent extension movements.

Fourth, there were changes in the induction of the neural ectoderm by dorsal mesoderm in animal x compared to the mitrate embryo. In extant craniates, neural induction begins through the plane of the tissues before gastrulation begins (planar induction) and is reinforced when the dorsal mesoderm underlies the prospective neural tissue (vertical induction).⁵² Probably in the embryos of both the mitrates and animal x, one set of inducing signals induced forebrain, and a different set induced the tail.^{53,54} In embryos of mitrates, probably a planar inductive interaction between the tail tissues and the forebrain produced a deuterencephalon, or primitive hind brain, from a portion of the prospective forebrain. We suggest that in the early embryo of animal x, planar induction between tail tissues and the forebrain was soon reinforced by induction from underlying dorsal mesoderm of posterior head and trunk, producing a possibly more complex hindbrain, as well as a spinal cord in the trunk. Some support for this suggestion comes from experiments on the frog *Xenopus laevis*. Tail axial tissue, when recombined with forebrain, induces a hind brain, and when hindbrain was recombined with tail tis-

sue, trunk spinal cord was induced from the hind brain.⁵⁵ Regional-specific molecular markers and lineage tracers were used to verify these results.

Amphibian and amniote embryos appear to recapitulate some of the neural repositionings necessary to transform mitrates into the latest common ancestor of extant craniates. In a fate map of the gastrula of a newt (*Taricha torosa*) embryo (Fig. 14), most of the dorsal hemisphere of ectoderm is prospective brain with the prospective spinal cord being but a thin transverse strip at the posterior end.⁴⁹ As the neural plate forms, it is reshaped from a hemisphere to a pear shape mainly by a repositioning of the constituent cells of the trunk spinal cord in a set of forward convergent extension movements.⁵⁶ Similar fate maps have been made for a frog embryo (*Xenopus laevis*).⁵⁷ The underlying prospective mesoderm at these stages is similarly disposed, with head mesoderm residing beneath the prospective brain, and posterior notochord and trunk and tail somites being beneath the transverse strip near the blastopore that will form the spinal cord portion of the neural plate. Convergent extension movements in both the neural plate and the underlying mesoderm largely are responsible for shaping the anterior-posterior body axis.^{56,58}

The Heart

The heart of mitrates was in the head and must have arisen from head mesoderm. Most likely, the mitrate heart was much like the heart of extant tunicates. The heart of the tunicate *Ciona* arises in the tadpole from left and right anlagen of dorsal head mesoderm just anterior to the junction of the tail,⁵⁹ then these rudiments unite in the ventral midline just behind the pharynx.⁶⁰ There is a spindle-shaped hollow in cornutes just to the right of the esophagus that may have accommodated the heart.¹⁰ Mitrates were descended from cornutes, the most important single difference between them being the origin of the right pharynx and right gill slits. This change would displace the heart from a right posterior position in the head, as in cornutes, to a new position just right of the esophagus as in tunicates.³

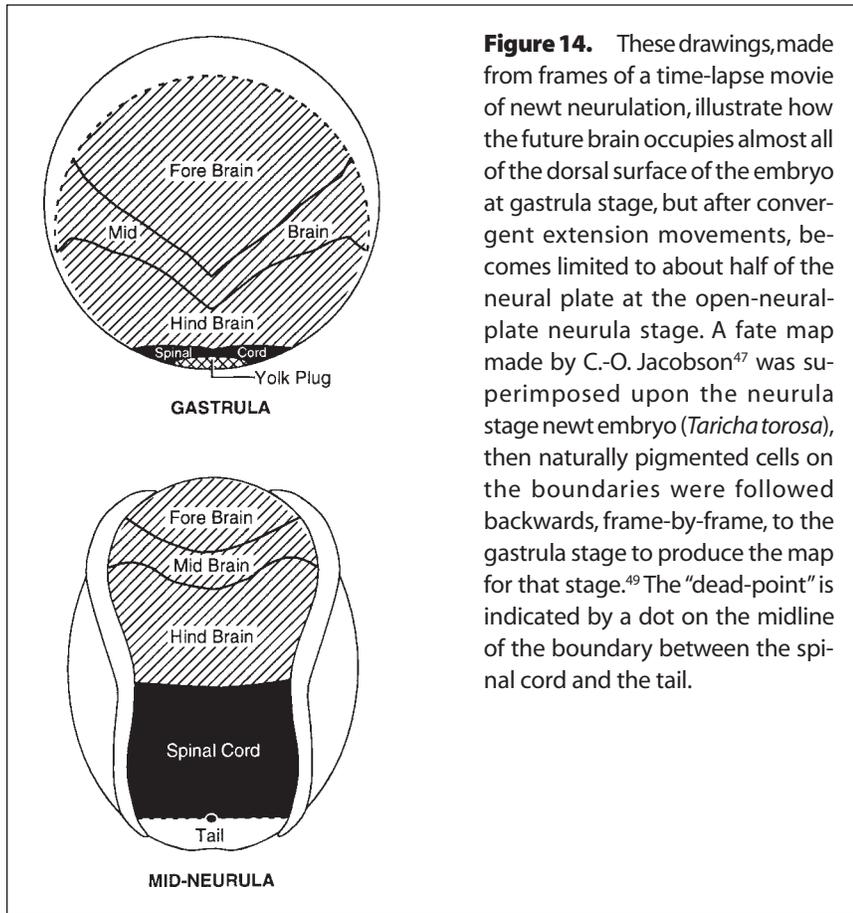


Figure 14. These drawings, made from frames of a time-lapse movie of newt neurulation, illustrate how the future brain occupies almost all of the dorsal surface of the embryo at gastrula stage, but after convergent extension movements, becomes limited to about half of the neural plate at the open-neural-plate neurula stage. A fate map made by C.-O. Jacobson⁴⁷ was superimposed upon the neurula stage newt embryo (*Taricha torosa*), then naturally pigmented cells on the boundaries were followed backwards, frame-by-frame, to the gastrula stage to produce the map for that stage.⁴⁹ The “dead-point” is indicated by a dot on the midline of the boundary between the spinal cord and the tail.

It seems likely that the cranioventral edge of the hyoid somitomeres may, in fact, be the ancestral as well as the present source of the heart rudiments. There is a ventral crotch of cells between the mandibular and the hyoid somites that is the likely source of the heart-producing cells. At the neurula stage of the newt, the heart rudiments are at the cranioventral edges of the hyoid (third) somitomeres (Fig. 15).⁶¹ There is no lateral mesoderm associated with the premandibular and mandibular somitomeres of the amphibian. Mesoderm begins to angle off laterally and caudad beneath the cranial edge of the hyoid somitomeres, and this most-anterior edge of the “lateral” mesoderm consists of the heart rudiments. These heart rudiments emerge from the ventral edge of the somitomere files, between the mandibular and hyoid segments. The induction history of the heart in amphibian embryos is consistent with the idea that the heart is dorsal mesoderm,⁶² as is the presence of large circumferential hearts in extreme dorsoanterior enhanced frog embryos.⁶³

Hearts appear, therefore, to arise from dorsal head mesoderm at a transverse level corresponding to the posterior margin of the mitrate head, but they eventually reside in a midventral position in the trunk, posterior to the head

Most textbooks suggest that the vertebrate heart arises from splanchnic lateral plate mesoderm (which the mitrate did not have). Actually, vertebrate

heart rudiments are much translocated during development, and their positions make ambiguous the judgment of what mesoderm gives rise to them.

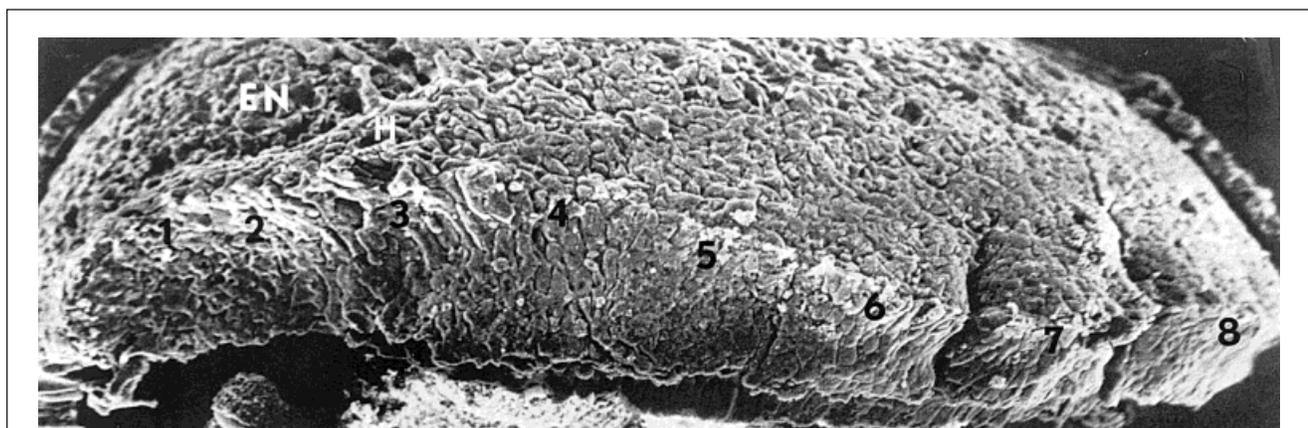


Figure 15. This scanning electron micrograph is a dorso-lateral view of a *Taricha torosa* (newt) embryo at stage 17, an open-plate stage when the embryo has one somite (number 7). The epidermis and neural plate were removed. The somitomeres and somite are numbered 1-8. The salamander heart rudiments were located with vital staining at the open-neural-plate stage by Sally Wilens (1955).⁶⁹ The right heart rudiment (H) is shown here in an SEM from Jacobson and Meier (1984).⁶¹ The heart rudiment is at the cranioventral edge of the hyoid (third) somitomere, which underlies the otic placode of the ear (removed with the ectoderm). EN = endoderm anterior to the mesodermal mantle.

in adult craniates. The heart rudiments of craniates are translocated to this more ventro-posterior position by combinations of wheeling movements, migration of the prospective heart cells, and by the displacement that occurs when the head fold of the body forms and undercuts the anterior end of the embryo. Head folds probably arose as a result of the new anteriorly directed convergent extension movements.

Origin of the heart in the head, anterior to the front end of the notochord, and its displacement into the trunk is seen in myxinooids,⁶⁴ in lamprey embryos,³² in zebrafish,⁶⁵ in amphibia as described above, and in the amniotes.⁶⁶⁻⁶⁸ These movements essentially recapitulate what happened in phylogeny in the transition from mitrates to animal x.

Summary of the Transitions From Mitrate to Animal X

In the progress from a mitrate to animal x, a process of tail-head overlap occurred by somewhat subtle means. The notochord-somite field of the tail of mitrates expanded in the earliest embryo and from the anterior part of the expanded field, a trunk was formed, some of which came to occupy the posterior part of the former "head" of the mitrates because the convergent extension movements of the new trunk are directed anteriorly rather than posteriorly as these movements go in the tail.

Anteriorly directed convergent extension movements during trunk formation and extension of the head of the embryo beyond the yolk mass created a head fold which helped displace some organs, such as the heart, posteriorly.

Forward-directed convergent extension movements that occur in the prospective somites and notochord also occur concurrently in the overlying neural plate, as mentioned before. The part of the neural plate that directly overlies, and is attached to, the prospective notochord is the "notoplate," which is in the midline position of the future floor plate of the nervous system.⁵⁶ Prospective somites underlie the neural plate lateral to the notoplate.

When the former tail tissues doing forward convergent extension collided with the old mitrate brain, the deu-

terencephalon became part of the forward extending system and the mitrate forebrain was displaced forwards to the most-anterior part of the head. New hindbrain parts were induced along with the spinal cord of the trunk. At the midline, the mitrate forebrain plate was moved forwards intact, but anterior and lateral parts wheeled about laterally then posteriorly. We suggest that lateral parts of the mitrate forebrain plate were displaced posteriorly where they became lateral to forward converging and extending tissue at the midline. When the neural plate rolled into a tube, these lateral parts from the forebrain composed the dorsal part of the midbrain, and the anterior end of the converging and extending tissues composed the ventral part of the midbrain. The midbrain thus is a composite of old forebrain and old hindbrain (deuterencephalon) parts. Starck has for years held the view that midbrain is composed of forebrain dorsally and hindbrain ventrally.⁷⁰ Recent studies at the molecular level reveal that forebrain-specific and anterior hindbrain-specific genes are both expressed in midbrain.³⁴ The most anterior part of the rhombencephalon may also be a part of the old mitrate deuterencephalon.

Forward-directed convergent extension of the notochord displaced anteriorly the premandibular somites of the mitrates, while the mandibular somites wheeled about to eventually lie posterior to the premandibular segments. The loop of gut in the mitrate head was straightened and came to lie beneath the newly formed trunk, leaving only the pharynx in the new head. The gonad, in the head in mitrates, was displaced by the straightening gut loop to lie to the right of the gut in the trunk in animal x, as it now is in myxinooids and lampreys. The new arrangement of gut beneath the somites of the trunk permitted the gut to induce coelomic spaces within the lateral plate, and either the gut or its progenitor endoderm induced the lateral plate from the ventral aspects of the somites or the somite field. Organs such as the heart and the gonad were carried posteriorly into the trunk by wheeling movements during gastrulation, by cell migration, by posterior extension of the head fold, and by the straightening of the gut.

Thus, by combining evidence from fossils with developmental biology, we can reconstruct the anatomical changes that occurred in an important episode of craniate evolution and suggest the causal mechanisms behind them.

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