Endocranial Morphology and Phylogeny of Palaeozoic Gnathostomes (Jawed Vertebrates)

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Abstract

Gnathostomes, or jawed vertebrates, make up the overwhelming majority of modern vertebrate diversity. Among living vertebrates, they comprise the chondrichthysans (“cartilaginous fishes” such as sharks, skates, rays, chimaeras) and the osteichthysans (“bony fishes” or bony vertebrates, inclusive of tetrapods). Gnathostomes appear to have originated in the early Palaeozoic Era, but their early fossil record is fairly scant. The best fossils appear first in the Late Silurian and Devonian periods. Much of gnathostome diversity owes to unique adaptations in the internal skeleton of their head (the endocranium). The endocranium is composed of the braincase, jaws, hyoid arch, and branchial arches, which sometimes fossilise when they are composed of bone or calcified cartilage.

The purpose of this thesis is to describe and compare the fossilised cranial endoskeletons of a variety of different Palaeozoic gnathostomes. The objective is to test current conceptions of gnathostome interrelationships (i.e. phylogeny) and infer aspects of key morphological transformations that took place during the evolution of Palaeozoic members of this group. Two key areas are examined: the morphology and interrelationships of Palaeozoic gnathostomes and the morphology of the visceral arches in sarcopterygian fishes.

New data on the visceral arches are described from the stem tetrapods Pandelichthys and rhizodontids. These provide insight into the sequence of character acquisition leading to the tetrapod middle ear. Pandelichthys shows key features of the tetrapod middle ear chamber were established prior to the origin of digited limbs. New morphological data are described from the “acanthodian” fish Ptomacanthus. Ptomacanthus provides only the second example of a well-preserved braincase from any member of this group. It shows dramatic differences from that of its counterpart, Acanthodes, providing new evidence for acanthodian paraphyly. New interpretations of basal gnathostome and osteichthyans phylogeny are presented, challenging or enriching existing views of these problems.

Keywords: systematics, palaeontology, anatomy, evolution

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urn:nbn:se:uu:diva-9360 (http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-9360)
To my four parents
But to do science it is necessary to be rigorous and break out of many of the modes of thought imposed by the natural thinking associated with ‘common sense’

Lewis Wolpert

[If I suppressed what will seem extravagant and incredible, there would be nothing left.]

H.P. Lovecraft’s
At the Mountains of Madness
This thesis is based on the following papers, which will be referred to in the text by their Roman numerals:


IV Friedman, M. and **Brazeau, M. D.** A reappraisal of the origin and basal radiation of the Osteichthyes. Submitted, *Journal of Vertebrate Paleontology*.


VI **Brazeau, M. D.** A revision of the anatomy of *Ptomacanthus anglicus* Miles with comments on the comparative head morphology of early gnathostomes. Manuscript.

The following paper was written during the course of my doctoral studies but is not part of the present dissertation.


In Paper I, MDB described the material and produced all figures, and shared in the interpretation. In Paper II, MDB did the majority of figures, descriptions, and had a majority part in the interpretation and discussion. In paper III, MDB shared the work and writing equally with MF. In Paper IV, MDB contributed to all aspects, but specifically wrote the sections on characters specifically related to acanthodians, shared writing equally with the introduction and review of methodological and conceptual content, and composed most of the figures.
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Introduction

The jawed vertebrates, or gnathostomes, make up the overwhelming majority of vertebrate life (Figure 1). From humans to sharks, all vertebrate animals with jaws belong to a single group that shared a common ancestor more than 430 million years ago. They comprise the Chondrichthyes (“cartilaginous fishes” including sharks, skates, rays, chimaeras) and the Osteichthyes (literally “bony fishes”, but also including tetrapods: vertebrates with digit-bearing limbs). In addition to jaws, modern gnathostomes are characterised by having paired appendages (fins or limbs), as well as three semicircular canals of the inner ear, an adaptive immune system, and nerve fibers covered in a fatty myelin sheath, all inherited from our last common ancestor.

The diversity of gnathostomes and the features that define them have been of special interest to biologists for centuries. Their myriad forms owe, in large part, to the modification of the head skeleton and jaws. This partly gives rise to the numerous feeding mechanisms and the unique modes of life in gnathostomes. In spite of all this diversity, early embryologists discovered that gnathostomes, and indeed all vertebrates, share profoundly similar head morphologies as early embryos. Following Darwin, the significance of these embryological and anatomical similarities became considered a reflection of the common ancestry of gnathostomes.

The origin of gnathostomes occurred at an extremely remote time in vertebrate evolution. Fossils give us some clues as to what the earliest gnathostomes and their relatives may have looked like. Fossils are currently known for representatives of the early members of the gnathostome groups familiar to us today (chondrichthyan and osteichthyan), as well as an array of bizarre extinct forms whose relationships are uncertain. From the remains of these early gnathostomes, we can piece together clues about the group’s origin and early radiation. However, the fossil record still leaves little evidence on the transformation from jawless to jawed vertebrate, even after almost 200 years of finding Palaeozoic gnathostome fossils.
The head and jaws of gnathostomes have attracted a great deal of interest among developmental biologists and palaeontologists. Their multitude of forms among living and fossil gnathostomes, and the mystery of their origin pose classical problems in vertebrate evolution that are still intensely researched to this day.

The skull and jaws are formed of either cartilage or a combination of cartilage and bone. The outer part of the skull is formed of dermal bones, bones that develop within the skin. Beneath this is the endocranium, or the part of the skull formed either entirely out of cartilage, or endochondral bone that has replaced the cartilage. These components make up the braincase, jaws, and the pharyngeal or branchial (gill) arches behind the jaws.

This is a basic organization or “plan”, but it does not illustrate the enormously diverse evolutionary paths that have modified the gnathostome head skeleton. In groups such as mammals, these basic components of the skull have become so modified that they are very difficult to distinguish in adult form. Some of these transformations were so dramatic that it is often difficult to recognise the correspondence of some features in the adult skulls of modern vertebrates.

The rich diversity and complexity of the head skeleton provides an excellent source of data for reconstructing the relationships of fossil and living species. Braincases, with their numerous passages for blood vessels and nerves, muscle attachment sites, and generally complex construction contain lots of information for comparative studies. They yield important characters that can be used to reconstruct the interrelationships of these animals.
The focus of this thesis is to describe and compare the morphology of the internal head skeleton (endocranium) in some of the earliest fossil gnathostomes from the Palaeozoic Era (570-248 million years ago). Two classical areas in early vertebrate evolution are investigated: the evolution of the spiracle and components of the hyoid arch in lobe-finned (sarcopterygian) fishes and early tetrapods (Papers I and II); and the morphology of the braincase and interrelationships of very early gnathostomes (Papers III-VI).
Theoretical framework

Before discussing fossil gnathostomes it is necessary to discuss the context in which and methodology by which they are understood. This section discusses methodology and the theoretical basis for the work done in this thesis.

Systematics and phylogeny

It is difficult, perhaps impossible, for evolutionary biologists completely to forget their training, their long soak in theory, and to think like non-evolutionists.


A (very) brief history of modern systematics

The theoretical approach that dominates this thesis is that the analysis of evolutionary events in the remote past requires knowledge of phylogeny: how organisms are related to one another. However, because there are no witnesses to gnathostome evolution in the Palaeozoic, and historical events are never repeatable, this type of science encounters a singularly difficult problem: phylogeny can never be known. However, we can infer it from patterns we observe among living things.

Prior to Darwin, classifications of life were viewed as reflecting a very real pattern that represented the plan of a creator god. Darwin (1859) argued forcefully that these early systematists were indeed recovering a real pattern, but that they were “unconsciously” uncovering the Tree of Life: the actual system of genetic relationships among taxa. As Darwin’s theory of common ancestry became widely accepted among naturalists, systematics became inextricably intertwined with the study of phylogeny.

However, it was not until the 1966 publication of the English translation of Willi Hennig’s *Phylogenetic Systematics* did a truly “evolutionary” classification system emerge. Hennig’s phylogenetic systematics (which came to be known as “cladistics”) emphasised shared unique characteristics (termed “synapomorphies”) as key to uncovering evolutionary interrelationships. In this way, Hennig recognised how a natural system of classification was obtained not through groups based on overall similarity, but through a hierarchy of unique features that define groups within groups (i.e. nested groups).
These relationships could then be presented in the form of a bifurcating tree called a **cladogram**.

During the 1970s and early 1980s, the school of “transformed cladism” emerged. This is a rather unpopular approach to systematics, as its chief proponents argue that evolutionary theory has no value in systematic biology. Perhaps what is underappreciated about the transformed cladists is that their effort aims to keep evolutionary theory from reliance on circular reasoning. Introducing presupposed law-like generalizations about how evolution proceeds (or, we think, ought to proceed) renders our systematic hypothesis incapable of detecting instances where those generalizations do not hold (Platnick, 1980).

**Inferring phylogeny**

To reconstruct phylogeny, character data must be gathered that can then be analyzed. **Characters** can come in the form of any attribute of an organism that can be compared with another organism. There is much debate about what constitutes a character, but for practical purposes it suffices to say that it is any aspect of an organisms which may be described and compared. Characters may take the form of anatomical features, behaviour, or the very molecules that make up an organism. For the purposes of this thesis, molecules and behaviour are unavailable and only the morphology of fossils can be studied and compared.

![Figure 2. Three possible ways of arranging the relationships of a shark, salmon, and a monkey and characters that might be used to define each grouping.](image)

To meaningfully discuss relationships, we need a group of at least three different organisms which we assume form a natural group, such as a species or genus (referred to as taxa, singular: taxon), that we can compare. A two-taxon statement is meaningless and trivial. A three-taxon statement can,
However, be arranged three different ways (Figure 2). Thus, in the case of the figure presented, we can resolve the relationships of a monkey, a salmon, and shark in a three different ways.

But just how do we do this? The salmon and the shark are overall more similar: they live in the water, have gills (obtain oxygen from the water), and have fins. The salmon and the monkey seem to share fewer things in common, such as the presence of endochondral bone and large plate-like dermal bones in the skull, while the shark has a skeleton made of cartilage and lacks large dermal skull bones. If we were grouping on the basis of overall similarity, the choice would be obvious: salmon + shark. In phylogenetic systematics, we recognise that overall similarity can be due to closeness of relationship or to the retention of primitive features. Thus, we need to know if two taxa are similar because of shared “primitiveness” or because they are more closely related to each other than either is to anything else. To determine this, we need a fourth taxon, one that we accept to be “outside” our group of three taxa. We call the outside taxon the “outgroup” and the taxa whose relationships we’re trying to resolve in the “ingroup”.

In this example, we take the jawless fish, the lamprey to be the outgroup (Figure 3). The lamprey has a cartilaginous skeleton, breathes through a series of gill openings, as does the shark. It also has a dorsal and tail fin (though no paired fins). The salmon and the monkey have skeletons made of bone. We have thus established polarity for these characters: the “directionality” we give characters in classification and in interpretations about their evolution. Thus, fins and gills do not establish close relationships between the salmon and the shark. These features are shared with the outgroup. The unique feature that is not possessed by the outgroup is endochondral bone, and so we group the salmon with the monkey (Figure 3). Knowing polarity allows us to identify the characters that unite the monkey and the salmon. Such characters are called synapomorphies, and the groups united by synapomorphies are termed monophyletic or a clade. Characters that are found to have evolved twice or more in a tree are convergences or homoplasies (singular homoplasy). Characters that are found to be primitive for the whole ingroup are referred to as “primitive” or plesiomorphic.

The introduction of cladistics into biology brought the recognition that many classical groupings were not monophyletic. For instance, mammals and birds were both agreed to be descended from some reptile ancestor (Romer 1958). Reptiles are not a group that excludes mammals or birds, but rather includes them. However, the definition of reptiles (scaly skin, “cold-blooded”, laying of soft-shelled eggs, etc.) does exclude mammals and birds (or most of them). As a consequence, we consider the grouping “Reptilia” to be paraphyletic, and excludes recognised groups.
Figure 3. The cladistic solution to the three-taxon problem in Figure 2. Gills and fins are plesiomorphic (primitive), and endochondral bone and dermal skull bones are a synapomorphy (homology) uniting the salmon and monkey. Internal fertilisation is independently derived for the shark and monkey (alternatively, one could propose that it was lost in salmon), an example of homoplaspy or convergence.

Another form of non-monophyly is called polyphly or polyphyletic. These are groupings that are composed of many distantly related taxa. A grouping of vertebrates that fly (bats, birds, pterosaurs) would be polyphyletic because each is a member of distantly related groups with non-flying ancestors.

The underlying theme with non-monophyletic groups is that they emphasise similarity alone, and not a combination of similarity and polarity. The significance of this to the thesis is discussed below.

Homology

One simply cannot escape the conclusion that the brain of a rat and a human are actually the "same" in spite of their obvious differences.

G. Wagner (1989, p. 51)

Controversies [surrounding the definition of homology] are frequently delimited by a homology proposition about which "most biologists would agree", as if this fact represented a valid argument per se.

M.G.G. de Pinna (1991, p. 368)

An introduction to the homology concept

Perhaps no other concept in biology is more unnecessarily mystified than homology. Homology is the foundational concept in comparative biology, upon which all systematic and evolutionary biology depends. This pre-Darwinian concept of the correspondence of parts of organisms dates to early comparative morphologists such as Geoffroy Saint-Hilaire and later elaborated upon by Sir Richard Owen. Since Darwin’s time, however, the
concept has become muddied by its newly ascribed evolutionary connotations (Patterson, 1982a). Today, the most common definition found in biology textbooks is typically as follows: ‘any similarity between two organisms occurring due to shared common ancestry’. For many, this has also become a prescriptive or operational definition, implying that homologies can be known independently of hypotheses of relationships.

The innate circularity of this is obvious: if homology is similarity due to common ancestry, how do we know if two organisms have a common ancestor? Because they share homologous characters, of course! As a result, biologists have sought to ground the concept of homology in some set of principles (often embryology) before phylogenetic analysis is conducted (e.g. Wagner, 1989; Laubichler, 2000). The result has been a proliferation of definitions and concepts that seek to circumvent this circularity. Hall (2003) counts some 19 definitions and forms of homology!

In my view, equating homology with synapomorphy (see Patterson, 1982a) satisfactorily (and simultaneously) avoids circularity, recognises the pre-evolutionary foundations of the concept, and accommodates evolutionary interpretations. Homologies are thus discovered by their congruence with other proposed homologies according to some optimality principle. Usually parsimony (simplicity) is the criterion of optimality, but work on molecular biology has led to a range of model- and probability-based methods that add sophistication. What is important is that homology is assessed through a combination of similarity and taxic distribution.

The quote by Wagner in the epigraph of this section misses the point about why the “sameness” of the human and rat brain is an inescapable conclusion. Wagner contrasts the eye and the brain, noting that the camera-type eye of octopi and vertebrates are not considered homologous, but the brain of a rat and the brain of a human are.

Rats and humans are both mammals, and all mammals have a brain (as do all vertebrates). By contrast, the eyes of octopi and vertebrates are similar in being constructed for a camera-type function. We do not see the eyes of humans and octopi as homologous because we know that both humans and octopi share closer relationships with other groups that do not have such eyes. Camera-type eyes are not widely distributed in the animal kingdom and so we have grounds to propose that they evolved independently in these two groups.

Identifying homologies
There is a desire among biologists to have certainty about homology before conducting phylogenetic analysis. The rationale is obvious: if homology can be known before phylogenetic analysis begins, then the greater confidence one can have in the resulting estimate of phylogeny. Although this approach is laudable for its effort to introduce rigor, evolutionary processes in the remote past can never be studied independently of the patterns used to infer
them (Platnick, 1980). Such prior confidence is therefore impossible to achieve.

On the other hand, some basic criteria must be established for homology proposal, or else one could arbitrarily choose any features, declare that they are homologous, and proceed to use it to support a preferred scheme of relationships. Sound comparative analysis must still form the basis of character selection and one must still endeavour to compare topographically equivalent parts. In molecular systematics, this is achieved through conducting a sequence alignment. Morphologists attempt a similar initial step (de Pinna, 1991; Brower and Schawaroch, 1996), with the initial proposal of primary hypotheses of homology taken to be topographically corresponding similarities. The initial proposal of a homology is called a primary hypothesis of homology (or “primary homology”). Those primary homologies which have passed the tests discussed below become secondary hypotheses of homology (or “secondary homology”).

Patterson (1982a) reviewed three tests of homology and the logic of passing any combination of these tests: similarity, conjunction, and congruence. The similarity criterion is doubtful as a test. It merely justifies a proposed homology, but beyond that it is of little use (Patterson, 1982a). Biologists can debate similarity until the end of days. How much similarity or difference is enough to determine whether or not structures shared by two different taxa are homologous? We must, therefore, assess other criteria in order to test homology.

**The test of conjunction** simply states that, if a feature proposed to be homologous is found in repeated instances within the same individual, it is not homologous. This test, however, does not rule out serial homologues (such as teeth, or fingers) which certainly are repeated within the same individual, by definition. But serial homology is a somewhat different comparative claim to homology itself (Patterson, 1982a)

**The test of congruence** is the condition of taxic distribution mentioned earlier. It is the strongest and perhaps only real test of homology (Patterson, 1982a; de Pinna, 1991). Any proposed homology implies a grouping based on the taxa that exhibit the structure in question. A proposed homology passes the test of congruence if it defines a group that is a unique subset of the groups defined by other proposed homologies. A proposed homology fails the test of congruence if it cannot define a unique subset of other groups established on congruent characters. That is, if it is not a synapomorphy of a group it is not a homology. In this way, homologies are identified though the groups they give rise to.

Cladogram construction is a congruence test. The identification of synapomorphies (=homologies) by a cladistic analysis is the means by which secondary hypotheses of homology are deduced. Thus homologies are identified by phylogenetic analysis itself, through the discovery of congruent character distributions. In this way, homology is not characterised by any
amount or degree of similarity, but as a combination of similarity and distribution.

Fossils, stem groups, and crown groups

Let us now look to the affinities of extinct and living species. They all fall into one grand natural system... That extinct forms of life help to fill up the wide intervals between existing genera, families, and orders cannot be disputed.

C. Darwin (1859, p.329)

While it is common to think of fossils as documenting evolutionary events, it is probably more that they activate our imaginings of these events. However evocative fossils may be, the depictions of evolutionary events they inspire are entirely imaginary. Patterson (1981) argued forcefully that fossils are not a key to recovering evolutionary relationships among living taxa, nor can they be expected to represented “ancestral” morphologies to which we can tie living forms and establish groups. Notions of fossils being necessarily “primitive” or “ancestral” (i.e. “missing links”) must be abandoned before attempting to determine their evolutionary significance.

Fossils tell us about the parts of the Tree of Life that have no living representatives and are thus important in helping reconstruct evolutionary history in revealing novel combinations of characters and testing proposed homologies in living forms. Fossils add information about the diversity of groups in their early history and can thus lead us to inferences about character transformation.

A phylogeny can be divided up into stem groups and crown groups. A **crown group** is defined by the last common ancestor and all descendent of the living representatives of a group. The **stem group** is the paraphyletic array of extinct taxa that are more closely related to the crown group in question than they are to any other crown group (Figure 4). Any crown group can contain within it any number of subordinate crown groups and stem groups. However, a stem group is, by definition, composed only of extinct species. Therefore, it is useful to discuss stem groups when discussing fossils, because fossil taxa are stem groups by definition.
Figure 4. Explanation of the stem group and crown group concepts. Members of crown groups B and C are composed exclusively of living taxa (e.g. B and C might each represent a distinct species or genus). Their immediate sister taxa (marked by a †) are extinct. These form the stem group. Groups B and C form a crown group (Crown group A).

The task of a palaeontologist is to discover which stem group a fossil belongs to. In this way, fossils fit into phylogenies that have already been established for living groups (Patterson, 1981). Thus, in order to identify fossils, we must have established a hypothesis of relationships for living groups. For the question of deep gnathostome evolution, we are fortunate to have the relationships of living groups quite well resolved (Figure 1).

A paraphyletic series of fossil sister groups is a useful arrangement, as it permits inferences of character acquisition leading up to the crown group. They then present evidence on the origin of the character complement that defines modern groups. Part of the aim of the present thesis is to help elucidate membership of the chondrichthyan and osteichthyan stem groups. However, it also aims to at clarify aspects of the upper part of the gnathostome stem group.

Character polarity and outgroups

Fitting fossils into a phylogenetic scheme requires the recognition of synapomorphies of crown groups (or, minimally, the groups thought to represent crown groups, since many analyses of fossil taxa do not include Recent forms). Questions of this nature are dealt with most extensively in Papers IV and V. Polarity decisions require the use of an outgroup. The outgroup is, ideally, the nearest sister taxon to the ingroup, whenever this can be known.
The problem with this approach is that a single outgroup does not always provide sufficient information to determine ingroup character polarity. This is especially problematic when fitting fossils into established phylogenetic frameworks. For any dichotomy between the ingroup and outgroup character state, there is the equally parsimonious interpretation that either the ingroup or outgroup presents the derived state of a character. Maddison et al. (1984) proposed the doublet rule of character polarity where two successive outgroups eliminates this uncertainty.

Multistate characters are characters for which there are more than two variable states. Often, a character is described as either “present” or “absent”. But values of characters, such as colour or shape, can often be more complex than simple presence/absence. DNA and amino acid characters present further examples of this case. Multistate characters easily give rise to situations where doublet outgroups are not decisive, and the polarity is ambiguous.

This problem is almost thematic for studies of early gnathostome phylogeny. Paper IV deals with this problem in relation to the study of osteichthyan origins. Paper V deals partly with this problem more deeply in relation to chondrichthyans and placoderms.
The Gnathostomata (Gegenbaur, 1874)

Basic gnathostome endocranial anatomy

The gnathostome internal head skeleton (endocranium) is composed of a braincase (or neurocranium), the jaws (or mandibular arch), the hyoid arch, and branchial arches (Figure 5). These arches, the pharyngeal arches, surround the mouth and throat (or pharynx) and fall in a series with each other. The head skeleton of gnathostomes (and all vertebrates) is endochondral, meaning that it is formed of cartilage or pre-formed in cartilage before being replaced by bone during development.

![Figure 5. The head skeleton of Mustelus (houndshark) showing the basic construction and arrangement of elements in the gnathostome endocranium. Pharyngeal arches are colour coded. Modified from Goodrich (1930).](image)

The braincase, or neurocranium, of jawed vertebrates is not unique to this group, but is a central structure of the vertebrate head and is here described first. As the name implies, it encases the brain and houses the nerves that emanate from it, as well as the blood vessels that supply it and drain from it. The braincase also contains the paired sensory organs: paired nasal capsules at the anterior, paired orbital (or eye) capsules behind those, and paired otic (or ear) capsules posterior to the orbital capsules. Primitively in vertebrates, there is a notochord, a cartilaginous rod about which (and partly from which in some groups, such as humans) the vertebral column forms.

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The notochord is present in the adults of the most primitive gnathostomes. In these forms, the braincase partially surrounds or includes the notochord beneath the brain and between the otic capsules. Behind the otic capsules, forming the midline back wall of the braincase, is the occiput. The occiput is considered to be formed of an indeterminate number of embryonic vertebrae in different gnathostome groups. True to its vertebral origin, the occiput surrounds the notochord and contains the spinal nerve cord and roots of the spino-occipital nerves. In primitive chondrichthyans and osteichthyans, it is at least partially separated from the braincase by a fissure known as the otico-occipital or metotic fissure.

The jaws, or mandibular arch, are composed of an upper part, the palatoquadrate, and a lower part, known as Meckel’s cartilage. They form a hinged linkage at the corners of the mouth, with the upper component of the hinge termed the quadrate and the lower (Meckelian) component termed the articular. The jaws may be linked to the braincase through joints or ligamentous attachments, or through the fusion of the palatoquadrate to the braincase. Primitively in living gnathostomes, the jaws are lined with teeth, though they have been lost in some groups.

Immediately behind the jaws is the hyoid arch, linked to the braincase at the level of the inner ear capsule. Like the jaws, it is formed primarily of an upper part, the hyomandibula, and a lower part, the ceratohyal. The dorsal part of the hyoid arch primitively acts as a link between the jaws and the braincase. The lower part primitively anchors jaw depressor muscles (in concert with the more posterior arches and the pectoral girdle) that function to open the mouth. Together, the jaws and hyoid arch form a series termed visceral arches and are a defining feature of modern gnathostomes (Reichert, 1837, cited in Rieppel, 1993).

Behind the hyoid arch are the branchial arches which, at least in fishes, support the gills. These generally follow a similar structure to the jaws and hyoid arch, in that they are hinged at the dorso-ventral mid-point. Dorsally, they are usually composed of a pharyngobranchial and an epibranchial. The pharyngobranchial attaches either to the braincase or vertebral column. The epibranchial attaches to the pharyngobranchial and the ventral branchial elements. Ventrally, they are composed of ceratobranchials. The branchial and hyoid skeleton meet a series of bones at the ventral midline. These are the basibranchials (for branchial arches) and the basihyal (for the hyoid arch), which may connect to the ceratobranchials (or ceratohyals) through paired hyobranchials (or hypohyals, known only in osteichthyans) (Figure 5).

The braincase and jaws are pre-formed in cartilage during growth. In many groups, there is an external, or perichondral, bone layer around the cartilage. But it is only in osteichthyans that the internal, or endochondral, part of these structures is replaced by bone.
Basic embryology of the gnathostome endocranium

It is often difficult to discuss the comparative morphology of the skull without reference to developmental criteria. Regions of the skull are frequently discussed through the use of terms with embryological connotations (i.e. a region of the skull may be described as “parachordal” or “trabecular”).

The embryonic neurocranium as it first begins to appear is a series of separate cartilage cell condensations. Ideally, it can be divided into two sets of midline structures, along with the paired sensory capsules which appear early in development as cartilage cell condensations. During development, these structures grow and join up to form the complete adult neurocranium.

The paired midline structures form the base of the neurocranium. The posterior pair which flank the notochord are the parachodral plates. Immediately anterior to them and to the anterior limit of the notochord are the paired rods known as the trabeculae cranii. The nasal capsules form at the anterior extremity of the trabeculae while the optic capsules form dorsally to them, and immediately posterior to the nasal capsules. The otic capsules form immediately behind these, and above the parachordals to which they are frequently fused. (Figure 6).

The bones of the pharyngeal arches form within elongated, ordered swellings of tissue separated by grooves (the grooves are termed “clefts” externally, and “pouches” internally). In fishes, the clefts between the arches corresponding to the branchial arches become the gill openings. The cleft between the mandibular and hyoid arches gives rise to the spiracle in fishes and the middle ear chamber and Eustachian tube in tetrapods.

The head skeleton is a complex mosaic of different embryonic cell populations. The bones of the pharyngeal arches are formed from neural crest tissue. This tissue arises at the margins of the developing nerve cord which initiates as a longitudinal invagination along the embryo’s back. The neural
crest cells become detatched (delaminate) from their position at the marginal ridges of the nerve cord invagination. From here, they move into the developing pharyngeal arches where they give rise to the skeletal elements. Most of the neurocranium is mesoderm, a compact embryonic tissue layer that “fills” the embryo between the ectoderm (the outer layer of the skin) and the endoderm (the wall of the gut). The trabeculae cranii are formed of neural crest tissue, even though they are incorporated into the braincase.
Historical and taxonomic review

The origin and early evolution of jaws

The idea that the jaw is a transformed [pharyngeal arch] fits the developmental sequence of the embryo better than the actual fossil record.

S. Kuratani (2004, p. 336)

Classical hypotheses

From Figure 5, it is easy to see the similarities between jaws and the more posterior arches. Indeed, this led many early morphologists to speculate that jaws were merely modified gill arches of an ancestral jawless form (reviewed in Janvier, 1996). These gill arches were said to have become enlarged, equipped with more powerful adductor muscles and armed with teeth. I have not been able to track down the original source for the actual transformational hypothesis, but for much of the twentieth century, it was taken to be a simple undisputed fact (“no doubt”, de Beer, 1937:418; Romer, 1958; Romer and Parsons, 1977). Goodrich (1930:404), however, expressed some doubt, citing the lack of palaeontological and embryological support.

If jaws and the hyoid arch are, in fact, modified gill arches, then it stands to reason that they should retain many of the primitive features of gill arches. This has led to considerable speculation by many authors about the existence of certain “primitive” jaw and hyoid morphologies in either fossils or embryos.

In the early twentieth century, morphologists speculated on the presence of a pharyngomandibular (Sewertzoff and Disler, 1924, cited in De Beer, 1937:419) and a pharyngohyal (see De Beer, 1937) to correspond with the pharyngobranchials of the more posterior arches (Figure 7). Holocephalans (or chimaeras, a highly specialised group of chondrichthians) are sometimes considered as having a “complete” or “unspecialised” hyoid arch, based on what is considered by some to be a pharyngohyal (De Beer and Moy-Thomas, 1935; Patterson, 1965; see also Grogan and Lund, 2000). However, Maisey (1984) shows that the hyoid arches of holocephalans are probably highly modified, and thus it is misleading to describe them as “unspecialised”. The hyomandibula of Acanthodes is composed of two discrete
ossifications, with a more proximal element suggestive of a pharyngohyal (Dean, 1907; Miles, 1964, 1968, 1973; Nelson, 1968). However, in this latter case, there is no evidence that the hyomandibula is formed of two discrete cartilages, as would be necessary to satisfy the identification of a separate pharyngohyal. It’s still possible (and fairly common) for a single cartilage to ossify at two separate points (c.f. hyomandibula and symplectic of neopterygian fishes).

Various theories have been proposed to explain the absence of a pharyngohyal in most other gnathostome taxa than holoccephalans. One proposed hypothesis is that the pharyngohyal was incorporated into the braincase or into the epihyal. However, it is equally probable that it never existed, or was never a component of the adult hyoid arch in the last common ancestor of living gnathostomes.

![Figure 7. Hypothetical ancestral gnathostome showing inferred pharyngomandibular and pharyngohyal elements as well as a premandibular arch. Black lines between arches represent gill openings. No living or fossil organism has ever demonstrated this complement of characters and it probably never existed.](image)

The complete absence of a pharyngomandibular has been particularly interesting. It has motivated some workers to seek its remnants in embryos and resulted in arguments that this hypothetical element has been incorporated into the braincase (Jarvik, 1954).

Whether or not pharyngohyals and pharyngomandibulars exist or ever existed may be both an uninteresting and unnecessary hypothesis. From a taxic perpective, pharyngohyals have only been “confirmed” in holoccephalans (de Beer and Moy-Thomas, 1935; Patterson, 1965) and a holoccephalan-like chondrichthyan Debeerius ellefseni (Grogan and Lund, 2000). Thus, there is no wider taxonomic distribution for this character that would suggest it was primitive in gnathostomes. Moreover, resolution of this problem is unlikely to alter conceptions about gnathostome phylogeny or their relationships to other vertebrates, as the relevant structures are supposedly unique to and primitive for all gnathostomes.

The existence of pharyngohyals and pharyngomandibulars is a simple empirical question: at present, there is no palaeontological evidence for the
existence of pharyngomandibulars, and pharyngohyals are not widely distributed. Attempts to divine them from or imagine them in embryos would seem to reflect a commitment to the theories from which they are derived. Moreover, even if they had existed in adult gnathostomes at one time, there is no reason to suppose that their remnants should be found in embryos today.

The “aphetohyoidean” theory speculated that early gnathostomes should be found to have a complete gill slit behind their jaws, and possibly even with the jaw arches supporting actual gills. Watson (1937) argued that the acanthodians (see below, as they figure prominently in this thesis) exhibited the aphetohyoidean condition. He interpreted numerous acanthodian fossils as having the primary gill cover attached to the jaws, rather than to the hyoid arch as in bony fishes and placoderms. However, Miles (1973), in re-examining much of this material, found no evidence for such a condition and found that the bony filaments of the gill covers were attached to the hyoid arch. One specimen of an isolated hyoid arch from the acanthodian Ischnacanthus examined by the author (Natural History Museum, London P 7000) clearly shows the gill cover plates attached to the hyomandibula, which verifies the claims of Miles. The aphetohyoidean hypothesis was later revived by Zangerl and Williams (1975) based on their interpretation of chondrichthyan, rather than acanthodian material. However, in this latter case, the evidence depends too much on soft tissue inferences on disarticulated fossil material.

Testing these classical theories on the origin and evolution of jaws is perhaps beyond the means of present data and methods. They seem to be inventions for rescuing segmentalist theories which imaginations must sometimes follow, but which Nature needn’t ever.

At present, there is ample reason to consider the velar region of agnathans as corresponding positionally with the jaws of gnathostomes. In the embryos of lamprey, the velum corresponds topographically with the mandibular somite of gnathostomes (de Beer, 1937). Like the jaws, it is innervated by the trigeminal nerve in both living and fossil agnathans (see Schaeffer, 1975; Janvier, 1996).

The mystery of jaw origins thus becomes one regarding the morphology of the precursors of jaws. In fossil agnathans considered closely related to gnathostomes, such as osteostracans (Forey and Janvier, 1993; Donoghue et al. 2000; Pradel et al. 2007), there appears to have been a muscular pump (Janvier, 1981; 1985). However, the actual skeletal arch structures are never preserved and so the morphological form of the immediate precursors of jaws remain mysterious. Nevertheless, it seems clear that the immediate precursors of jaws were specialised structures in their own way, and were not gill arches. The hyoid arch, by contrast, in fossil and living agnathans appears to correspond in form to the more posterior branchial arches, as far as one can tell. There is no evidence of its differentiation from more poste-
rior arches in agnathans, except in the hyoid arch being specially innervated by the facial nerve.

**Gene expression: a modern approach**

The question of the origin of jaws has taken a decidedly modern turn with the advent of molecular developmental biology. Recent work on lamprey and tetrapod embryos (reviewed in Kuratani, 2004) have revealed comparative gene expression patterns in these groups.

What has emerged from this research has been the discovery of genetic patterns that underlie the differentiation of jaw and pharyngeal arch structures. “Codes” of nested gene expression in the embryo are argued to divide the embryo into dorso-ventral, and anteroposterior blocks of tissue, each with its own specific genetic identity, specified by the overlap of different genetic “switches” (e.g. Depew et al. 2002).

The picture of jaw origins that has emerged from comparative gene expression studies complicates the morphological picture. Functionally equivalent parts of the lamprey and gnathostome mouth, as well as their respective embryonic mandibular arches, exhibit different gene expression patterns. This has been argued as being indicative of a “heterotopic shift” (Shigetani et al. 2002). According to this theory, neither the upper lip nor the entire lamprey velar skeleton can be said to correspond to the jaws of gnathostomes. The authors preferentially assign this shift to the gnathostome lineage though it is noted that the difference could be specific to the lamprey lineage (Kuratani, 2004:344).

The problem faced by molecular developmental studies is that the key players have diverged long ago in earth’s history. Furthermore, it is wrong to assume that lamprey and hagfish, because they lack jaws and paired fins, are somehow essentially primitive. They are both specialised groups with long evolutionary histories. Moreover, it is unclear to what extent gene expression patterns can tell us about the factors driving evolutionary change (Budd, 1999, 2006). Nevertheless, a study of comparative embryology has given rise to some interesting and important insights in gnathostome evolutionary history.

**Origin of the tetrapod middle ear**

One of the hallmark theories that emerged from the embryological inquest into gnathostome morphology concerns the origin of the middle ear of tetrapods. Tetrapods possess a stapes bone that fits into a hole in the otic capsule. In tetrapod groups capable of hearing, the stapes is the principle bone that conducts sound from the tympanum (‘eardrum’) to the inner ear vesicle. This novel adaptation is completely absent in fishes, and appears to
have emerged several times in different tetrapod groups (see Clack, 2002a; Müller and Tsuji, 2007).

German embryologist Carl Reichert (reviewed in Rieppel, 1993) recognised that, in tetrapods, the stapes is formed from the tissues of the embryonic hyoid arch. Although Reichert’s ideas did not imply transformation, Carl Gegenbaur working in the post-Darwin late 1800s, applied the transformational approach to this discovery and identified the stapes as a modified hyomandibular bone (Rieppel, 1993).

A stapes is found in all living groups of tetrapods, but it is not known in any fishes, where a hyomandibula is found instead (Figure 8). Thus, the stapes originated some time prior to the last common ancestor of all living tetrapods. Indeed, the very earliest and most basal (“primitive”) tetrapods had a well-developed stapes (Clack, 1989; Clack et al. 2003).

Figure 8. Comparison of the hyoid and branchial arches of A, a chondrichthyan, Cobelodus, and B, an early tetrapod Acanthostega showing the positional equivalence of the hyomandibula and stapes (marked in red). (A, modified from Zangerl and Williams, 1975; B, modified from Clack, 2002b).

Thus, the study of the origin of the middle ear has, in a sense, become a palaeontological pursuit. Papers I and II of this thesis deal with aspects of the hyoid arch, jaw, and spiracle morphology in fish-like members of the tetrapod stem group. Paper I shows that many attributes of the middle ear space seen in early tetrapods evolved prior to the origin of digited limbs, and in indisputably aquatic animals. The morphology of the sarcopterygian hyomandibula has been of interest to a number of researchers for its potential in shedding light on the origin of the stapes (Eaton, 1939; Romer, 1941; Smithsonian and Thomson, 1982; Lombard and Bolt, 1988). Paper II provides new data on hyomandibular morphology from a poorly understood group of stem-tetrapods, the rhizodonts. Data presented in these papers later figures in discussions of characters used in papers IV, V, and VI.

Early representatives of the Gnathostomata
Palaeozoic gnathostomes have been recognised in the fossil record for close to 200 years (see Janvier, 1996). They have always been of interest to scien-
tists investigating the early history of this group. The following is a short description of key groups considered in this thesis followed by a discussion of recent hypotheses of their interrelationships.

The “Placodermi”

Placoderms (Figure 9) are fishes characterised by heavy dermal armour and a moveable articulation between the head and shoulder girdle. They underwent a massive diversification during the Devonian before suddenly vanishing at the end of that period. They are quite possibly the most diverse group of Devonian fishes (Janvier, 1996) in spite of their very limited temporal range.

Figure 9. A selection of placoderm diversity. A, rhenanid; B, ptyctodontid; C, petalichthyid; D, antiarch; E, arthrodire. (A, C, E, redrawn from Denison 1978; B, redrawn from Miles 1967; D, redrawn from Arsenault et al., 2004).

Placoderms ranged from relatively small forms, not more than a few centimeters long, to the giant arthrodires such as Dunkleosteus from North America. Their diversity encompasses a number of different groups ranging from the more ‘conventional’ looking arthrodires, to the extremely bizarre forms such as rhenanids and ptyctodontids.

Overall, their morphology is characterised by simple jaws, often bearing heavy dermal plates, dermal armour forming a complete ring around the trunk, a paired articulation between the dermal shoulder girdle and the skull, an epiphyal element fused to an opercular plate and articulating directly with the braincase, and a special type of dermal tissue called semidentine (Goujet, 1984a).

These characters have been cited numerous times as synapomorphies of the “Placodermi” (Goujet, 1984a, 2001; Goujet and Young 2004). It is gen-
erally accepted that placoderms form a monophyletic group, in spite of the absence of any systematic tests of this hypothesis. Papers V and VII test placoderm monophyly and find that characters of the braincase and postcranial skeleton suggest placoderm paraphyly with respect to crown-group gnathostomes.

The braincase, and sometimes the jaws, are well known in a number of placoderms and have provided a wealth of character data used in this thesis. The first detailed works were by Stensiö (1925, 1950, 1963, 1969). Goujet (1975, 1984b) described the braincase, jaws, and epiphyal or opercular cartilage in excellently preserved, mechanically prepared specimens of the arthrodire Dicksonosteus. Acid-prepared specimens from limestones in Australia have proven especially informative for revealing the structure of the jaws and braincase in a number of peculiar placoderm forms (Miles, 1977; Miles and Young, 1977; Young, 1979, 1980, 1984).

The “Acanthodii”

The “Acanthodii” are an assemblage of fishes characterised by the presence of a sharp spine at the leading edge of every fin except the caudal (tail) fin (Figure 10). They have a peculiar scale morphology which, when examined in cross-section reveals a concentric series of growth layers, often referred to as an “onion-skin” pattern. They may sometimes have a row of short spines or scutes along the ventrolateral edges of the body, anterior to the pelvic fins, or a number of small spines anterior to the pectoral fins.

![Figure 10. Representatives of three different groups of the “Acanthodii”: A, a clamiid; B, an ischnacanthid; C, an acanthodiform. (Redrawn from Watson, 1937, with modifications from Miles, 1973, in A).](image)

Acanthodians have been of interest in studies of early gnathostomes because they are among the earliest to appear in the fossil record, but also because of the unique mix of chondrichthyan- and osteichthyan-like characters they exhibit. Like chondrichthyans, acanthodians typically did not have endochondral bone, so their internal skeletons rarely fossilised. Also, like chondrichthyans, the lateral line canal is flanked by the body scales, rather than passing through them, as in most other groups (see Paper IV).
ever, acanthodians share with osteichthians the presence of branchiostegal gill covers and certain features of the endocranium.

The internal skeleton, including the head, jaws, and fin skeleton is best preserved in the ironstone moulds of *Acanthodes bronni*, from the Permian of Lebach, Germany. From these specimens, we have been able to obtain a detailed account of the braincase for this lone acanthodian genus (e.g. Watson, 1937; Miles, 1973 and references cited by these authors). Thus, this important source of phylogenetic data is wanting from all other acanthodians.

These braincase data have formed the basis for competing hypotheses of relationships for acanthodians. Jarvik (1977, 1980) preferred to interpret acanthodians as the sister group of chondrichthians. Miles (1973), however, interpreted evidence in a cladistic framework, using outgroup comparison rather than inferences about the essential importance of certain characters. Thus, the hypothesis of Miles has since become a preferred solution (Denison, 1979).

The Chondrichthyes

The chondrichthians are the so-called “cartilaginous fishes”, though a cartilage internal skeleton is found in all vertebrate groups at some point in their life history. The chondrichthians include sharks, skates, rays, and chimaeras and are characterised by a skeleton that is composed of prismatically calcified cartilage. Chondrichthians are also characterised by the possession of paired pelvic claspers, a set of external reproductive structures in males. These are formed as elongated appendages of the pelvic fin skeleton. Although there is evidence of claspers in ptyctodontid placoderms, they do not appear to be homologous with those of chondrichthians (Young 1986; Papers V and VI).

Figure 11 shows an array of Palaeozoic chondrichthians. For many decades, the earliest articulated chondrichthyan was *Cladoselache* from the Late Devonian Cleveland Shale of Ohio (Dean, 1909). As the oldest chondrichthyan and notable for its apparent lack of pelvic claspers, *Cladoselache* earned a status as the most “primitive” chondrichthyan (Moy-Thomas and Miles, 1971; Romer, 1958; Carroll, 1988). However, new data on articulated Devonian and Carboniferous chondrichthians from the last half-century have greatly altered modern conceptions of chondrichthyan interrelationships.
Figure 11. Some representative Palaeozoic shark-like chondrichthyans that featured in this dissertation: A, a stethacanthid; B, a cladoselachian; C, a xenacanth. (A, redrawn from Coates and Sequeira, 2001b).

Chondrichthyans are frequently divided into the Holocephali (chimaeras) and the Elasmobranchii (more shark-like fishes and rays/skates). However, when fossil groups are concerned, this division becomes unclear and there is much disagreement about which taxa belong on the elasmobranch and holocephalan stem lineages (e.g. Grogan and Lund, 2000; Lund and Grogan, 2004a,b; Coates and Sequeira, 2001a,b; Maisey, 2001).

Recent cladistic analyses (e.g. Coates and Sequeira, 2001a,b; Maisey, 2001) have ousted *Cladoselache* from its position as “most primitive” chondrichthyan. Perhaps most interesting is that Coates and Sequeira find *Cladoselache*, along with a number of other similar forms, to be members of the holocephalan stem lineage. These latter analyses have recovered tree topologies suggesting that the chondrichthyan stem is devoid of recognised chondrichthyan taxa. Papers V and VI attempt to identify “acanthodians” that may be stem-group chondrichthyans and clarify characters used to diagnose potential stem chondrichthyans.

A growing body of data on the braincase and pharyngeal arch skeleton of chondrichthyans has been helping re-shape chondrichthyan phylogeny. Well-preserved, three-dimensional (or nearly three-dimensional) braincases of Devonian and Carboniferous chondrichthyans have provided a wealth of new data (Schaeffer, 1981; Williams, 1998; Coates and Sequeira, 1998; Maisey, 2005, 2007, Maisey et al., in press).

The most surprising discovery among chondrichthyans is *Pucapampella*, the enigmatic chondrichthyan from the Middle Devonian of Bolivia and South Africa (Maisey, 2001; Maisey and Anderson 2001). Perhaps its most surprising features are a ventral cranial fissure and basipterygoid articulations, features previously thought to define the Osteichthyes (Schaeffer,
1968; Miles, 1973). This taxon has thus induced serious reconsideration of the character compliment defining the gnathostome crown group.

The Osteichthyes

By far the largest of all these groups is the bony vertebrates, or osteichthans. They comprise nearly 30,000 species of ray-finned fishes and nearly as many species of tetrapods, or four-limbed vertebrates. Their key defining attribute is endochondral bone (Figure 12), creating a solid internal skeleton. The Osteichthyes are divided into two large groups: the Actinopterygii, or ray-finned fishes, and the Sarcopterygii, or lobe-finned “fishes”/vertebrates which includes tetrapods.

The fossil record of these groups extends well into the Devonian. Perhaps owing to their significance in understanding the origin of tetrapods, sarcopterygians seem to be better represented in the Devonian and have been more thoroughly investigated (e.g. Jarvik, 1980) than actinopterygians. However, many of these studies on sarcopterygians have revealed a great deal about basic osteichthyan endocranial morphology (e.g. Säve-Söderberg, 1936; Romer, 1937, 1941; Jessen, 1980; Jarvik, 1954, 1972, 1980). Along with these earlier well-studied forms, a host of new data from China (Chang, 1982, 2004; Chang and Yu, 1984; Yu, 1998; Zhu and Yu, 2002; Zhu et al. 2001, 2006) and acid-prepared material from Australia (Fox et al. 1995; Long et al., 1997; 2006) have provided a wealth of anatomical data on primitive sarcopterygian braincases.

Figure 12. Representatives of some early osteichthians from the Palaeozoic; A, a porolepiform sarcopterygian; B, an actinopterygian; C, cross-section through the snout of the Devonian sarcopterygian Eusthenopteron, showing the defining osteichthyan feature, endochondral bone. Heavy black elements represent cross sections of dermal bone. (A, C modified from Jarvik, 1980; B, redrawn from Gardiner, 1984).
The record of Devonian actinopterygians is fairly sparse, but endocranial data are well known from the forms *Mimia* and *Moythomasia* (Gardiner, 1973, 1984). Although little is known of its endoskeleton, *Cheirolepis* has played a significant role in studies of actinopterygian evolution, as it has widely been considered one of the most basal actinopterygians (e.g. Moy-Thomas and Miles, 1971; Pearson and Westoll, 1979; Patterson, 1982b; Gardiner, 1984; Carroll, 1988; Cloutier and Arratia, 2004, and results cited therein; Friedman and Blom, 2006). A large amount of well preserved material of this taxon has been recovered from Scotland and Canada, including some clues to the structure of the braincase and jaw cartilages (Pearson and Westoll 1979; Arratia and Cloutier, 1996). *Howqualepis* (Long, 1988), an actinopterygian from the Devonian of Australia, also presents some evidence of the endocranium, though it is preserved as natural moulds and subsequently cast in rubber.

**Papers I, II, and IV** concern osteichthyans specifically. They provide new observations on osteichthyan morphology and review hypotheses of osteichthyan interrelationships. Paper IV, in particular, reviews and re-evaluates the characters considered to define primitive osteichthyans. This paper also addresses the problem of identifying members of the osteichthyan stem. Until recently, the only accepted members of the osteichthyan stem were the acanthodians. However, Paper IV, in addition to previous works (Basden et al. 2000; Friedman, 2007) identifies the enigmatic forms *Ligu-lalepis* (Basden et al., 2000; Basden and Young, 2001) and *Dialipina sal-gueiroensis* (Schultze and Cumbaa, 2001) as probable stem osteichthyans.

**Gnathostome phylogeny and ‘jawless gnathostomes’**

The interrelationships of Palaeozoic gnathostome groups is a contentious topic with a diverse and complex history. Before the advent of cladistics as a means of inferring relationships, palaeontologists focused on the nomination of particular fossils or fossil groups as candidate ancestors (reviewed by Thomson, 1981; Janvier 1996). By the end of the 1960s, vertebrate palaeontologists had begun applying Hennig’s (1966) phylogenetic systematics to the study of vertebrate interrelationships and the question of fossils.

Amongst the first questions to receive a cladistic treatment by vertebrate palaeontologists and neontologists was the interrelationships of both fossil and Recent gnathostomes (e.g. Nelson, 1969; Miles 1973; Wiley, 1979). Among early fossil gnathostome groups, placoderms have had a rich history of proposed cladistic solutions to their interrelationships (Miles and Young 1977, Denison, 1978, Young 1979, 1980, 1986, Goujet, 1984a; Forey and Gardiner, 1986; Goujet and Young 1995).

Over the past four decades, a number of alternative cladistic solutions have been proposed for the relationships of basal gnathostomes, inclusive of fossil taxa.
Nelson (1969) regarded acanthodians as the sister group of chondrichthyans, primarily supported by similarities in the orientation of the pharyngobranchials. However, Nelson did not explicitly include placoderms.

Miles (1973) focused specifically on the question of acanthodian relationships with the Chondrichthyes and Osteichthyes. In light of a revised description of the endocranium of *Acanthodes*, Miles evaluated three competing hypotheses: acanthodians as the sister group of crown gnathostomes; acanthodians as the sister group of chondrichthyans; and acanthodians as the sister group of osteichthyans. As previously mentioned, Miles hypothesised sister-group relationships between acanthodians and osteichthyans.

The cladistic solution proposed by Rosen et al. (1981) represents the third option for the position of the acanthodians: as the sister group of Osteichthyes + Chondrichthyes, thereby placing them as stem-group gnathostomes. However, these authors acknowledged explicitly that they were considering *Acanthodes bronni*, rather than a composite acanthodian as in other analyses.

Gardiner (1984) later proposed that both acanthodians and placoderms were crown-group gnathostomes on the osteichthyan stem. Based on their dermal bone covering, placoderms were argued as being the nearest sister group of the Osteichthyes.

Schaeffer (1975) favoured the view that placoderms were stem gnathostomes. This view was later upheld by Young (1986), citing strong evidence from the orbital morphology of placoderms, “agnathans”, osteichthyans, and chondrichthyans. This last picture (Figure 13) is a generally accepted, though not uncontroversial, picture of gnathostome interrelationships.

*Figure 13. Summary of Palaeozoic gnathostome groups including extinct groups and the jawless stem gnathostome group, Osteostraci (extinct groups marked by a dagger symbol †). Consensus relationships based on Janvier (1996).*
The overall scheme in which placoderms are stem gnathostomes and acanthodians are the sister group of osteichthyans has been upheld by several analyses (Coates and Sequeira 2001a,b; Friedman, 2007), although not all of these data matrices were specifically targeted at this question.

The question of gnathostome origins at a broad level has been greatly informed through a study of jawless vertebrate interrelationships. The fossil jawless fishes, collectively termed ‘ostracoderms’, form a paraphyletic series of sister taxa to the Gnathostomata (Forey and Janvier, 1993; Donoghue et al. 2000; Gess et al. 2006). This total-group view highlights the deeper portion of the gnathostome stem lineage and provides insights into the origin of paired fins and the patterning of the tail fin (e.g. Wilson and Caldwell, 1998; Pradel et al. 2007).

The problems emerging in recent years have been the pre-supposed monophyly of certain fossil groups. Of interest in this thesis are the placoderms and the acanthodians. Acanthodian monophyly has been in doubt for some time (e.g. Schaeffer, 1968; Janvier, 1996; Coates, 2003). In the past decade, the discovery of paired and median fin spines in an osteichthyan, Psarolepis (Zhu et al. 1999), and paired fin spines in a chondrichthyan, Doliodus (Miller et al. 2003), have overturned this character’s utility as an acanthodian synapomorphy. Additionally, peculiar ‘acanthodian’-like teleostomes from northern Canada (Gagnier and Wilson, 1996; Hanke 2002; Hanke and Wilson 2004; Wilson et al. 2007) and Australia (Burrow and Young, 1999) demonstrate incongruent distributions of fin spine and scale characters previously used to diagnose the acanthodians.

Johanson (2002) and Friedman (2007) have recently challenged placoderm monophyly and are the first to do so in an explicitly cladistic framework. Young (2008) has disputed the character interpretations cited by Johanson in support of an alternative relationships scheme in which antiarchs are more basally stemming than other placoderms. Before the publication of Paper V, a comprehensive generic-level test of this question had never been accomplished.
Conclusions and prospectus

This dissertation has provided the following novel data and insights on questions related to basal gnathostome evolution:

1. Spiracular and hyomandibular morphology transformed to a tetrapod-like morphology before the origin of digited limbs in tetrapods (Paper I).
2. The investigation of rhizodontid hyomandibulae offers new clues on the complement of muscles in the hyoid region of basal stem-group tetrapods, as well as phylogenetic characters (Paper II).
3. The canal piercing the osteichthyan hyomandibula may be formed by the ontogenetic closure of a sulcus (Paper II). This feature is important in understanding both the origin of the osteichthyan hyomandibular canal and the origin of the tetrapod stapes.
4. Paper IV offers a reconsideration of the basal character complement of osteichthyan and increased support for novel interpretations of the phylogeny of the most primitive members of this group. It provides the first comprehensive review of this problem in 40 years and suggests a series of candidates (or supports earlier proposals) for stem osteichthyan.
5. The first known braincase and articulated jaws of a Devonian acanthodian (Ptomacanthus) are described (Paper V) offering significant new data on the relationships of acanthodians.
6. The first comprehensive genus-level cladistic analyses for basal gnathostomes are conducted (Papers V and VI). These results challenge placoderm and acanthodian monophyly, and uphold osteichthyan and chondrichthyan monophyly. They identify characters and taxa that give rise to character distributions incongruent with traditional conceptions of basal gnathostome interrelationships.
7. The anatomical details of Ptomacanthus are expanded upon and comparisons made in light of new data (Paper VI).

None of these results present a definitive, complete, or final answer to the questions they address. In light of this work, I have identified a number of problems or suggested tasks that will help guide future research on the anatomy and phylogeny of basal gnathostomes:
• Braincase and endoskeletal data from acanthodians may be more common than previously thought. A re-examination of existing museum collections may yield more important data that can test or corroborate the conclusions drawn from *Ptomacanthus* and *Acanthodes* regarding the relationships of “acanthodians”.

• “Placoderms” as a whole must be re-considered with the possibility that they are paraphyletic with respect to gnathostomes. This could help reveal jaw morphologies that are intermediate between the “agnathan” condition and gnathostomes.

• Scale morphology and histology must be studied in a wider range of undisputed chondrichthyans and “placoderms”. These will provide key insight into the significance of scale morphology characters in diagnosing taxa.
Svensk sammanfattning

Inledning

Teoretiskt ramverk
Fossila organismers evolutionära betydelse kan bara diskuteras mot bakgrund av, och i relation till, deras släktskapsförhållanden. I denna avhandling används ett kladistiskt ramverk för att uttrycka släktskapshypoteser om fossila organismer och de levande grupper med vilka de tros vara besläktade. Genom att placera fossil och nulevande grupper i gemensamma släktskapshypoteser är det möjligt att rekonstruera sekvenserna av morfologiska förändringar som ledde till de nulevande gruppernas uppkomst.

Gnathostomernas morfologi
Historisk och taxonomisk översikt

Käkar tros ha uppkommit som en modifikation av primitiva gälbågar, men den detaljerade bilden från jämförande anatomi, paleontologi och embryologi är betydligt mer komplicerad. Teoretiska ursprungsformer och arketyper är dessutom inte representerade varken bland fossilen eller i den nulevande faunan. Utvecklingsbiologiska studier av grundläggande gnathostommorfologi har dock givit upphov till en del viktiga hypoteser som till exempel uppkomsten av tetrapodernas (landryggradsdjurens) mellanöra från komponenter av fiskarnas hyoidbåge.

De tidiga gnathostomerna representeras av en mängd sinsemellan olika former: placodermerna, acanthoderna och primitiva medlemmar av chondrichthyiderna och osteichthyiderna. Syftet med denna avhandling är att beskriva och jämföra de fossiliserade craniala endoskeletten från ett antal olika paleozoiska gnathostomer. Målet är att testa vedertagna ideer om släktskapsförhållandena bland gnathostomerna och dra slutsatser om viktiga morfologiska omvandlingar som ägde rum inom gruppen under paleozoikum. Två huvudområden har studerats: de paleozoiska gnathostomernas morfologi och släktskapsförhållanden, och svalgbågarnas morfologi hos de sarcopterygiska (kvastfeniga) fiskarna.
Completing this work would have been impossible if not for the generous help and support of many people.

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