The Anterior-Most Vertebrae and Occiput of Eusthenopteron: Implications in the Origin of the Tetrapod Atlas-Axis Complex

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ABSTRACT

The anterior-most elements of the vertebral column of Eusthenopteron foordi are examined by direct observation of articulated material. Large blade-like supraneural spines are present above neural arches 1, 3, and 5, but not 2 or 4. The supraneural spines support a muscular complex involved in feeding, not only through raising the snout, but also in depressing the lower jaws by the forward swing of the quadrate. The similarity in skulls of osteolepiforms, and between osteolepiforms and Paleozoic tetrapods implies that a cranio-vertebral joint of similar function existed in the ancestor of tetrapods, forming the precursor of the tetrapod atlas-axis complex.

The distinct nature of the basioccipital and exoccipitals of tetrapods is the result of reduced ossification of the occiput, and not the incorporation of vertebral elements onto the back of the braincase relative to the rhipidistian condition. The similarity between the occiput and succeeding vertebrae of some primitive tetrapods is due to analogous ossification of notochordal tissue. Bony occipital condyles arose separately in many lineages of Paleozoic tetrapods. The atlas-axis complex of tetrapods is constrained by the pattern of occipital articulation. It is an excellent character for diagnosis of particular groups, but a poor character for determining relationships between separate lineages.

RÉSUMÉ

Un spécimen articulé d'Eusthenopteron foordi permet d'examinées les éléments antérieurs de la colonne vertébrale. De grandes lames supra-neurales sont présentes au-dessus des arcs 1, 3, et 5, mais non sur les arcs 2 et 4. Les éléments supra-neuraux supportent un complexe musculaire épaxial responsable, non seulement de l'élévation de la tête, mais aussi de l'ouverture de la mâchoire par la projection avant du carré. La similarité des crânes des ostéolépiformes indique qu'un complexe cranio-vertébrale semblable existait chez l'ancêtre des tétrapodes. Ceci suggère un morphoclyne entre un complexe de ce type et l'atlas-axis des tétrapodes.

Consideront la condition des ostéolépiformes comme primitive, le basioccipital et les exoccipitaux des tétrapodes sont le résultat d'une réduction de la solidite de l'occiput, et non pas de l'incorporation d'éléments vertebraux rhipidistiens. La similarité entre l'occiput est les vertèbres de certains tetrapodes semble due au même processus d'ossification des tissues chordaux. Les articulations occipitalles se sont dévélopées séparément chez plusieurs groupes de tétrapodes paléozoiques. Le complexe atlas-axis des tétrapodes est affecté par la morphologie de l'occiput. Il est donc un bon caractère pour l'identification des differents groupes, mais peu informatif sur les relations entre les groupes.

PREFACE

The preparation, description and functional interpretation of the anterior-most vertebral elements of _Eusthenopteron foordi_ is entirely original work. Analysis of the function of the various components of the head during feeding is new, but founded on considerable previous work on _Eusthenopteron_ and on other fishes. The discussion of the function and phylogeny of the atlas-axis complex of tetrapods is a new synthesis of information present in the literature, in conjunction with information obtained in this study.

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I would also like to thank Peter Forey at the British Museum for allowing me to study material there, Dr. Oleg Lebedev for allowing me to examine an osteolepid specimen from the Soviet Union, and Drs. Jenny Clack and Mike Coates at the Cambridge University Museum of Zoology for allowing me to see their specimens of *Acanthostega*, and along with Dr. Per Ahlberg, providing stimulating discussion on the origin of tetrapods.

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INTRODUCTION

The first great radiation of tetrapods in the Late Devonian and Early Carboniferous followed soon after their divergence from rhipidistian fish. This transition involved numerous changes in anatomy and physiology. Out of water there is an increased dependence on the skeleton for support. While suspended in water the entire body is supported uniformly, but on land the body is stressed by gravity around a few points of contact with the ground. Accordingly, there is increased ossification of the vertebral column, the development of an ossified pelvic girdle and the evolution of limbs from fins. Other skeletal changes include the separation of the pectoral girdle from the back of the skull, leaving the head cantilevered forward.

The decoupling of the skull and pectoral girdle provides increased flexibility to allow rotation along the axis as well as lateral and vertical flexion, while the trunk remains stationary. The anterior two vertebral segments, termed the atlas-axis complex, are specially modified in tetrapods to allow for this rotation while providing the required support.

Rotation of the head is much more important for feeding in terrestrial vertebrates than in fish. Fish are suspended in the water, may flex the body as desired, and are not anchored to the substrate. If a fish needs to orient on prey, it can re-orient the entire body; thus no separation of pectoral girdle and skull is required and the vertebral column does not provide the kind of support to the skull that is achieved in the cervical vertebrae of tetrapods. No fish has a specialized atlas-axis complex comparable with that of tetrapods. The problem investigated in this thesis is to determine the condition of the anterior vertebrae in the group ancestral to tetrapods, in order to shed some light on the origin of the tetrapod atlas-axis complex.

The osteolepiform rhipidistians are considered by most paleontologists to be the sister-group of tetrapods, or the group from which the tetrapods arose (Panchen and Smithson, 1987; Carroll, 1987; Romer, 1966, but for an alternate view see Rosen et al., 1981; Patterson, 1980). Many of the bones of the skull, vertebral column and limbs in these fish can be directly homologized with those of early tetrapods. The presence of choanae is considered by many to be the most important character in establishing this relationship. The choanate condition is defined by Panchen and Smithson (1988) as "a fenestra endochoanalis in the nasal capsule, lying dorsal (deep) to a fenestra exochoanalis bounded by the premaxillary and maxillary laterally and the vomer and palatine medially." Panchen and Smithson (1987, 1988) dispute the claim that porolepiforms (Jarvik, 1980) and

Dipnoi (Rosen et al, 1981) are choanate. The choanate condition is thus shared solely by the osteolepiform rhipidistians and tetrapods.

Previous descriptions of the anterior-most region of the vertebral column in one of the best known osteolepiform rhipidistians, Eusthenopteron foordi, based on grinding series (Jarvik 1975, 1980) and disarticulated remains (Andrews and Westoll 1970), conflict with one another. My intent in this thesis is to examine in detail the articulated anterior-most vertebral segments in RM 14 234, a three dimensional skull of Eusthenopteron in which the anterior part of the vertebral column is intact, establish their natural structural relationships, and determine the functional significance of these elements in conjunction with structures of the cranium. The structure and function of this region in Eusthenopteron will be used as a basis for considering the adaptive changes of the cranio-cervical joint in Paleozoic tetrapods.

There are three related problems covered by this thesis. The first is the description and functional interpretation of the anterior-most vertebrae of Eusthenopteron. Because this region is associated with the epaxial muscles involved in skull movement, this problem also involves the functional morphology of feeding mechanics in this fish. The second problem is to determine the implications of the structure and function of this region in Eusthenopteron in the origin of the tetrapod atlas-axis complex. The third problem involves the diversity of patterns of the atlas-axis complex in Paleozoic tetrapods, which requires an examination of functional and developmental aspects of the vertebral column and occiput of these animals.

MATERIALS AND METHODS

All the specimens of Eusthenopteron examined were originally collected from Escuminac Bay on the Restigouche River, on the south coast of the Gaspé Peninsula, Quebec, Canada. This site is now a provincial park, Parc Miguasha, and is the location of the Musée d'Histoire Naturel Miguasha.

The specimens used in this study are as follows.

(i) GN790 (Cambridge university Museum of Zoology) - a short series of vertebrae.

(ii) MHNM 6-216 (Musée d'Histoire Naturel Miguasha) - an articulated series of trunk vertebrae.

(iii) MHNM 6-12-196 - the ventral half of the otoccipital portion of the endocranium, on which considerable preparation was done for this thesis.

(iv) ROM 1234 (Royal Ontario Museum) - an endocranium, first described by Sternberg (1941).

(v) ROM 1245 - an almost complete vertebral column with some skull material exposed in ventral view.

(vi) P6796a (Natural History Museum, London) - a large three dimensional skull, behind which lies much postcranial material, mostly disarticulated.

(vii) RM 14 234 (Redpath Museum) - a complete three dimensional skull. Mechanical preparation exposes the anterior portion of the vertebral column and the occiput. This specimen forms the primary basis of this research.

Mechanical preparation of RM 14 234 and MHNM 6-12-196 was done using a Chicago Pneumatic CP-9361-1 Air Scribe. Delicate preparation was performed using a mounted needle. Some chemical preparation was done using 10% acetic acid. VINAC B-15 polyvinyl acetate was used as a consolidant.

THE SKULL IN RHIPIDISTIANS AND TETRAPODS

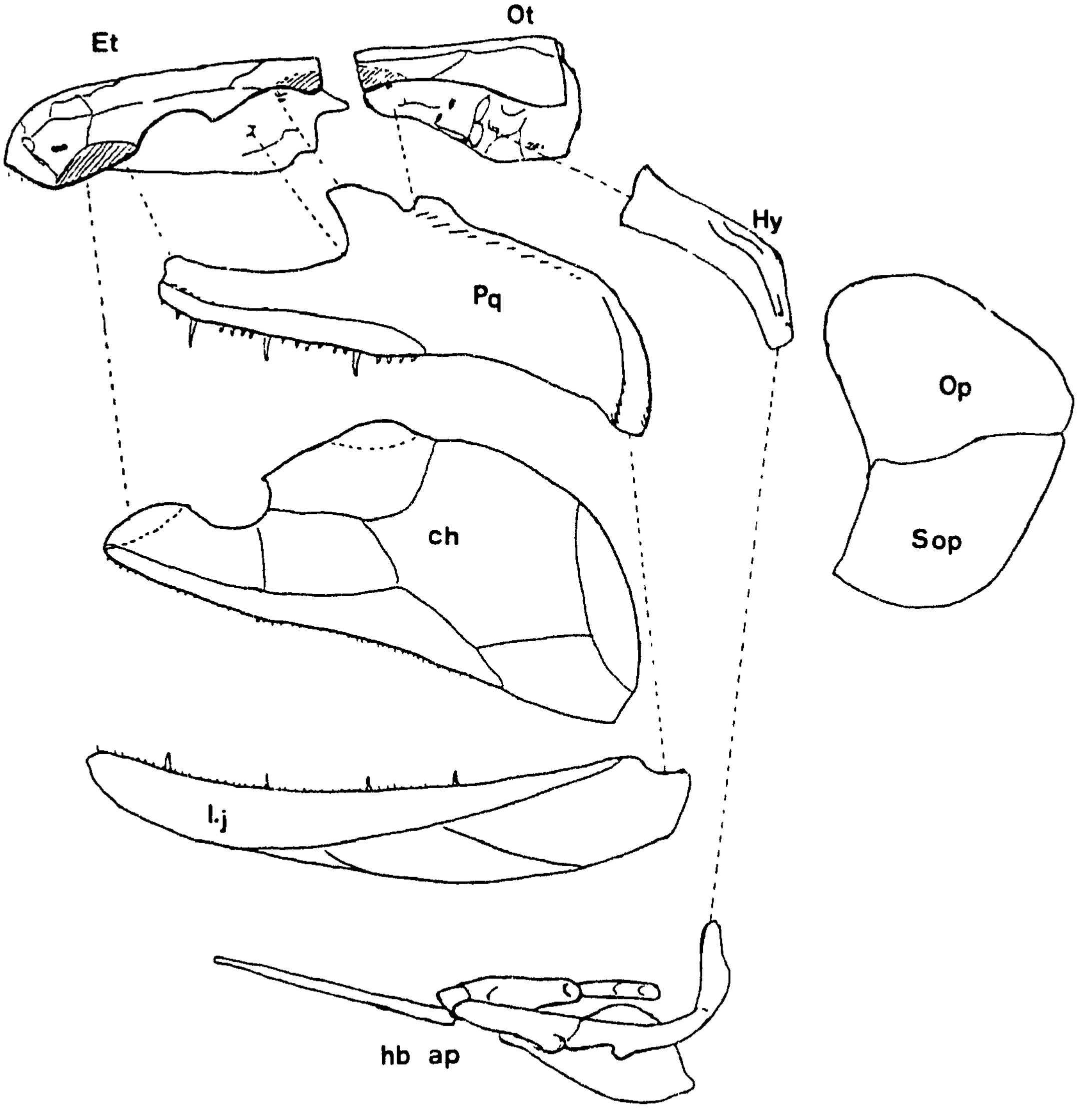
Description of the head region of *Eusthenopteron*

Most the bones of the skull of rhipidistians may be readily homologized with those of tetrapods. In contrast, the skulls differ greatly in their mechanical specializations for feeding and respiration. Both of these activities also involve the anterior vertebrae.

In order to understand the many changes that occurred in the rhipidistian-tetrapod transition, the cranial structures must be fully appreciated.

The skull of Eusthenopteron (Figures 1-3) comprises several articulated units (Jarvik 1980). The braincase consists of two segments, the anterior ethmosphenoid and the posterior otoccipital. The palatoquadrate lies lateral to the braincase and articulates with it. The cheek plate lies lateral to the palatoquadrate and articulates with the snout and skull roof. The lower jaws articulate with the quadrate. Below and between the lower jaws is the hypobranchial apparatus, and behind the skull lie the opercular bones and the pectoral girdle.

Figure 1. The separate units that comprise the head of *Eusthenopteron*. The hatched areas on the snout and skull roof indicate the region of overlap by the cheek plate. Abbreviations are as follows: ch- cheek plate; Et- ethmosphenoid; Hb ap- hypobranchial apparatus; Hy- hyomandibular; l.j- lower jaw; Op- opercular; Ot- otoccipital; Pq- palatoquadrate; Sop- subopercular. Based primarily on specimen RM 14 234 and Jarvik (1980).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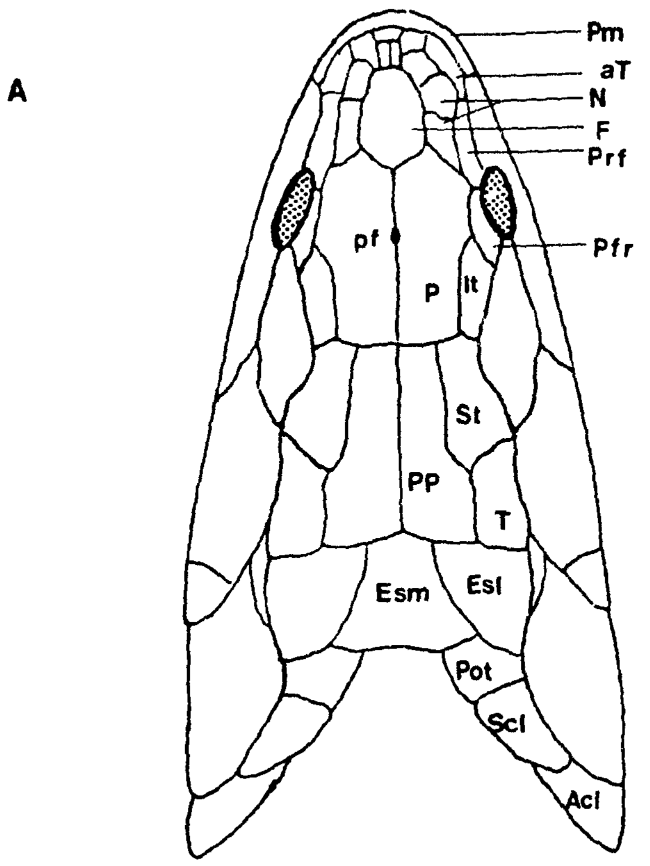
The dermal skull and braincase of Eusthenopteron (Figures 2 and 3) have been thoroughly described (Jarvik 1942, 1944, 1954, 1963, 1980, Sternberg 1941, Westoll 1937, 1940). There is some debate as to the specific homology of some of the dermal bones of the skull roof (Borgen, 1983; Jarvik, 1967, 1980; Panchen and Smithson, 1987; Parrington, 1967a), the terminology used here is that accepted by Panchen and Smithson (1987).

At the posterior edge of the skull roof are the median and lateral extrascapulars, which form the connection between the skull roof and the pectoral girdle. Anterior to this are paired postparietals (parietals of Jarvik 1980) medially, and paired tabulars (supratemporals of Jarvik). Supratemporals (intertemporals of Jarvik) lie anterior to the tabulars. There is an almost straight line across the anterior margin of the supratemporals and postparietals isolating this part of the skull roof from the more anterior part. This is a hinge line that lies dorsal to the separation between anterior and posterior portions of the braincase. There are processes extending forward from the ventral side of the supratemporal, but there is no interdigitation or solid connection across this line. Anterior to the hinge line medially lie the paired parietals (frontals of Jarvik) bearing the pineal opening. Lateral to the parietals are paired intertemporals (dermosphenotic of

Figure 2. The dermal skeletal elements of the Head region of *Eusthenopteron*. A, dorsal and B, left lateral views. Acl- anocleithrum; aT- anterior tectal; Cl- cleithrum; D- dentary; Esl- lateral extrascapular; Esm- median extrascapular; F- frontal; Id- infradentary; It- intertemporal; J- jugal; La- lachrymal; Max- maxillary; N- nasal series; Op- opercular; P- parietal; pf- pineal foramen; Pfr- postfrontal; Pm- premaxillary; Po- postorbital; Pot- posttemporal; PP- postparietal; Prf- prefrontal; Prop- preopercular; Qj- quadratojugal; Scl- supracleithrum; Sop- subopercular; Sq- squamosal; St- supratemporal; T- temporal.

Based on specimen RM 14 234, Jarvik (1980) and Panchen and Smithson (1987).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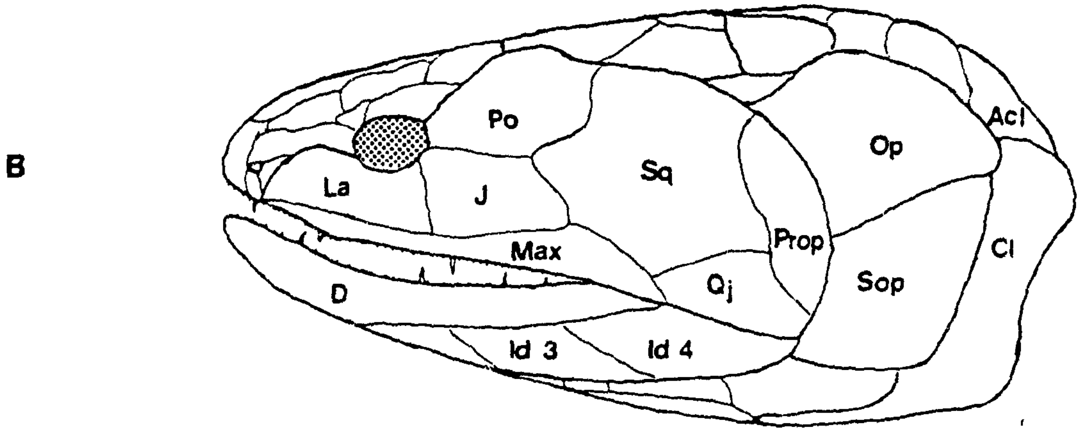
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Jarvik) and postfrontals (supraorbitals of Jarvik) which lie dorsal to the orbit. Dorsal and anterior to the orbit lies a bone which may be a prefrontal or a posterior tectal. Anterior to the parietals is a single median bone (postrostral of Jarvik) that may be homologous with the frontals of tetrapods. The dermal bones of the rostral region include paired premaxillae, and a series of small bones including numerous nasals, postrostrals, lateral rostrals and tectals.

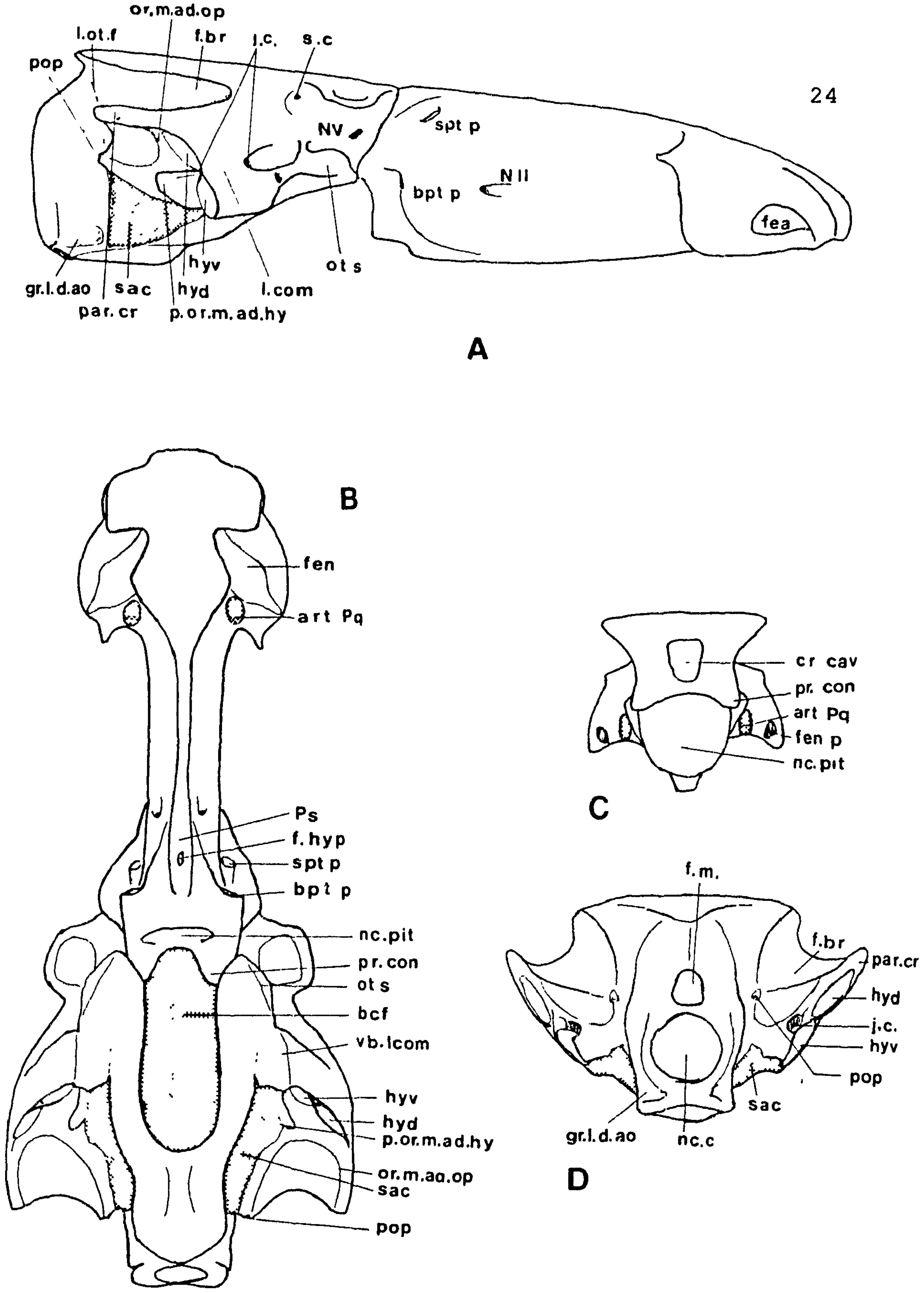
The cheek region is similar to that of early tetrapods, with a lachrymal and jugal bordering the maxillary dorsally, and a postorbital dorsal to the jugal. A large squamosal lies posterior to the postorbital but, unlike the condition in tetrapods, the squamosal extends down to the maxillary so that there is no jugal-quadratojugal contact. The quadratojugal lies at the posteroventral corner of the cheek, overlying the quadrate articulation. Posterior to the quadratojugal and squamosal is the preopercular which, in contrast with the preopercular of actinopterygian fishes, is solidly attached to the cheek plate and is not a movable element of the opercular series.

The cheek and skull roof are only connected by two areas of overlap. A dorsal extension of the lachrymal overlaps the lateral rostral and posterior tectal (prefrontal?), and a dorsal extension of the postorbital overlaps the intertemporal and supratemporal (dermosphenotic and intertemporal of Jarvik) across the hinge line. In both cases the area of overlap is smooth, with no solid connection or interdigitation. It is likely that both of these areas of overlap would allow a slight degree of freedom of movement.

The anterior portion of the endocranium, the ethmosphenoid (Figure 3), comprises the anterior ethmoidal region and posterior orbitotemporal regions. The posterior portion of the endocranium comprises the otic and occipital regions, and is termed the otico-occipital, or otoccipital region.

The laterally expanded ethmoidal region contains the nasal capsules. In the lateral wall of the nasal capsule is the fenestra endonarina anterior, which opens to the external naris. On the posterior wall of the nasal capsule lies the fenestra endonarina posterior, and medial to this are the surfaces of articulation with the anterior end of the palatoquadrate. The orbitotemporal region is narrower than the ethmoidal region, with a thicker region posteriorly. The ventral surface is sheathed by the parasphenoid, and is pierced by the hypophyseal fossa. The dorsal surface of the orbitotemporal region is pierced by the pineal opening. The ventral half of the posterior face of the ethmosphenoid bears a circular depression for the

Figure 3. The braincase of Eusthenopteron in A, right lateral and B, ventral views, and posterior views of C, ethmosphenoid, and D, otoccipital portions of the braincase. art Pq- area of articulation o the palatoquadrate on the posterior face of the nasal capsule; bcf- basicranial fenestra; bpt p - basipterygoid process; cr cav- cranial cavity; f.br- fossa bridgei; f.hyp - fossa hypophyseos; f.m.- foramen magnum; fea- fenestra endonarina anterior; fen- fenestra endochoanalis; fen p - fenestra endonarina posterior; gr.l.d.ao- groove for the lateral dorsal aorta; hyd- dorsal articular are for the hyomandibular; hyv- ventral articular area for the hyomandibular; j.c.- jugular canal; l. com- lateral commissure; l.ot.f- lateral otic fissure; N II- foramen for second cranial nerve; N V- foramen for trigeminal nerve; nc.c- notochordal canal; nc.pit- notochordal pit; nr.c- neural canal; or.m.ad.op.- origin of a'ductor opercularis muscle; ot s- otical shelf; p.or.m.ad.hy- process for the origin of the adductor hyomandibularis muscle; par.cr- parotic crest; pf- pineal foramen; pop- postotical process; pr.con- processus connectens; s.c.- spiracular canal; sac- cartilaginous region containing the saccule; spt p- suprapterygoid process; vb.lcom- ventral buttress of lateral commissure. Based on specimens MHNM 6-12-196 and ROM 1234, and on Jarvik, 1980)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anterior extremity of the notochord. Level with the top of the notochordal pit at the lateral edge of the posterior face are the paired posteriorly projecting, processus connectens, which insert into the anterior face of the otoccipital. In the dorsal half of the posterior wall of the ethmosphenoid is the opening for the cranial cavity. On the lateral wall, just anterior to the processus connectens are the paired basipterygoid processes, which articulate with the processus basalis of the palatoquadrate. Anterodorsal to the basipterygoid processes, the suprapterygoid processes articulate with the processus ascendens of the palatoquadrate.

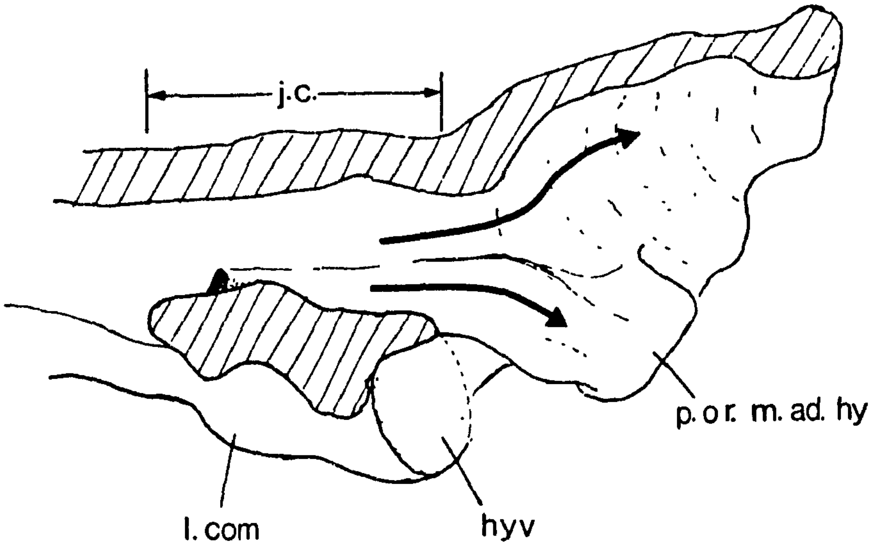
The ventral surface of the otoccipital is a bony shield marked with scars for the subcephalic (basicranial) muscles. The basicranial fenestra for the notochord is in the shape of a "U", open anteriorly. On either side of this opening, the bony shield slopes anterodorsally and forms the otical shelf. The lateral face of the otic region is divided by the lateral commissure, an almost vertical flange that extends outward and is pierced by the jugular canal. Ventrally the lateral commissure is buttressed anteriorly to the otical shelf. Dorsal to the otical shelf is the jugular groove, and dorsal to this lie openings for the fifth cranial nerve and the spiracular canal. In the anterior end of the medial face of the walls of the basicranial fenestra, adjacent to the otical shelf, are depressions to accept the processus connectens of the ethmosphenoid.

The posterodorsal part of the lateral commissure is continuous with the parotic crest (crista parotica) which forms the floor of the large fossa bridgei (sometimes termed post-temporal fossa or supraotic fossa) for the insertion of the epaxial musculature. The posterolateral margin of the lateral commissure is oblique posterodorsolaterally. Along the posterior face of this surface lie the dorsal and ventral surfaces for articulation with the hyomandibular. The jugular canal opens on the posterior face of the lateral commissure, medial to the hyomandibular articulations.

Posterior to the jugular canal lies a process, presumably for the origin of the adductor hyomandibularis (Bjerring 1971, Jarvik 1980) which has not previously been described in detail (Figure 4). The lateral face of this process bears a groove continuous with the jugular canal. The dorsal margin of this process forms a slight ridge that extends anteriorly into the jugular canal so that it appears as if the jugular vein bifurcates as it does in Latimeria. One vessel passes medial to the process and follows the contour of the braincase, while another passes between this process and the hyomandibular. A groove for a large vessel on the medial face of the proximal end of the hyomandibular of Eusthenopteron and an osteolepid in the possession of Dr.

Figure 4. The left jugular canal of specimen MHNM 6-12-196 in dorsolateral view. Hatching indicates sectioned bone, and arrows indicate the direction of vessels leaving the canal posteriorly.

hyv- ventral facet for articulation with the hyomandibular; jc- jugular canal; l. com- lateral commissure; p.o.m.add. hy- process for the origin of the adductor hyomandibularis.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Lebedev (personal communication and observation) substantiates this. The groove along the side of the braincase ends posteriorly at the lateral occipital fissure. Dorsal to the end of this groove is the postotical process, which presumably articulates with the ascending suprapharyngobranchial of branchial arch 1.

Medial to the process for the origin of the adductor hyomandibularis, and extending anterior from the postotical process on the ventral surface of the parotic crest is the large crescentic ridge of a muscle scar (Figures 9 and 13). The ventral portion of this scar forms the dorsal margin of the jugular groove, and has been termed the jugular ridge (Jarvik, 1980). This was first documented in Ectosteorhachis (identified as Megalichthys)(Romer, 1937), and was interpreted as the origin for the adductor opercularis. This is corroborated by the position of the origin of this muscle in Latimeria (Millot and Anthony 1958), which lies dorsal to the origin of the adductor hyomandibularis and posterior to the dorsal articulation of the hyomandibular.

Ventral to the jugular groove and posterior to the ventral head of the hyomandibular is a region without ossification in any of the specimens of Eusthenopteron previously described or examined in this study. In an acid prepared osteolepid skull in the possession of Dr. Lebedev, it can be seen that this area is continuous with the cranial cavity. Jarvik (1980) suggests this area probably contained the saccule, and also suggests that the surface was pierced by a fenestra ovalis. This surface of this region is ossified in Ectosteorhachis (Romer, 1937), but shows no evidence of a fenestra ovalis. Without direct evidence of an opening comparable to the fenestra ovalis of tetrapods, a claim that a fenestra ovalis is present in Eusthenopteron is premature.

The occipital region of the endocranium is narrower than the otic region, and is essentially an ossified tube extending a short distance over the notochord and spinal cord. The lateral margins are marked by grooves for the dorsal vertebral and occipitovertebral arteries. A deep groove along the ventral margin is thought to have been occupied by the lateral dorsal aorta (Jarvik 1954, 1980). On the posterior face of the otoccipital are the notochordal canal and foramen magnum.

The palatoquadrate is connected to the endocranium at seven points in three principal regions (Jarvik 1980): three points close together on the posterior wall of the nasal capsule; the basipterygoid and suprapterygoid processes on the orbitotemporal region; and the otical shelf. It is likely that the palatoquadrate was capable of some rotation outward and upward. The posterior articulations between the palatoquadrate and otoccipital lie directly lateral to the articulation of the processus connectens between the otoccipital and the ethmosphenoid. As the ethmosphenoid pivots on the otoccipital, the palatoquadrate, which is anchored to the anterior and posterior ends of the ethmosphenoid, may move with it, pivoting about the connection with the otical shelf. Thomson (1967) states that the palatoquadrate was not connected to the otical shelf, but whether or not this connection was present is of little importance to its mobility.

The quadrate articulation between the palatoquadrate complex and lower jaw lies at the posteroventral extremity of the palatoquadrate. The lower jaws are loosely connected at the symphysis, and the medial face of the lower jaw is abutted by the ceratohyal of the hypobranchial apparatus. The posterior extremity of ceratohyal 2 was connected to the stylohyal, which was connected to the hyomandibular by cartilage (Jarvik 1954, 1980). The two heads of the anterodorsal end of the hyomandibular articulate with the posterior face of the lateral commissure. The dorsal head is more posterior and lateral than the ventral head, an arrangement which allows the hyomandibular to hinge out horizontally as though the axis of articulation were vertical. A pit on the medial face of the opercular accepts a process of the hyomandibular, most probably a cartilaginous process from the posterodorsal margin (Jarvik 1954, 1980). A similar pit on the subopercular accepts a process from ceratohyal 2 or the stylohyal.

Skull Kinetics and Feeding Mechanics

The function and degree of kinetism of the skull in Eusthenopteron and other osteolepiforms remains a controversial issue. It is believed by many paleontologists (Thomson 1967, 1969, Romer 1966, Carroll 1987) that significant movement was possible between ethmosphenoid and otoccipital portions of the braincase, while others (Bjerring 1970, 1978, Jarvik 1954, 1980) believe that kinetism is impossible if the interconnections between all the components are considered.

The following examination of the components of the head, starting from the hypobranchial apparatus and working up, describes the mobility of which the skull was capable. The ceratohyals of the hypobranchial apparatus are braced against the inner surface of the lower jaw. The principal function of this apparatus is the ventral expansion of the orobranchial cavity. Such an expansion is produced by contraction of the sternohyoideus muscle pulling the basket posteriorly. This also generates a strong lateral force on the posterior extremity of the jaws, as in modern bony fish (Alexander, 1970). The loose symphysial connection of the lower jaws implies that the angle between them was not fixed. If the posterior end of the lower jaws moved laterally, the quadrate must follow or the jaws would disarticulate. There must therefore be some degree of lateral movement of the palatoquadrate with respect to the endocranium. The articulation of the palatoquadrate to the otical shelf lies in line with the articulation of the processus connectens and does not prevent movement at this joint. If the palatoquadrate hinges laterally then there must also be some flexibility of the cheek, because the ectopterygoid abuts the medial surface of the maxilla. The small areas where the cheek overlaps the skull roof and snout likely allowed some sliding and would not prevent the cheek from moving laterally. The overlap of the postorbital across the hinge line would not prevent mobility of the intracranial joint, for the sliding nature of this overlap area would allow movement between the intertemporal and supratemporal. The processes of the supratemporal extending below the hinge line would limit, but not prevent movement at this joint. Muscle scars on the ventral surface of the braincase indicate the presence of a large subcephalic (or basicranial) muscle mass, which in the living Latimeria is responsible for flexion of the intracranial joint.

The feeding mechanism in Eusthenopteron was probably much like that proposed for Latimeria by Lauder (1980), which differs from the interpretation by Thomson (1968). The initial action in the feeding mechanism of <u>Eusthenopteron</u> (Figure 5) was the contraction of the anterior epaxial muscles to raise the skull. The result of this was not only to raise the upper jaws, but also to depress the lower jaws. Contraction of the strong anterior epaxial muscles resulted in the posterodorsal rotation of the endocranium, which pivoted around a point posterior to the occiput, at the dorsal margin of the notochord. The palatoquadrate, which is attached to the endocranium at several points, rotated with it, thrusting the quadrate joint forward. In this initial phase of jaw opening, as the endocranium is swung upward, the quadrate joint is swung like a pendulum through an arc from a point below and behind the occiput to a point below and in front. The effective lever has the dorsal part of the occiput as the short arm, the occipital-vertebral joint as the fulcrum, and the quadrate articulation as the distal point of the long arm. The motion of the short arm (dorsal part of occiput) is magnified in the long arm (Quadrate) by a factor of about twelve to one.

The lower jaw is a lever with the short arm between the quadrate articulation and the lateral process of the ceratohyal. The long arm is from this articulation to the symphysis, and is about five times as long as the short arm. The fulcrum is below and in front of the articular so that the rotation of the mandible is in the opposite direction to that of the palatoquadrate. The motion of the skull is magnified in the motion of the quadrate and is again magnified in the swing of the symphysis. Thus the short powerful contraction of the epaxial muscles not only raises the skull and upper jaws, but is also responsible for the rapid lowering of the mandibles.

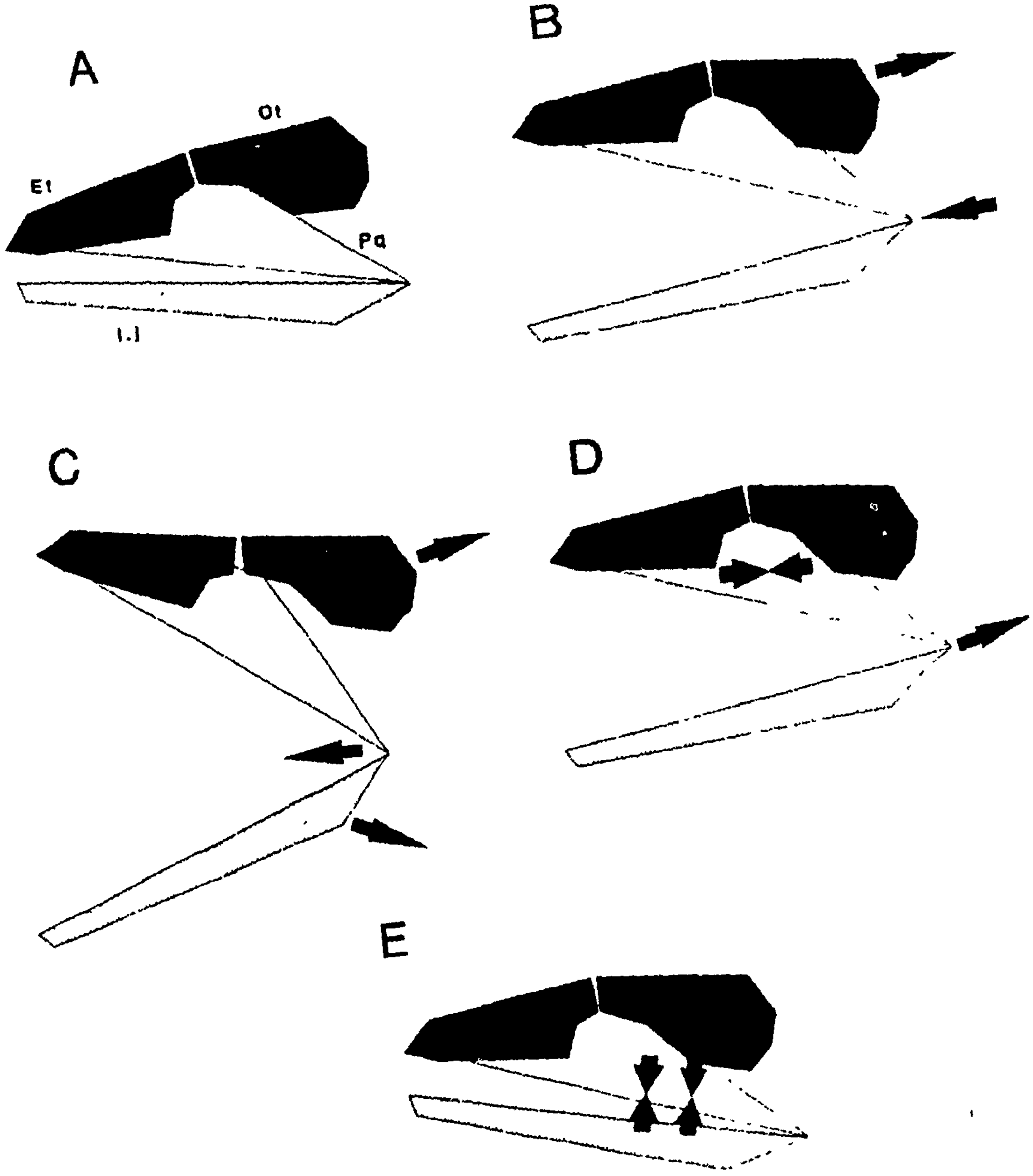
Since the skull is raised as a unit there is no need for a large muscle mass to raise the ethmosphenoid with respect to the otoccipital, and indeed none has been found (Thomson 1967, Millot et al 1958, Jarvik 1980). The ethmosphenoid may be slow in raising, due to some compressibility of the notochord, but this compressibility may have played a part in jaw opening and closing (see below).

If the lower jaw is depressed by a forward swing of the quadrate, then initiation of jaw closure may be by way of a rearward swing of the quadrate. Such a swing may be induced by means of the subcephalic (or basicranial) muscles (Figure 5, D). Contraction of these muscles produces a rotation of the ethmosphenoid and palatoquadrate around the processus connectens, and the quadrate is thrust posteriorly, swinging the lower jaw in the reverse of the manner of opening, without having to overcome the inertia of the entire skull. The fulcrum this time is the intracranial joint. The long lever arm is longer than in the opening sequence, and the short lever arm is the effective position of the subcephalic muscles. The fulcrum of the mandible initially is the area of insertion of the anterior most (deep) portion of the adductor mandibulae, which has the most posteriorly directed fibres (Jarvik 1980, Thomson 1967). Since the intracranial joint is more anterior than the occiput, the swing of the quadrate has a greater vertical component than in the opening sequence, so that in the later stage of its swing both the quadrate and the adductors act to lift the mandible. In this way a slight flexure of the intracranial joint has a large effect on the gape. Final jaw closure is by contraction of the posterior (lateral) portions of the adductor mandibulae, which pull the jaw up against the skull.

This model is also in agreement with Lund, Lund and Klein (1979), who claim that the crushing aspect of ethmosphenoid flexion (ie Thomson's model of rhipidistians (1967) and Lauder's model of Latimeria (1980), in which ethmosphenoid contraction is the last phase of jaw closure and is used to puncture prey) has been exaggerated, particularly when it concerns coelacanths with feeble dentition.

Figure 5. The feeding mechanism of Eusthenopteron. From the resting position (A), the epaxial musculature inserting in the fossa bridgei contracts, pulling the skull up and back (B). The notochord compresses slightly, then releases the stored energy, hyperextending the ethmosphenoid (C). This snaps the quadrate forward, rotating the lower jaw around the articulation with the hypobranchial apparatus. Initiation of jaw closure is through contraction of the subcephalic muscles (D), which swings the quadrate posteriorly, rotating the lower jaw into position for final jaw closure through contraction of the adductor muscles (E).

Et- ethmosphenoid; l.j- lower jaw; Ot- otoccipital; Pq- palatoquadrate.


A
Ot
Et
Pa
I.J
B
C
D
E

Simultaneous ventral and lateral expansion of the hypobranchial apparatus and cheeks increases the volume of the orobranchial cavity. This also forces the stylohyal laterally, and in conjunction with the protraction of the hyomandibular the operculars are forced open. All of these actions help to produces suction to aid prey capture. This may well continue late in the cycle to compensate for the volume reduction caused by closing the jaws, as in <u>Amia</u> (Lauder 1979). Use of the subcephalic muscles to initiate jaw closure does not draw the palatoquadrate complex medially, while muscular action directly on the palatoquadrate would. This would help prevent the orobranchial cavity from becoming prematurely reduced in volume during jaw closure.

In addition to the mechanics just described, the notochord may act as an elastic element in the intracranial joint, so that as the otoccipital is pulled back and up, rotation of the ethmosphenoid is delayed by its inertia and the energy is stored in the notochord like a compressed spring. When the otoccipital is maximally extended, the notochord spring releases its energy and the ethmosphenoid snaps up and becomes hyperextended, further increasing the swing of the quadrate. The stretched notochord would then help in the downward acceleration of the ethmosphenoid during the initial phase of jaw closure.

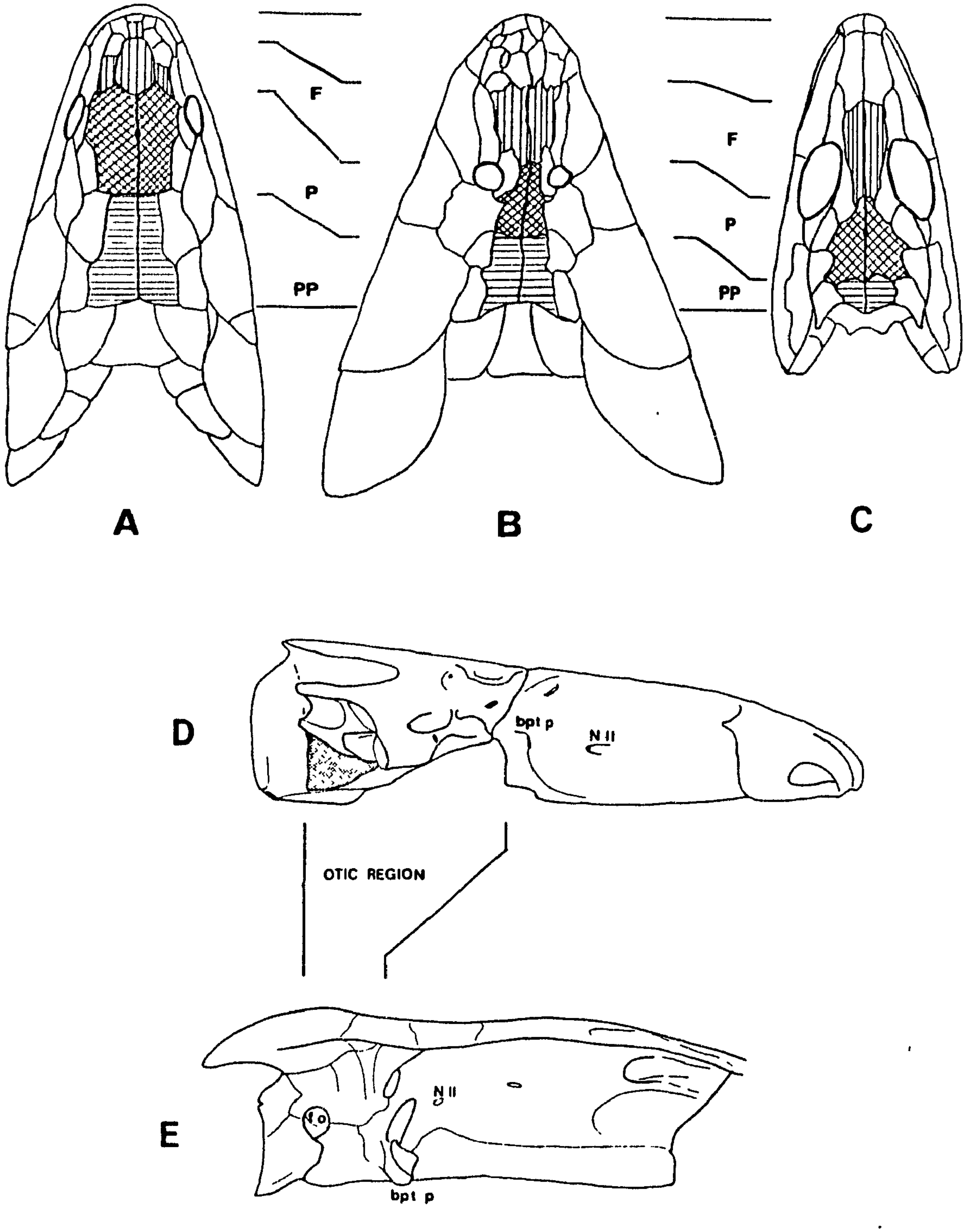
Changes in the Skull in the fish - tetrapod transition

Most of the dermal bones and much of the braincase of tetrapods may be directly homologized with rhipidistians. However, the entire skull of tetrapods becomes more consolidated. The cheek and skull roof are more solidly connected, at least anterior to the orbit (a line of kinesis persists behind the orbit in some Paleozoic tetrapods). In many cases the skull is dorso-ventrally flattened.

In the transition from fish to tetrapod there is a consistent trend towards a reduction in the relative length of the posterior part of the skull table and elongation of the snout (Figure 6). In this shift the panderichthyid fishes are intermediate in form between other osteolepiforms, such as Eusthenopteron, and tetrapods (Schulze and Arsenault, 1985). Accompanying this change in the pattern of roofing bones there is also a change in the morphology of the braincase. The ethmosphenoid becomes more elongated with the snout, while the otic region, which underlies the postparietals, becomes shortened (Figure 6, D-E). In Ichthyostega and Acanthostega (Clack, personal communication cited in Carroll 1992) the anterior and posterior elements of the neurocranium remain separate as in rhipidistians. The notochordal canal persists through the otoccipital in Ichthyostega, but not Acanthostega. In later tetrapods the two elements of the neurocranium coossify.

Figure 6. The relative increase of the snout region and decrease of the otic region of the skull in the transition from rhipidistian fish to tetrapod. A - C, the skull roof, D, E, the braincase. A, Eusthenopteron; B, Elpistostege, after Schulze and Arsenault (1985); C, Proterogyrinus, after Holmes (1984); D, Eusthenopteron; E, Archeria, after Clack and Holmes (1988)

bpt p- basipterygoid process; F- frontal; fo- fenestra ovalis; N II- foramen for second cranial nerve; P- parietal; PP- postparietal.


F
P
PP
F
P
PP
A
B
C
D
bpt p
N II
OTIC REGION
E
N II
bpt p

The parasphenoid extends posteriorly to cover the ventral surface of the otic portion of the braincase, covering the former intracranial joint from below.

The larger marginal teeth in tetrapods indicate that biting played a more important role in feeding. In the earliest tetrapods with a flattened, elongate snout and no intracranial kinesis the feeding mechanism employed by Eusthenopteron would not be possible (Thomson, 1967). Suction feeding in aquatic forms could still be accomplished through the use of the hypobranchial apparatus. Jaw opening could be accomplished through muscular depression of the lower jaws, or by gravity in some terrestrial forms. In some forms feeding may have been crocodile-like, accomplished by raising the upper jaws while keeping the lower jaws in place. This would have been necessary in cases where the proximity of the skull to the ground would have prohibited lowering of the jaws.

The Occiput of Rhipidistians and Tetrapods

In rhipidistians the occipital region is a solidly ossified tube surrounding the notochord and spinal cord, extending a short distance posteriorly from the otic region of the braincase (Figures 6 and 7). It is separated from the otic region by the lateral occipital fissure. There is no indication of sutures on the occipital region to distinguish separately ossified elements. A groove for a blood vessel along the posterior margin of the lateral face of the occiput may be homologous with the groove for the intersegmental artery of the intercentra (Jarvik, 1980). The notochordal canal penetrates the braincase to the level of the ethmosphenoid. There is no occipital condyle for the articulation between the first vertebra and the occiput. However, Jarvik (1980) describes a pair of posterior occipital processes, small bosses at the level of the ventral end of the first neural arch. There is a slight thickening of the ventral part of the first neural arch in RM 14 234, but there is no evidence that the arch and occiput were in contact, and this does not qualify the posterior occipital processes as condyles. In _Eusthenopteron_ the foramen for the vagus (tenth cranial) nerve opens near the anterior margin of the occipital region, at the lateral occipital fissure, dorsomedial to the postotical process (Jarvik, 1980). In _Ectosteorhachis_, Romer (1937) describes the hypoglossal (twelfth cranial) nerve foramen as being posteroventral to the vagus foramen.

The portion of the occiput of Paleozoic tetrapods (Figure 7) that articulates with the vertebral column is comprised of a ventral median basioccipital, and dorsal to this are paired exoccipitals. There are distinct sutures to show these as separate ossifications. The occipital condyle, when present, may form from either the basioccipital or the exoccipitals, or both. The pattern of this bony articulation is fairly conservative within groups, but varies significantly between groups. In many Paleozoic tetrapods there is a median supraoccipital bone dorsal to the foramen magnum. The foramen for the vagus nerve lies on the suture between the exoccipitals and opisthotic in anthracosaurs (Clack and Holmes, 1988; Panchen 1970), and microsaurs (Carroll and Gaskill, 1978). A foramen possibly for the hypoglossal nerve lies on the suture between exoccipital and basioccipital in Archeria (Clack and Holmes, 1988). In Adelogyrinids (Andrews and Carroll, 1991) the exoccipital bears foramina for the eleventh and twelfth cranial nerves.

The homology of the elements of the rhipidistian and tetrapod occiputs is difficult to establish because the basioccipital and exoccipitals are distinctly separate ossifications in tetrapods, while in rhipidistians the occiput is a solid ossification. It is widely believed that the basioccipital of tetrapods is serially homologous with the centrum of succeeding vertebrae (Goodrich, 1930; de Beer, 1937; Romer 1966). That is, it is formed from the ventral part of a sclerotome that has been incorporated into the back of the braincase. Likewise the exoccipitals have been suggested as being serially homologous with the neural arches of the vertebrae. The problem is determining whether the basioccipital and exoccipital are in fact serially homologous with vertebral elements, and if so, at what evolutionary stage were they incorporated into the braincase.

A narrow occipital portion of the braincase is present in arthrodires, elasmobranchs, acanthodians, and palaeoniscoids (Carroll, 1987), as well as sarcopterygians. This implies that such a condition is primitive for jawed vertebrates. In most of these groups the occipital region is a single solid ossification, except for elasmobranchs (which have a cartilaginous braincase), and the specialized acanthodian Acanthodes, which has separate ventral and lateral occipital ossifications (Miles, 1973). In the transition between palaeoniscoids and neopterygian fishes, as in the transition between rhipidistians and tetrapods, the number of separate bones in the occiput of the adult becomes greater. In both neopterygians and tetrapods there is a median ventral basioccipital and paired dorsal exoccipitals, and a supraoccipital is also present in many neopterygians and tetrapods. Patterson (1975) concludes that the presence of a basioccipital and exoccipitals are primitive for actinopterygians. It is likely therefore that this condition is primitive for all osteichthyans, if not all gnathostomes, and that the basioccipital and exoccipitals in tetrapods are not additions to the braincase subsequent to the rhipidistian condition. If these elements are serially homologous with the vertebrae, their incorporation into the braincase occurred very early in the evolution of vertebrates, and is of little relevance to the fish - tetrapod transition.

The similarity between the occipital condyle and vertebral elements in some early tetrapods may be due to evolutionary changes similar to those seen in actinopterygians. A conical plug in the notochordal pit develops in the same manner as the centra. In pholidophorids, which have endochondral dominated centra, the plug is of endochondral bone, and in leptolepids, with perichordal dominated centra, the plug is predominantly perichordal in origin (Patterson, 1975). This plug is analogous, but not homologous with the vertebral centra.

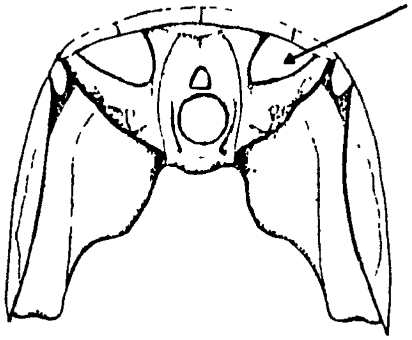
In the occipital surface of the skull of rhipidistians there is a large pocket that opens posteriorly on either side of the dorsal half of the otic region. This pocket is bordered ventrally and ventrolaterally by the parotic crest, medially by the bone surrounding the cranial cavity and dorsally by the tabular bone of the skull roof. This pocket is termed the fossa bridgei (Jarvik, 1980), supraotic fossa (Romer, 1937), or fossa supra-auditiva (Bjerring, 1984). It has also been labelled posttemporal fossa (Carroll, 1992;

Holmes, 1984). A depression in the ventral surface of this fossa may have accommodated a hemopoietic organ (Jarvik, 1980; Bjerring, 1984), while most of the fossa was filled with somatic musculature, involved in the feeding process described above. Many Paleozoic tetrapods also bear openings or depressions on the occipital face of the skull (Figure 7), and these too have been variously termed fossa bridgei and posttemporal fossa, the two terms being used interchangeably.

There are numerous problems in determining whether the posttemporal fossa of tetrapods is homologous with the fossa bridgei of rhipidistians, not the least of which is the wide variety of structures which have been given the name posttemporal fossa. Among microsaurs (Carroll and Gaskill, 1978) a notch on the ventrolateral margin of the tabular is labelled posttemporal fossa in Micraroter and Paladosotis, while in Pantylus the posttemporal fossa occupies a position along the suture between the occipital portions of the tabular and postparietal bones, bordered ventrally by the opisthotic. The posttemporal fossa of temnospondyls lies at the junction of the opisthotic and the occipital lappets of the tabular and postparietals and extends anteriorly between the skull roof and the paroccipital process, while in seymouriamorphs the posttemporal fossa is a depression in the posterior face of the opisthotic between a pair of

Figure 7. The Occiput of Rhipidistians and tetrapods. A, Eusthenopteron, B, the primitive labyrinthodont Greerepeton (based on Smithson, 1982), C and D, the microsaurs Pantylus and Palodosotis (redrawn from Carroll and Gaskill, 1978) E, Lysorophus (based on Carroll and Gaskill, 1978 and Sollas, 1908). The arrows indicate the structures termed post-temporal fossa. Not to scale.

A



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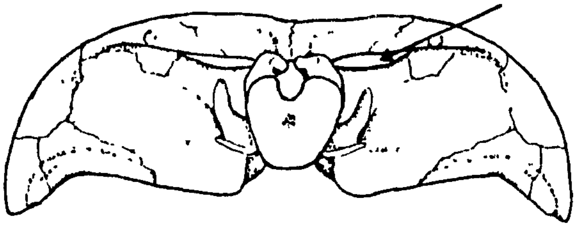

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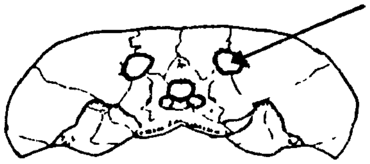
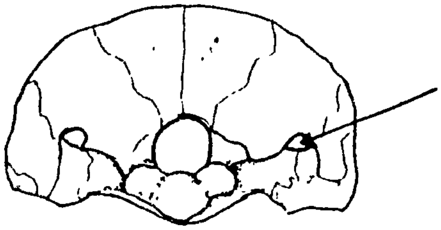
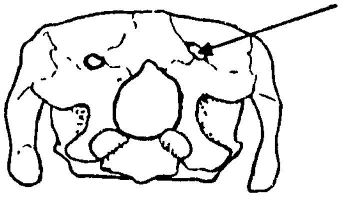


D



E



contacts with the tabular (Holmes, 1984). Embolomeres do not have posttemporal fossae, but do have concavities on the occipital surfaces of the postparietals and tabulars (Clack, 1987; Holmes, 1984, 1989; Panchen, 1970). Clearly a careful case by case examination, as well as fossil evidence from basal members of each lineage, is needed to determine the homology and function of this structure in tetrapods.

THE VERTEBRAL COLUMN OF RHIPIDISTIANS AND TETRAPODS

The Axial Skeleton of Rhipidistians

A stout notochord runs from the posterior end of the ethmosphenoid portion of the braincase to an almost terminal position in the caudal fin. Ossified vertebral elements are present in all rhipidistians, although the pattern varies widely between genera according to the locomotor requirements of each group (Andrews and Westoll, 1970b; Carroll, 1987). The pattern in Osteolepis and Eusthenopteron is similar to that of primitive labyrinthodonts. The centra comprise anterior ventral paired crescentic elements, and smaller posterior paired dorsal elements. Following the terminology in tetrapods, these elements are termed intercentra and pleurocentra for the ventral and dorsal elements, respectively. In some cases the two sides of the intercentrum are fused ventrally in anterior and posterior trunk and caudal segments, but this is variable. The neural arches are not firmly attached to the centra in these forms. The arches are paired anteriorly, but fuse into a median neural spine in more posterior trunk and tail segments.

In other forms, such as Megalichthys, there is a single cylindrical centrum per segment, to which the neural arch articulated. Ribs are present in forms with multipartite centra, articulating with a parapophysis on the intercentrum, but are absent in those forms with cylindrical centra.

The Vertebrae of *Eusthenopteron*

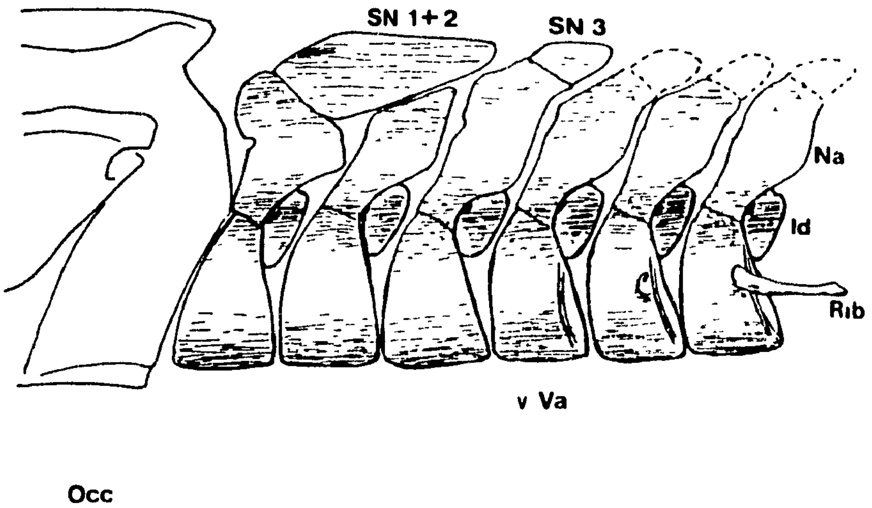
The vertebrae of Eusthenopteron are composed of three paired elements: the neural arch, dorsal pleurocentrum and ventral intercentrum (Andrews and Westoll, 1970a). Jarvik uses the term interdorsal following Gadow (1933) for the element between the bases of successive neural arches, and claims the ventral vertebral arch is composed of fused portions of both the anterior and posterior sclerotome on the evidence of the groove for the intersegmental artery along the lateral surface. The elements are here labelled pleurocentrum and intercentrum, following Andrews and Westoll (1970a).

The anterior portion of the vertebral column has been described previously by Jarvik (1980) based on serial grinding sections, and by Andrews and Westoll (1970) based on disarticulated material. Jarvik's reconstruction (Figure 8, A) shows a large supraneural blade over the first two neural arches, which he interpreted as the fused supraneurals of these two segments, and small supraneurals above each succeeding segment up to about segment 10. He also reconstructs the "interdorsals" with small flanges extending up to cup the ventral surface of the neural canal, and with foramina for the dorsal and ventral roots of the spinal nerves. In this reconstruction, ribs are present from the fifth or sixth segment back. The reconstruction by Andrews and Westoll (1970) includes no supraneurals, and the segments are spaced farther apart (Figure 8, B). There is little if any difference between the anterior and trunk vertebrae in this reconstruction. This reconstruction was made from disarticulated material, and the element shown as the neural arch of segment 3 (Andrews and Westoll 1970, fig. 20 a.) is likely a supraneural (personal observation). It is because of the discrepancies between these two previous reconstructions that this work has been undertaken. By preparation and direct observation of articulated material the problem of the discrepancies can be resolved.

Figure 8. Previous reconstructions of the cranio-vertebral joint in Eusthenopteron. A, after Jarvik (1980); B, after Andrews and Westoll (1970).

Ic- intercentrum; Id- interdorsal; Na- neural arch; Occ- occiput; Pc- pleurocentrum; SN- supraneural; v Va- ventral vertebral arch.

A



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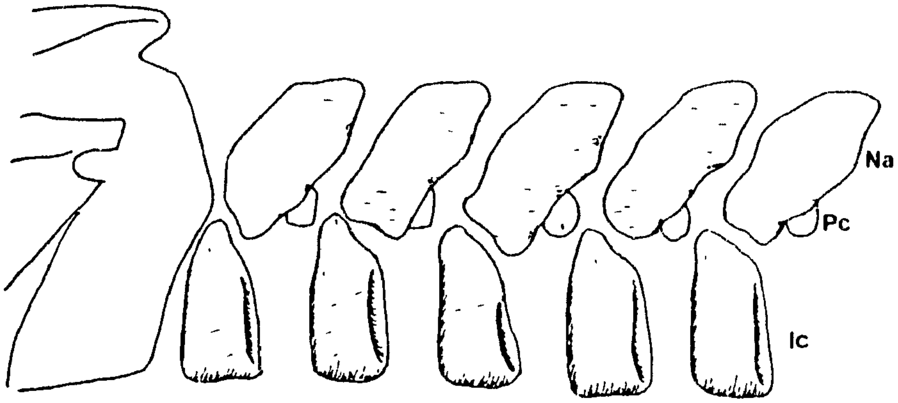
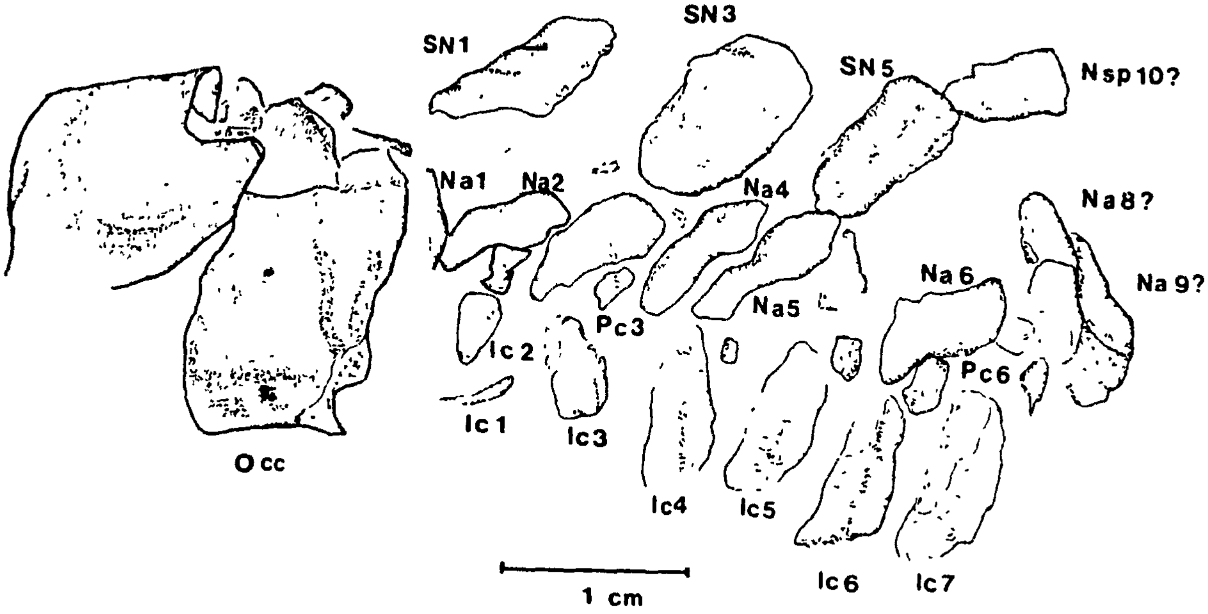


In RM 14 234 vertebrae 2 through 5 are articulated and are close to the position they would have held in life (Figure 9). The first neural arch is rotated horizontally, so that the nature of its articulation with the occiput cannot be seen. The first intercentrum is also disarticulated, lying ventrolateral to intercentrum 2. There is a gap between neural arches 5 and 6, due to arch 5 having been pushed anteriorly and arch 6 pushed ventrally. Intercentrum 7 is articulated with 6, but its arch is obscured by two or three disarticulated arches which lie at the posterior margin of the block. Supraneural spines are present above the neural arches of segments 1, 3, and 5, while there are no ossified spines above arches 2 and 4, and there is no indication of a neural or supraneural ossification above arch 6.

All the intercentra are paired crescents in ROM 1245. In P6796a in London and GN790 at Cambridge some of the intercentra are fused, producing horseshoe-shaped unitary intercentra. This does not seem to be size related, as the Cambridge specimen has intercentra 9 mm in diameter, while specimen P6796a has intercentra 18 mm in diameter. ROM 1245 has intercentra roughly 20 mm or more (these centra are splayed, so that the diameter is an estimate) in diameter but show no fusion. All the intercentra visible in ROM 1245 and RM 14 234 have a vertical ridge of unfinished bone on

Figure 9. The articulated anterior portion of the vertebral column exposed by preparation of specimen RM 14 234.

Ic- intercentrum; Na- neural arch; Nsp- neural spine; Occ- occiput; Pc- pleurocentrum.


SN1
SN3
SN5
Nsp10?
Na1
Na2
Na4
Na8?
Na6
Na9?
Na5
Pc3
Pc6
Ic2
Ic1
Ic3
Ic4
Ic5
Ic6
Ic7
Occ
1 cm

the lateral face, and immediately posterior to this a vertical groove for the intersegmental artery (Figure 10). The whole external surface of the posterior half of the centrum is of periosteal bone, except for the ridge which was probably continuous with the myoseptum. Anterior to the ridge there is some periosteal bone missing particularly in the dorsal half. This differs from the description by Andrews and Westoll (1970) in which the dorsal half of the entire centrum was described as being devoid of periosteal cover. The ventral surface of the intercentrum is flattened and smooth, with neither the ridge nor groove extending to this region. In life the two halves of the intercentrum would have abutted ventrally such that the flattened ventral regions would form a channel, concave ventrally, for the dorsal aorta (Andrews and Westoll 1970, Jarvik 1980). The dorsal end of the lateral face, which underlies the neural arch, bears a slight depression. Neither the ridge nor groove extend to this region. There is no evidence of sutural contact between intercentrum and arch. None of the first seven intercentra show evidence of parapophyses or ribs. The first and second intercentra in RM 14 234 appear to be narrower and less robust than in succeeding segments. This may be due to preservation, since in ROM 1245 all exposed intercentra appear to be equally robust, though they vary slightly in width.

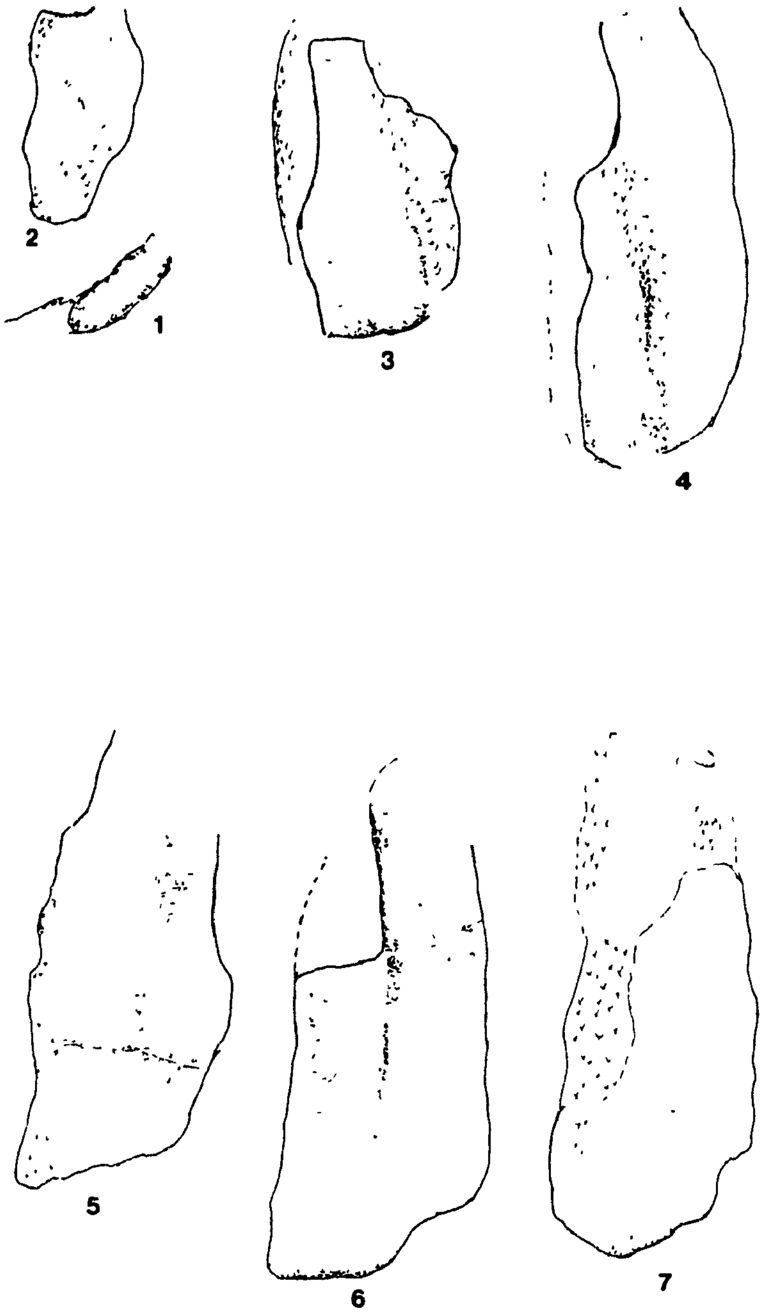


Figure 10. The intercentra exposed in Specimen RM 14 234.

The neural arches (Figure 11) are small, simple in shape, and closely spaced. Arches 2 through 6 are similar in shape, while arch 1 is rotated 90 degrees so that its posterior margin is obscured by arch 2, and its complete outline cannot be seen. The ventral portion of each arch that overlaps the intercentrum is more vertical when viewed laterally, and more oblique when viewed anteriorly or posteriorly. The dorsal portion, which covers the spinal cord, is angled posterodorsally when viewed laterally, but appears more vertical than the ventral half when viewed in anterior or posterior aspect (Figure 13, B-C). The lateral surface is smooth as is seen in more posterior arches and spines, with no striations or muscle scars, except for a longitudinal boss on the ventrolateral margin of arch 1. Because of the orientation of the dorsal portion of the arches, they lie close to one another, with the dorsal half of one arch extending over the ventral half of the following arch, although there are no articulating facets. These incipient zygapophyses occur lateral or ventrolateral to the spinal cord and are therefore paired, whereas in most trunk and caudal segments incipient zygapophyses occur dorsal to the nerve cord on the neural spines, and are median.

In RM 14 234 the pleurocentra (interdorsals of Jarvik) present between the ventral halves of successive neural arches are little more than nodules of bone(Figure 11), and

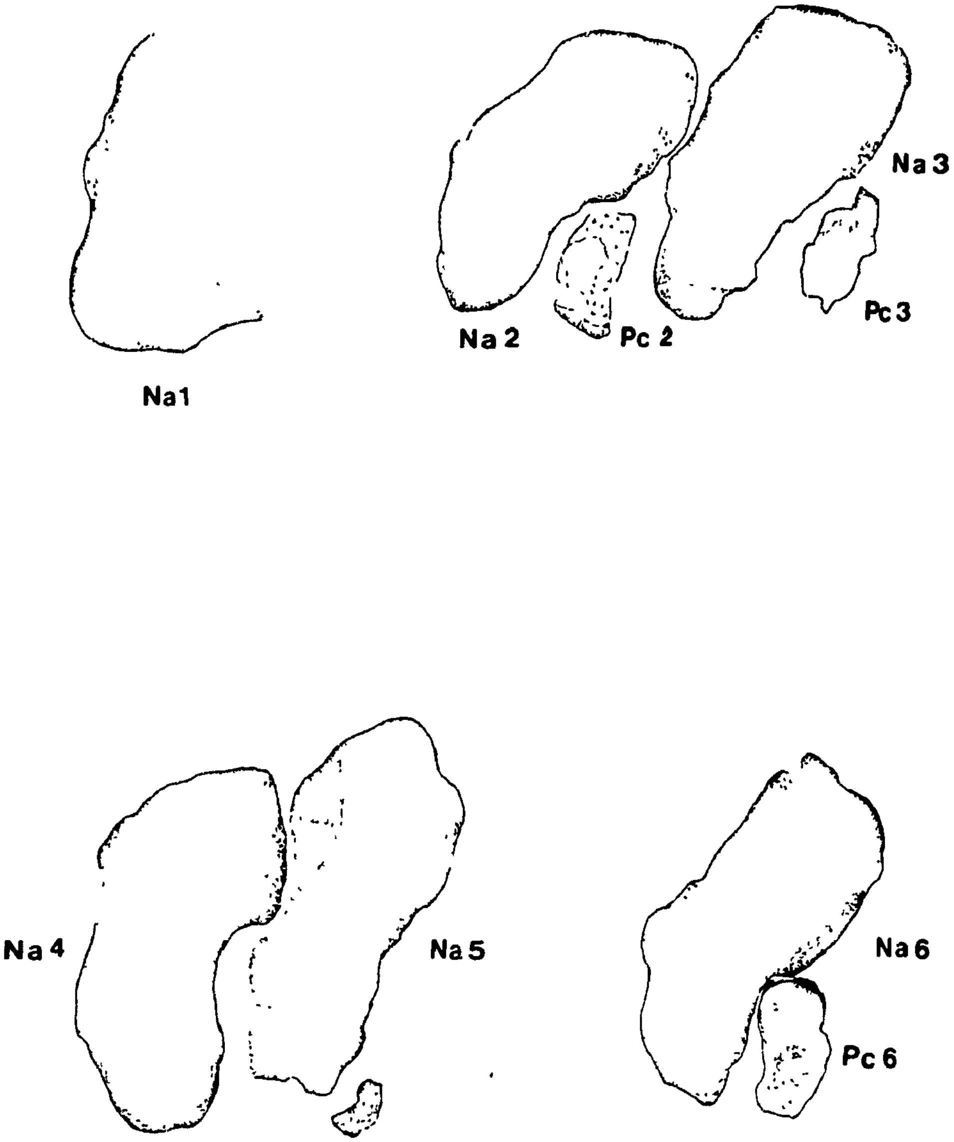
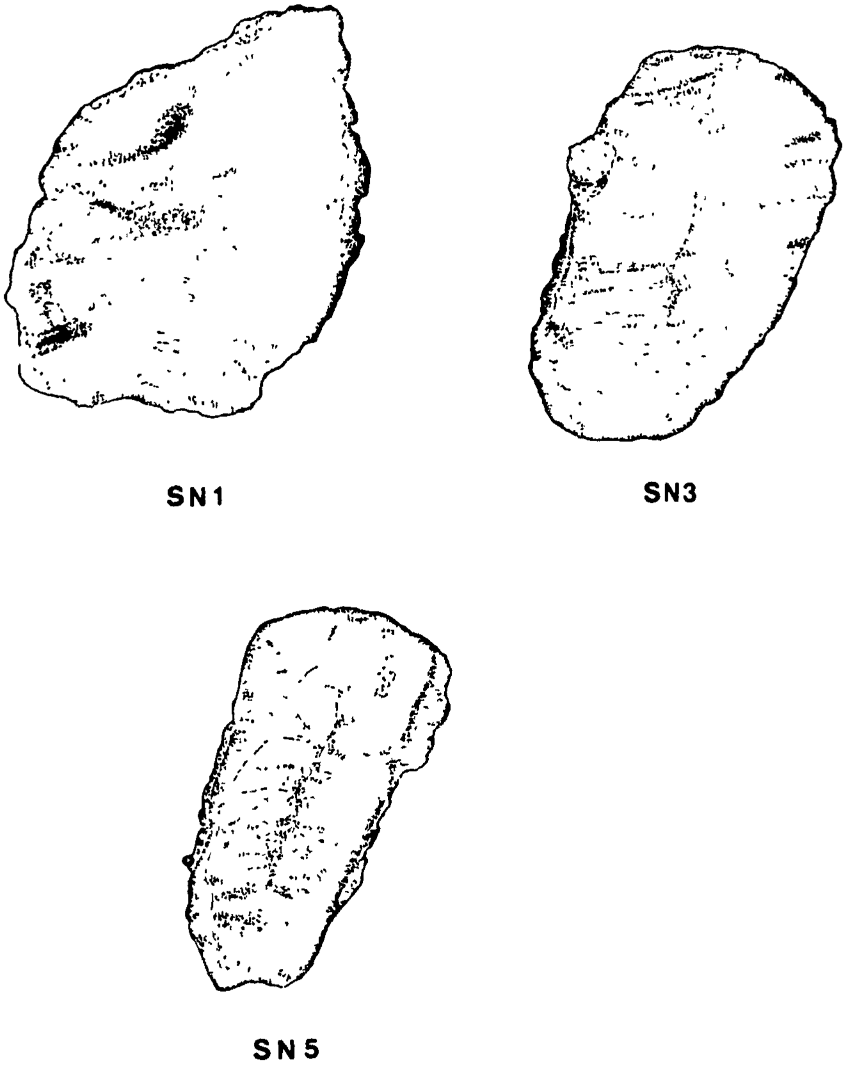


Figure 11. The pleurocentra and neural arches of RM 14 234

it is difficult to ascertain their exact shape. They are taller than wide, with a convex lateral surface of fragile periosteal bone. There is no evidence of nerve canals (Jarvik, 1980), and their position between the ventral halves of successive arches below the incipient zygapophyses and adjacent to the dorsal extremity of the intercentrum implies a position on the dorsolateral surface of the notochord, rather than lateral to the spinal cord.

The supraneural spines (Figures 9, 12 and 13) in RM 14 234 are larger than any previously described for Eusthenopteron. Supraneurals are present above arches 1, 3 and 5. There is insufficient space between successive supraneurals to accommodate supraneurals above arch 2 or 4. Each is broad, roughly oval in shape and lies in line with the dorsal portion of the arch with which it is associated. The lateral surface of each is marked with distinct longitudinal striations, and the anterior and posterior margins bear thin flanges and grooves. The ventral margins are neatly rounded, showing no evidence of articulation with the arches. They are at least as thick as the neural spines of the trunk segments, and are probably of cancellous bone, as indicated by the fact that supraneural 5 has been crushed in the middle, but suffered little deformation around the periphery. The spines are unpaired median elements.



SN1

SN3

SN5

Figure 12. The Supraneurals of RM 14 234

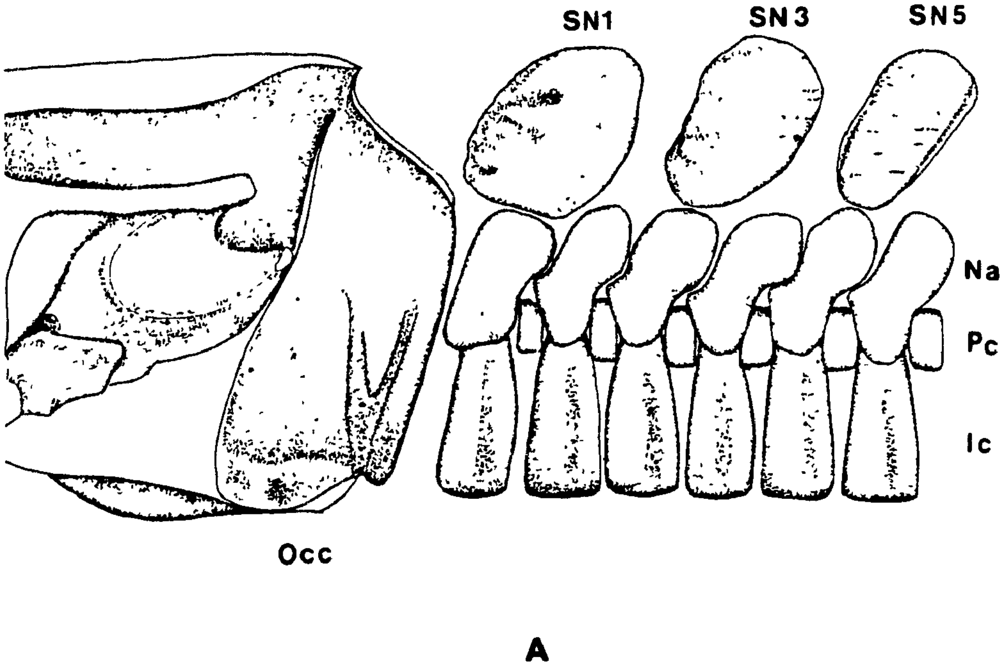
Supraneural 1 (Figure 12) has been deformed anterodorsally, but is roughly a flat-bottomed oval in outline. It is the broadest of the supraneurals, being almost as wide as high. The anterior margin is rough and uneven, with a thin median flange which was presumably continuous with the dorsal median septum. Three deep grooves run to the anterior margin, one ventrally and two dorsally. The dorsal grooves are separated by a ridge, and extend for almost one third of the width of the bone. The lateral surface is covered by tiny striations, mostly longitudinally, but some slightly oblique.

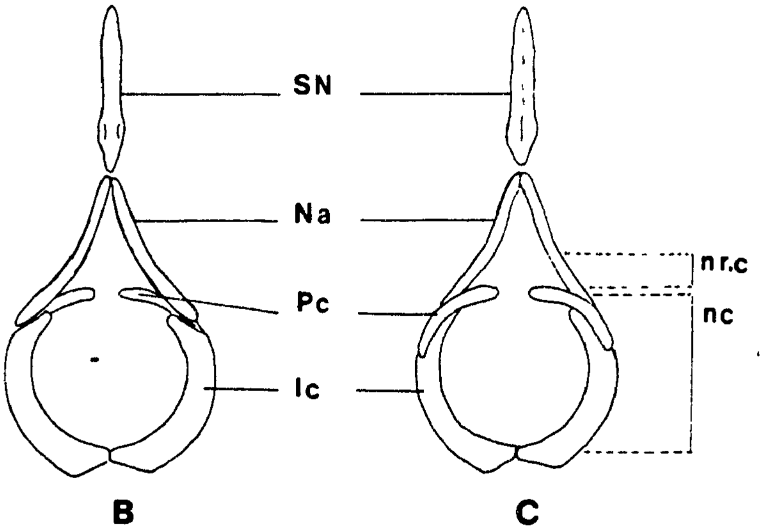
Supraneural 3 (Figure 12) is also oval, but narrower than SN 1. It too bears longitudinal striations and one deep groove across the dorsal tip. The anterior face bears a groove along its middle third, bordered top and bottom by raised processes, which are extensions of lateral ridges. The posterior margin of this element is not marked by a median flange. Supraneural 5 (Figure 12) is narrower than both SN 1 and 3, being almost rectangular in shape with the dorsal end slightly wider than the ventral end. The striations are less distinct, and this element is more crushed than the others. A distinct median flange lies along the posterior margin, while a short groove is visible in the upper part of the lower half of the anterior margin.

A portion of a spine, broken transversely, lies dorsal to the column at the posterior margin of the specimen. Unlike the first three supraneurals it is not crushed, and its surface is smoother, although it still bears striations and a small process. Unlike a neural arch, it bears a periosteal covering and is convex on both sides. It is uncertain whether it is a supraneural for segment 6 or 7, or if it is the dorsal half of a more posterior neural spine. The latter seems more likely, due to the texture of the bone and its resemblance to more posterior spines seen in other specimens.

Figure 13. A reconstruction of the anterior most vertebrae and occiput of specimen RM 14 234. A, left lateral view, B, anterior view, c, posterior view.

Ic- intercentrum; Na- neural arch; nc- notochord; nr.c- neural canal; Occ- occiput; Pc- pleurocentrum; SN- supraneural.


SN1
SN 3
SN5
Na
Pc
Ic
Occ
A


SN
Na
nr.c
Pc
nc
Ic
B
C

Development of Supraneurals

Ossified elements dorsal to the neural arches are common in fishes. Embryologically these elements may either grow upward from the neural arches as neural spines, or down towards the neural arches as derivatives of fin radials. In fossil fishes these elements may be fully formed in cartilage before becoming ossified, obscuring the direction of growth and confounding their developmental origins.

Eusthenopteron has long bladelike neural spines on trunk and tail segments. Rodlike dorsal fin radials are only found in association with the fins: one proximal radial with the first dorsal fin, two with the second dorsal fin (one of which is fused with the middle radials), and fused to the neural spines in the caudal fin. This suggests that the supraneurals were most probably derived from the neural spines.

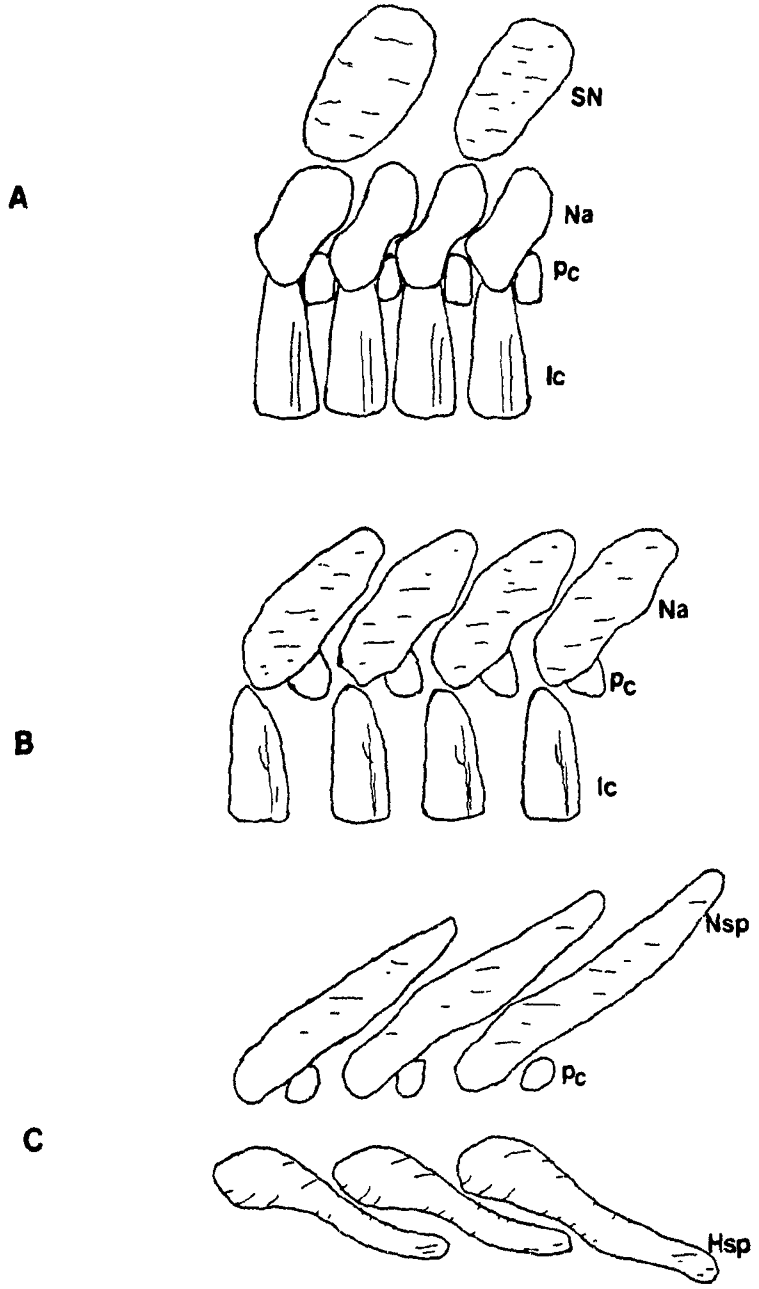
Elsewhere in the vertebral column of Eusthenopteron ossification is induced at the junction of the myoseptum and dorsal median septum immediately dorsal to the neural arches. No ossification is induced dorsal to neural arches 2, 4 and 6, which may indicate that the myoseptum does not intersect the median septum in these places (ie. that these myotomes are fused), but this cannot be proven.

Variation within the Vertebral Column of *Eusthenopteron*

The anterior-most segments of the vertebral column differ from the more posterior trunk and tail regions in *Eusthenopteron*. The trunk and tail segments have long neural and haemal spines projecting posterodorsally and posteroventrally, respectively, spanning several succeeding segments (Figure 14). In the trunk and tail of fishes, the myotomes of the right and left sides contract alternately, to produce a strong oscillation at the tail for locomotion. The neural and haemal spines act to limit the lateral flexibility of the trunk during locomotion so that the force can be maximized at the tail (Hildebrand 1988). This pattern does not absolutely restrict lateral flexion but allows for lateral flexibility of the body if the muscles of only one side are contracted. The myotomes in the region between the skull and the pectoral girdle are not used primarily for locomotion (Jarvik, 1980) but for respiration and feeding. The epaxial musculature has a large area of insertion on the posterior and lateral faces of the braincase in *Amia* (Jarvik 1980) and *Latimeria* (Millot et. al. 1958) and probably in *Eusthenopteron* as well judging by the deep fossa bridgei. For raising the skull or for ventilation of the gills, the muscles in this region act bilaterally, rather than alternately, so that both opercula are opened simultaneously, or in raising the head both sides

Figure 14. Regional variation in the vertebral column of Eusthenopteron. A, anterior, segments 3 to 6; B, mid trunk, approximately segments 20 to 23; C, posterior trunk, approximately segments 40 to 42. B and C modified from Andrews and Westoll (1970)

Hsp- haemal spine; Ic- intercentrum; Na- neural arch; Nsp- neural spine; Pc- pleurocentrum; SN- supraneural.


A
SN
Na
Pc
Ic
B
Na
Pc
Ic
C
Nsp
Pc
Hsp

of the back of the skull are pulled back simultaneously.

This explains why the morphology of the anterior-most vertebral elements differs from that of more posterior segments. Instead of acting to resist lateral flexion of the vertebral column, the spines in this region act to bridge the myotomes of the two sides with a solid connection. Bilateral contraction of the epaxial musculature would act to pull back the top of the skull, and raise the snout. The close proximity of the neural spines in more posterior segments severely restricts vertical flexion of the vertebral column. In the anterior region of the vertebral column, the lack of ossified elements above arches 2 and 4 allows the supraneurals of segments 1, 3 and 5 to be pulled closer together to allow dorsal flexion. The decoupling of neural arches and supraneurals allows the supraneurals to move independently of the arches. Thus the rapid movement of the supraneurals during a powerful contraction of the epaxial muscles would not place great stress on the spinal cord. This mechanism may have evolved in this fish due to the broad blade-like neural spines. In teleosts the neural spines are narrow, and do not restrict dorsal flexion in the same manner as the broad spines of rhipidistians.

Patterns of Vertebral Ossification of tetrapods

There are two basic patterns of the vertebral column of Paleozoic tetrapods. In the apsidospondylous condition (Carroll 1989; Romer, 1947; Godfrey, 1989), the elements of the centra are multipartite as in rhipidistians. In the lepospondylous condition the centra are formed of a single cylindrical element. Apsidospondylous vertebrae consist of a neural arch and two central elements, the anterior intercentrum and posterior pleurocentrum. The labyrinthodonts, which typify this pattern, are composed of two main lineages. Temnospondyls usually show either the rachitomous pattern which consists of a ventral intercentrum (occasionally paired) and dorsal paired pleurocentra, or the stereospondylous pattern in which there is a large cylindrical intercentrum and loss of the pleurocentrum (Carroll 1988). In anthracosaurs the pleurocentrum is the dominant element, being a complete or almost complete disk, while the smaller intercentrum may be crescentic or a disk (Holmes 1984, Panchen 1970, Carroll 1988). The pleurocentrum may become fused to the neural arch, as in Seymouria.

The lepospondyls can be divided into several main lineages: the aïstopods, nectrideans, microsaurs, adelogyrinids and lysorophids (Carroll, 1989, 1991). Aïstopods have holospondylous vertebrae, with only one element per segment. The neural arch is fused to the centrum and there are no haemal arches in the caudal region. Nectrideans also have a single element per segment, with a neural arch fused to a spool shaped centrum. Nectrideans have modified caudal haemal spines that are almost symmetrical with the caudal neural spines. Microsaurs have spool shaped centra that are fused or suturally attached to neural arches, but in many species an intercentrum is also present. Adelogyrinids have heavily ossified cylindrical centra, with no trace of trunk intercentra, but the arches are only loosely connected to the centra. In lysorophids there are no trunk intercentra, but there are haemal arches in the tail. The neural arches are paired, but solidly attached to the centra.

Development of Vertebrae

There have been numerous theories concerning the ontogeny of vertebral elements (Gadow, 1933; Goodrich, 1930; Laerm, 1979; Panchen, 1977; Jarvik, 1980) which address the problem of how the elements develop intersegmentally, alternating between successive blocks of axial musculature. Gadow's (1933) arcualia theory holds that the components of the axial sheath break into four blocks, which recombine to form the vertebral ossifications (Figure 15). Williams (1959) describes a pattern of resegmentation of the anterior and posterior halves of the segment, to reform in an intersegmental position.

Jarvik (1980) points out that Gadow's arcualia theory and Williams resegmentation theory may be readily combined. Early in embryonic development the mesodermal tissues surrounding the notochord coalesce into a row of block-like somites (Romer 1962). The medial surface of the somite surrounding the notochord and nerve tube forms the sclerotome, while the bulk of the somite differentiates to become the axial musculature. The sclerotome divides into anterior and posterior halves, and the posterior half sclerotome of one somite joins the anterior half of the next somite. Thus these new sclerotome bodies span between the myotomes of adjacent somites. These sclerotome bodies, or sclerotomites develop into the vertebral elements (Goodrich, 1930; Romer, 1962).

It is thought that the half sclerotomes produce separate dorsal and ventral elements, the arcualia (de Beer, 1937; Goodrich, 1930; Jarvik, 1980). The posterior half sclerotome (which is the anterior member of the pair) develops the basidorsal and basiventral, while the anterior half sclerotome (the posterior member of the pair) develops the interdorsal and interventral. These elements form the centres of ossification in the rhachitomous pattern of vertebrae. This poses problems, however, in the homologies

Figure 15. The classic interpretation of the development of tetrapod vertebrae from Gadow's arcualia. A, two adjacent sclerotomes. B, Sclerotomites recombine intersegmentally. C, tetrapod vertebra: dorsal arcualia form the neural arch, while the ventral arcualia form the intercentrum and pleurocentrum.

bd- basidorsal; bv- basiventral; Ic- intercentrum; id- interdorsal; iv- interventral; Na- neural arch; Pc- pleurocentrum.

Figure 16. Diagram showing the conflict between different interpretations of Gadow's arcualia. A, intersegmentally recombined sclerotomites, as in figure 15 B. B, vertebrae of Eusthenopteron derived from A, as interpreted by Jarvik (1980). C, tetrapod vertebra as in figure 15 C. D, tetrapod vertebra derived from B. Note that in D the intercentrum is formed by both ventral arcualia, and the pleurocentrum is formed from the interdorsal.

bd- basidorsal; bv- basiventral; Ic- intercentrum; id- interdorsal; iv- interventral; Na- neural arch; Pc- pleurocentrum; SN- supraneural; v Va- ventral vertebral arch.

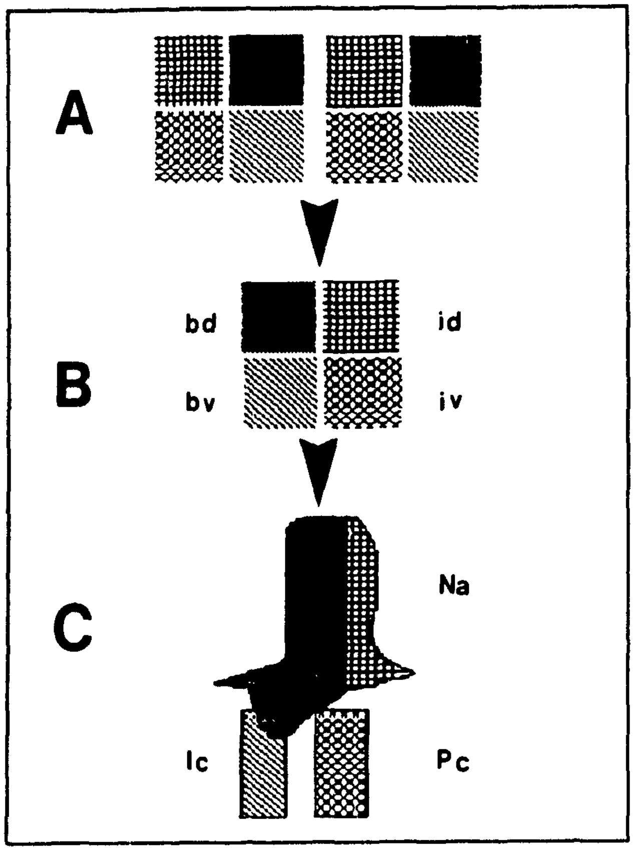


Figure 15

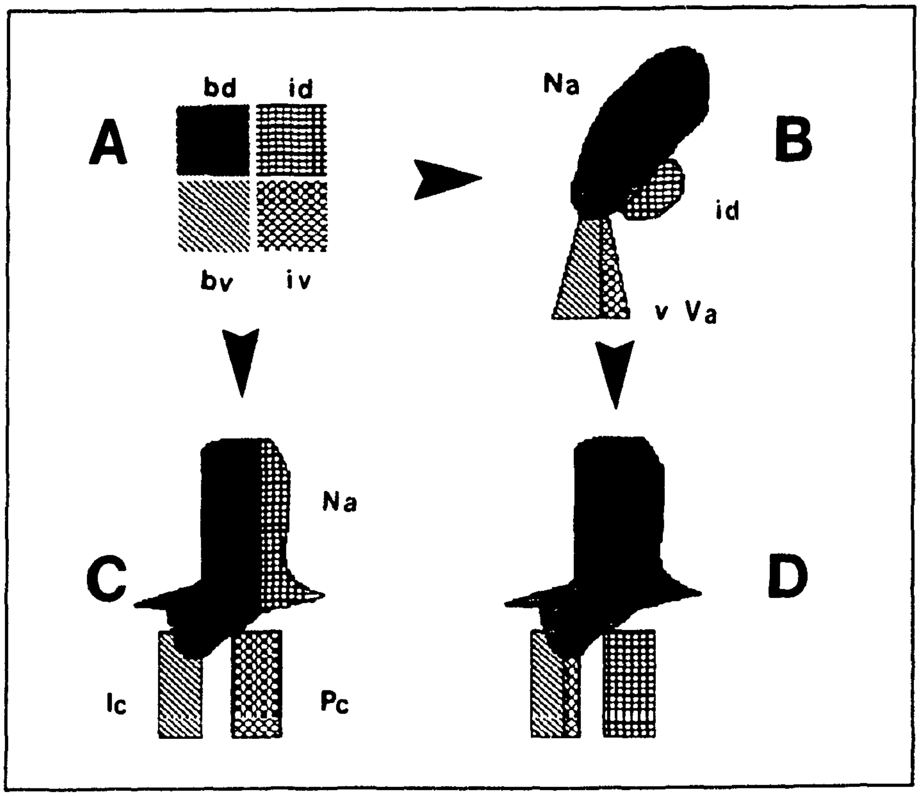


Figure 16

of the elements in fish and tetrapods (Figure 16). Jarvik (1980) proposed that the ventral vertebral element in Eusthenopteron is in fact formed by both the basiventral and interventral on the evidence of the groove for the intrametameric artery, and follows Gadow's (1933) terminology of interdorsal for the small element behind and below the neural arch because of its position dorsal to the notochord. This element is assumed to be homologous with the pleurocentrum of tetrapods (Andrews and Westoll, 1970; Carroll, 1987, 1991) which in many tetrapods forms as a ventral or cylindrical element. If these are homologous structures then it clearly cannot represent the interdorsal.

More recently, greater emphasis has been placed on function in the origin of Rhipidistian vertebrae (Laerm, 1979; Panchen, 1977). Laerm (1979) proposed the existence of three separate anlagen, a ventral arch, a neural arch, and a pleurocentrum, which may become modified as adult structures to meet functional demands. Modification of the anlagen is by direct induction of bone by mechanical stress, a mechanism which is well understood.

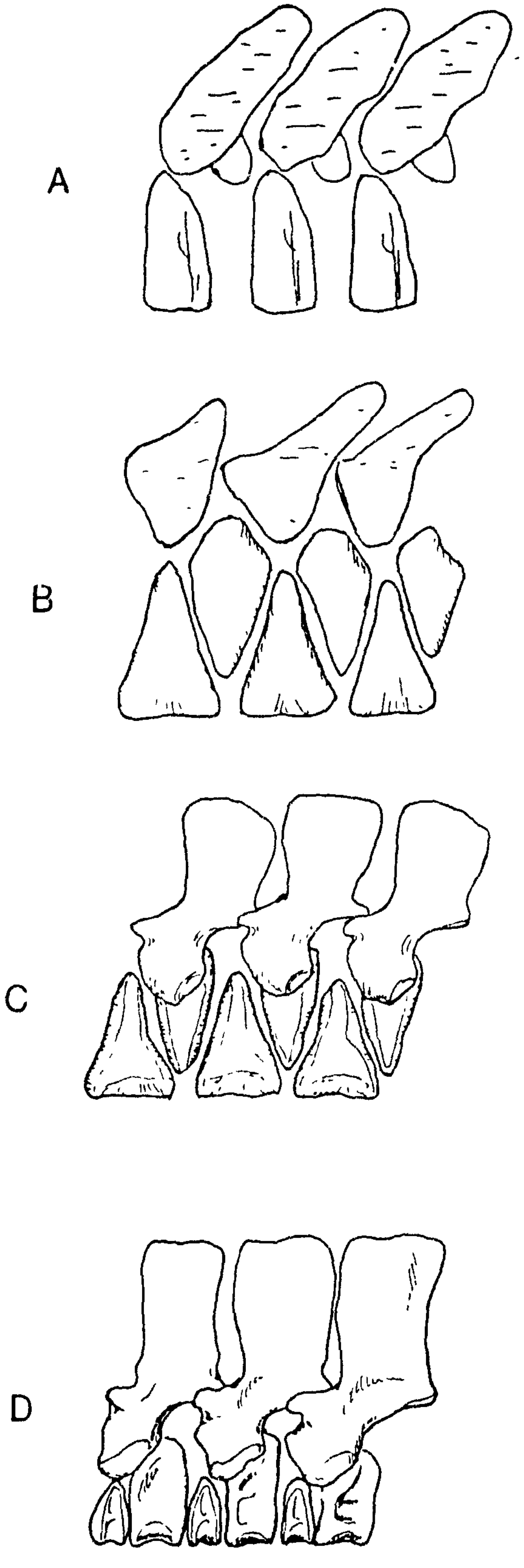
The pattern of the vertebrae in lepospondyls and early amniotes gives little evidence of formation from arcualia. The cylindrical centra might have evolved from either intercentra or pleurocentra, or through an entirely different developmental process. Carroll (1989) suggested that the lepospondylous condition may arise from precocious ossification of the perichordal sheath of the notochord, which prevents the cartilaginous elements from dominating the centrum as in labyrinthodonts. This condition has arisen numerous times within the teleosts (Carroll 1989, 1991; Laerm 1982), and separately in the amniotes, and most likely several times among the Paleozoic lepospondyls.

Vertebrae in the Fish - Tetrapod Transition

There is little debate as to the primitive condition of the vertebrae of tetrapods. The vertebral patterns of Ichthyostega (Jarvik, 1980) and primitive temnospondyls such as Greererpeton (Godfrey, 1989) are very similar to that of Osteolepis or Eusthenopteron, with a crescentic ventral wedge-shaped intercentrum, and small paired dorsal pleurocentra (Figure 17).

Innovations in the vertebrae of terrestrial vertebrates to provide greater support include the addition of zygapophyses on the neural arches, and a thickening of the centra, which restricts the notochord. If the tetrapods arose originally as aquatic animals then these adaptations would not have fully developed, as much of the support of the body would have been provided by the water. This is the case in Acanthostega (Coates and Clack, 1991).

Figure 17. The vertebrae of osteolepiforms and primitive labyrinthodonts. A, Eusthenopteron, (redrawn from Andrews and Westoll, 1970 a); B, Osteolepis, (redrawn from Andrews and Westoll, 1970 b); C, Greererpeton, (redrawn from Godfrey 1989); D, Proterogyrinus (redrawn from Holmes, 1984).


A
B
C
D

The Atlas-Axis Complex in the Fish-Tetrapod Transition

The presence of a specialized skeleto-muscular complex at the cranio-vertebral joint in Eusthenopteron emphasizes the fact that the specialization of the anterior vertebrae is not restricted to tetrapods. The origin of the tetrapod atlas-axis complex did not involve the evolution of entirely new structures, but the modification of existing structures to accommodate a change in feeding and support requirements.

As the ancestor of tetrapods has not yet been positively identified, the morphology of the anterior most vertebrae in the lineage leading to tetrapods is not known. Likewise there is little known of the atlas-axis complex of the earliest known tetrapods Ichthyostega, Acanthostega, and Tulerpeton, although the neural arches of the atlas and axis of Acanthostega have been uncovered (Clack, 1988; Clack and Coates, personal communication). Despite this gap in knowledge we may piece together a reasonable model of the atlas-axis complex in the transition from rhipidistian to tetrapod. It has already been shown that the anterior most vertebrae in Eusthenopteron are modified to form part of a musculoskeletal complex involved in raising the head in feeding. It is reasonable to assume that although the pattern of ossification in the anterior vertebrae of the tetrapod ancestor may not be identical to that of

Eusthenopteron, the feeding mechanics within the osteolepiform rhipidistians would have been consistent enough that a skeleto-muscular complex performing a similar function to that of Eusthenopteron would have been present. The role of this complex is altered during the transition from an aquatic to terrestrial lifestyle in two respects. Firstly, it becomes involved in support of the head, which requires modification of the vertebral elements to provide resistance to compression, and a change in the role of the musculature from short bursts of contraction to continuous tension. The second change involves the mobility of the head. As already discussed, a terrestrial lifestyle requires a mechanism to allow rotation of the head to compensate for the reduced mobility of the rest of the body held to the ground by gravity. This requires the modification of the anterior vertebrae to allow axial rotation, as well as horizontal and vertical flexion, without dislocation of the joints or occlusion of the spinal cord.

There are numerous unanswered questions concerning the early evolution of tetrapods, and among them the question of when or at what stage the early tetrapods became terrestrial is of importance to the problem of the origin of the tetrapod atlas axis complex. Acanthostega, though clearly a tetrapod with forelimbs composed of humerus, radius, ulna, carpals and phalanges, and the skull disconnected from the bony pectoral girdle, also shows many aquatic characteristics. These include the retention of an anocleithrum and well developed gill skeleton (Coates and Clack, 1991), and in contrast with Ichthyostega and most other early tetrapods, the zygapophyses are not developed. These characteristics are presumably retained from its fish ancestors, and not secondarily derived. This provides good evidence for an aquatic origin of the tetrapod limb, and hence of tetrapods.

If the earliest tetrapods were aquatic, then the atlas-axis complex would not have been fully developed as a mechanism for support, since the head would have been partially supported by the water. It would not necessarily allow a great deal of rotation, as an aquatic habitat allows a greater degree of movement of the body. It would likely have provided some support and allow some degree of rotation, as the head was separated from the pectoral girdle in Acanthostega (at least there is no bony connection). The atlas-axis complex of Acanthostega was likely intermediate in function between rhipidistian fish and terrestrial labyrinthodonts, in allowing dorsal flexion and increased mobility of the neck, but not providing a bony connection for support. Its morphology reflects this, as it roughly resembles the pattern of the atlas-axis complex of later labyrinthodonts, having paired atlas arches that are narrow and angled posteriorly towards the slightly modified axis arch. Another more posterior cervical vertebra has a shortened neural spine, as does Eryops, to allow dorsal flexion of the cervical region. This is consistent with the anterior vertebrae of Eusthenopteron which have supraneurals on alternate segments to allow dorsal flexion.

If the tetrapods evolved originally as aquatic animals, then the anterior-most vertebrae may have initially been little different from the stock of rhipidistians from which they arose. The great degree of specialization and variation of the atlas-axis complex of later tetrapods would have occurred during and after the radiation of the Paleozoic tetrapods.

THE ATLAS-AXIS COMPLEX IN THE RADIATION OF TETRAPODS

Patterns of the Atlas-Axis Complex of tetrapods

Corresponding with the wide variety of patterns of vertebral ossification in Paleozoic tetrapods there is a wide variation in the morphology of the atlas-axis complex in these groups (Figure 18). Within the labyrinthodonts, the atlas-axis complex is quite similar in temnospondyls and early anthracosaurs. Both have paired proatlas and atlas arches, and an axis arch modified to accommodate the rearward projecting atlas arch. Both have paired atlas pleurocentra, and a median atlas intercentrum (Carroll 1987, 1989, Godfrey 1989, Holmes 1984). Immature specimens of Greererpeton show paired atlas intercentra (Godfrey 1989). The articular surface of the occiput is a single cotyle, a depression which accepted a short anterior extension of the notochord. There was not a ball and socket joint as in modern amniotes, but the median atlas intercentrum may have acted as a pivot between the occipital cotyle and atlas pleurocentrum. In the Permian anthracosaur Archeria, both the atlas intercentrum and pleurocentrum are complete cylinders, and the intercentrum has a convex anterior face which fits into the occipital cotyle.

Since the pattern of the vertebral centra of Greererpeton is very close to that of rhipidistians, it is tempting to consider the atlas-axis complex of this animal as primitive for terrestrial labyrinthodonts. However, as Greererpeton was probably secondarily aquatic (Carroll, 1987; Godfrey, 1989) this cannot be unequivocally stated.

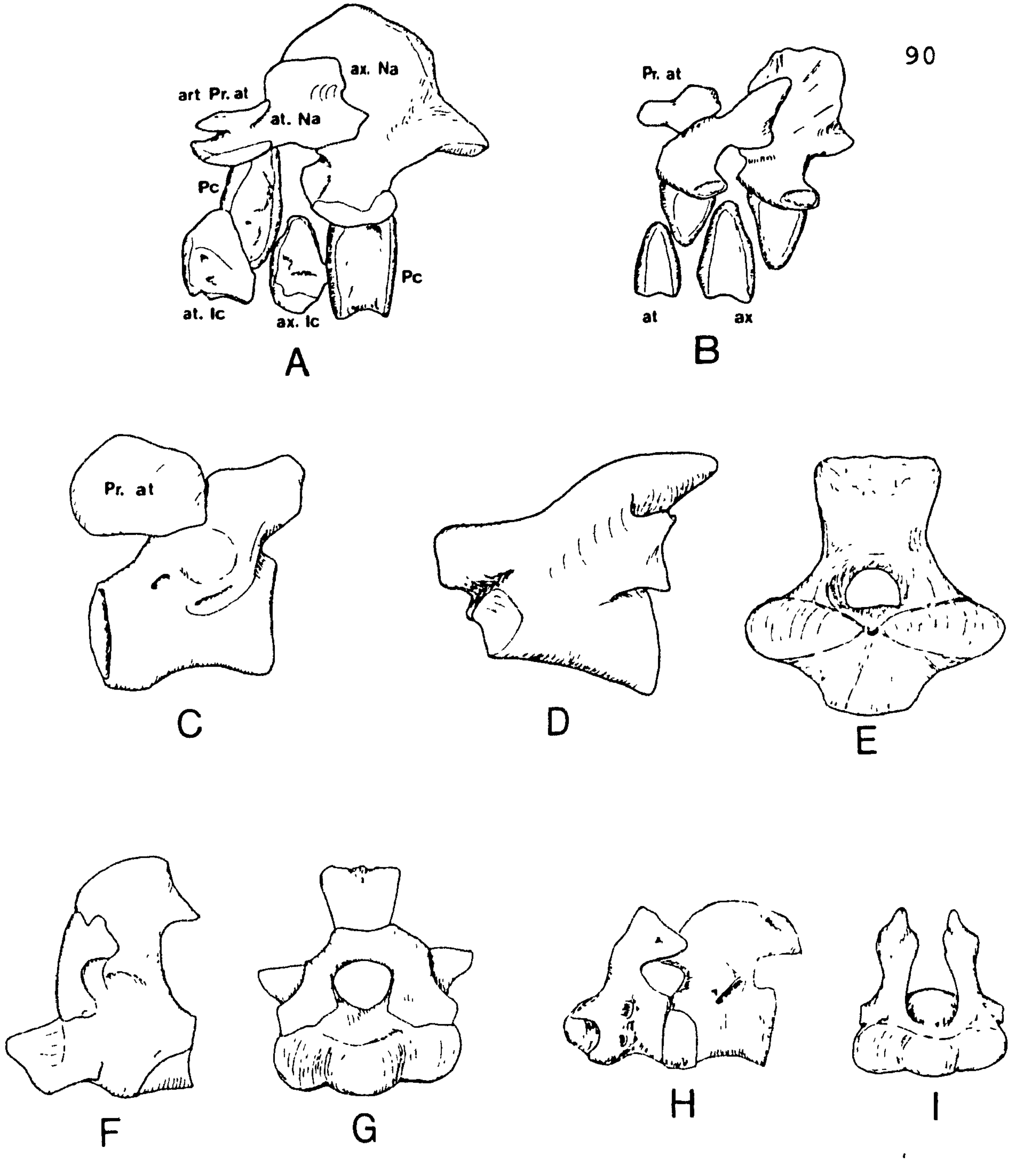
The pattern of the atlas-axis complex of the groups termed lepospondyls varies widely compared with that of labyrinthodonts. In aïstopods there is no clearly differentiated axis vertebra, and the connecting surface of both the first cervical vertebra (atlas) and the occiput are concave. A large median proatlas links the occiput and atlas arch (Carroll 1987, 1989, 1992).

The cranio-vertebral joint of nectrideans is formed by a single vertebra with a pair of broad and almost flat anterior surfaces for articulation with the occiput. A short spine-like process protrudes forward between them. The neural spine is wide and extends posteriorly to articulate with a zygantrum on the second vertebra, which is otherwise little differentiated from succeeding trunk vertebrae (Beerbower 1963).

The first cervical vertebra of microsaurs bears a pair of slightly concave anterior articular surfaces, with an anteriorly projecting process between them (Carroll 1988, 1989, Carroll and Currie 1975). Those specimens with intercentra in the trunk vertebrae also retain them between the first two cervical centra, but not between the first cervical centrum and occiput (Carroll 1988).

Figure 18. Atlas-axis complexes of labyrinthodonts (A, B) and lepospondyls (C - I). A, Proterogyrinus after Holmes (1984); B, Greererpeton after Godfrey (1989); C, the aistopod Ophiderpeton, after Carroll (1989); D and E, the nectridean Diploceraspis in left lateral and anterior views, after Beerbower (1963); F and G, the microsaur Pantylus in left lateral and anterior views; H and I, the microsaur Euryodus dalyae in left lateral and anterior views. F-I after Carroll and Gaskill (1978).

art Pr.at- articulation for proatlas on atlas arch; at- atlas; ax- axis; Ic- intercentrum; Na- neural arch; Pc- pleurocentrum; Pr.at - Proatlas.


ax. Na
art Pr. at
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In adelogyrinids the basioccipital is recessed to accept a ball-like condyle of the atlas centrum (Andrews and Carroll, 1991). The atlas is slightly shorter than other vertebral segments, but it is not expanded laterally as in microsaurs and nectrideans. The second vertebra is not differentiated from succeeding segments. In lysorophids the condyle is narrow, but made up of both the basioccipital and exoccipitals as in microsaurs.

Development of the Proatlas

In many tetrapods there is an extra element, the proatlas, which lies between the neural arch of the first (atlas) vertebra and the occiput. This has been explained as the separate ossification of the interdorsal of the last cranial sclerotome as a neural arch element (de Beer 1937; Goodrich, 1930). However, it is more likely that it is a neomorph.

It is unlikely that the occiput of tetrapods was formed from vertebrae incorporated into the back of the braincase subsequent to the rhipidistian level of evolution, rather the basioccipital and exoccipitals appear as distinct elements because of the decrease in the degree of ossification of the occipital elements. On this basis, it is likely that the first vertebra of tetrapods is homologous with the first vertebra of the rhipidistian ancestor. There is no evidence for the presence of a separate vertebra between the atlas and occiput that could have atrophied to leave only the proatlas arch. If the structure of the vertebrae were greatly influenced by mechanical stress, and if the occipital elements could mimic the pattern of the vertebrae as in some actinopterygians (Patterson, 1975), then it should be possible for the skeletogenous layer between the first neural arch and occiput to develop arch-like elements through induction by stress. These stresses are examined in the following section.

Function and Variation in the Atlas-Axis Complex

The atlas-axis complex plays the double role of providing support and controlling movement of the head. Any modification to allow rotation must occur without sacrificing supportive strength. The observed patterns of the atlas-axis complex arose as a compromise between selective pressures, the physical constraints of gravity, and developmental constraints of the vertebral elements.

Rotation of the head, either along or away from the body axis is accomplished through mobility of the joint between occiput and atlas, and between the vertebrae of the anterior portion of the vertebral column. Motion of the head may be accomplished either by the mobility of many articular surfaces among numerous vertebral segments, or of a small number of segments, such as that between the occiput and the atlas, or between the atlas and axis vertebrae as in later amniotes. In groups where rotation is accomplished primarily within the atlas-axis complex (eg. mammals), the axis is often differentiated to a greater degree from more posterior segments in order to perform this function. The atlas vertebra is invariably modified to some degree in order to articulate with the occiput.

Rotation about the atlanto-axis joint was probably limited in labyrinthodonts by the retention of zygapophyseal connection between these elements, but some rotation likely occurred about the atlas-occipital joint. The reduced atlas arch in labyrinthodonts and in early amniotes indicates a trend towards increased axial mobility between the atlas and axis. The role of the atlas arch as a tension member in the support of the head must be reduced in order to allow rotation, and the reduction of the atlas arch indicates that this was in fact occurring. Even in modern reptiles, the degree of rotation is limited at the atlas-axis joint (Jenkins 1971).

In the atlas-occipital joint of labyrinthodonts lateral flexure was possible, but vertical flexion of this joint around a single ventral condyle would have placed a great deal of stress on the brain stem, since it must be stretched or compressed to accommodate bending at this joint. Axial rotation was also likely possible, but must have been restricted to some degree at the atlas-occipital joint since the axis of rotation lies below the foramen magnum and extensive axial rotation of this joint would occlude the spinal cord. It appears that the proatlas acted both to restrict vertical flexion and to prevent occlusion of the foramen magnum by mediating axial rotation at the atlas-occipital joint. A partially ossified connection between the atlas and the occiput dorsal to the foramen magnum would have helped to compensate for the atlas' reduced role as a tension member in support of the head. The proatlas may also have acted in a way similar to that in mammal-like reptiles, increasing the degree of axial rotation by disarticulating the first neural arch (Kemp, 1969; Jenkins 1969, 1971).

The vertebral centra of lepospondyls are holospondylous and the vertebral column has somewhat different mechanical properties than those of labyrinthodonts. In lepospondyls the centra articulate with the centrum in front and behind, as does the neural arch, while in labyrinthodonts there is also an articulation in the middle of the centrum. The notochord plays a more major role in the flexibility of the vertebral column in labyrinthodonts than in lepospondyls.

Two methods by which holospondylous centra may be evolved are the gradual dominance of one of the centra per segment, or dominance of a unitary centrum by precocious ossification of perichordal tissue (Carroll 1989). Most lepospondyls have only a single centrum per segment, and this is well ossified even in very small individuals. This tends to indicate precocious perichordal ossification. Many microsaurs retain separate intercentra, which may imply a gradual dominance of the pleurocentrum as in the lineage leading to early amniotes. The intercentra may have been retained in order to increase dorso-ventral flexibility when needed, as described by Parrington (1977). Lepospondyly appears to be an evolutionary step in response to small size, but is not an inevitable consequence of small size; hence the retention of apsidospondylous vertebrae in a few small contemporary labyrinthodonts.

The pattern of the atlas-axis complex in Paleozoic lepospondyl amphibians differs from that of labyrinthodonts and early amniotes in that the first cervical centrum is always a single element, and the second cervical arch is little or not at all differentiated from succeeding vertebrae. The patterns of the occipital condyles are also different among the lepospondyl groups. Both nectrideans and microsaurs have broad condyles, while in aïstopods there is no condyle, the articulating surface of the occiput resembles that of the amphicoelous vertebrae of the cervical region. Since the morphology of the condyles differs, the physical constraints acting on the atlas and axis also differ, and therefore the morphologies of the atlas-axis complex differ.

The occipital "condyle" of aïstopods is notable in that it resembles the articulating surfaces of the amphicoelus vertebral centra. This likely evolved in a way similar to the occipital articulation in some actinopterygians (Patterson, 1975). A conical plug develops in the notochordal pit as a centrum analog. In this way the articulation between the occiput and the first vertebra acts in the same manner as the articulation between vertebrae. This articulation does not permit the degree of lateral or vertical flexibility of a ball and socket type of condyle. This type of articulation also has only the elasticity of the notochordal tissue in the joint to resist axial rotation, unlike the wide condyles of microsaurs and nectrideans. A large median proatlas likely acts to prevent occlusion of the spinal cord by restricting axial rotation and dorso-ventral flexion. In contrast, labyrinthodonts and early amniotes had multi-partite atlases with which the proatlas interacted in a complex manner with the atlas arches to allow some rotation without occlusion of the spinal cord. The proatlas of aïstopods may also have played a role in support as a dorsal tension element, but since it is not certain whether aïstopods were aquatic, terrestrial or fossorial, the importance of this aspect is uncertain.

Despite the limited movement of the cranio-cervical joint, aïstopods were undoubtedly capable of significant head movement. The lack of limbs allows snake-like flexibility through the limited flexibility of a large number of vertebral segments.

The cranio-vertebral joint in adelogyrinids is poorly known. The posterior part of the braincase is not well preserved in any specimen. It is known that the basioccipital is recessed, and that there is not a broad straplike condyle as in microsaurs. Little is known of the first cervical, save that in Adelogyrinus simorhynchus the first cervical is shorter than succeeding vertebra, and the anterior surface is reportedly convex.

Like the aïstopods, the adelogyrinids are limbless, although they do possess a dermal pectoral girdle. It would be expected that movement of the head would likewise be accomplished over a large number of vertebral segments. It is puzzling that the joint between the first cervical and occiput appears to form a ball and socket joint. This dilemma may be resolved by the consideration that this type of morphology may actually reduce the flexibility of this joint, rather than increase it. Neither the convex surface of the atlas nor the concave surface of the basioccipital is well defined. It may be that the connection between the first cervical and occiput was notochordal, as in labyrinthodonts and aïstopods, and not synovial. The anterior process of the first cervical may have acted to reduce the amount of soft notochordal tissue in the joint to make a firmer, less mobile connection, rather than to form a mobile ball and socket. No proatlas has been described in any adelogyrinid, but whether this is because the occipital articulation is firm enough to resist axial rotation, or simply because none has been found has yet to be determined.

The occipital condyle of lysorophids resembles that of microsaurs (Case, 1908; Carroll and Gaskill, 1978; Sollas, 1920; Bolt and Wassersug, 1975). The basioccipital is recessed, and convex facets of the exoccipitals form the lateral portions of the articulating surface. The overall width of the condyle is slightly less than in most microsaurs, being only slightly wider than the foramen magnum, and the majority of the surface is formed by the basioccipital. In most microsaurs each convex exoccipital portion of the condyle is almost as broad, if not broader than the concave basioccipital part. In contrast, the combined width of the exoccipital portions of the condyle of <u>Lysorophus</u> is not as great as the width of the basioccipital portion (Figure 7 E). The first cervical vertebra has not been described in detail. There is a central convex process, and the articulating surface is continuous with small depressions laterally for the exoccipitals. There is insufficient information for a proper analysis, but since lysorophids have greatly reduced limbs, it may be postulated that like aïstopods and adelogyrinids, the occipital articulation is no more mobile than the articulation between vertebrae, and that movement of the head is accomplished over many vertebral segments.

Microsaurs have a wide strap-shaped occipital condyle, with convex surfaces laterally on the exoccipitals, and a concave basioccipital medially. The articulating surface of the first cervical vertebra is correspondingly wide with concave facets laterally, and a median odontoid process. This arrangement of a single broad articulating surface would allow dorso-ventral flexion, while effectively precluding axial rotation and lateral flexion about the cranio-cervical joint.

There is no proatlas in microsaurs, which might be predicted, since there would be no need for a dorsal element to restrict axial rotation if this motion is effectively precluded by the condyle. The arches of the cervical vertebrae have well developed zygapophyses, restricting the axial rotation of these joints as well. Any axial rotation of the head must have been accomplished by the slight rotation of numerous vertebral segments. Since the atlanto-occipital joint is not adapted to axial rotation the atlas arch in most microsaurs is as tall as the second cervical arch, and likely played a greater part in the support of the back of the skull than in labyrinthodonts, in which rotation occurred about the occiput.

There is no atlas intercentrum in microsaurs. If the intercentra are retained for mechanical reasons outlined by Parrington (1977), an atlas intercentrum is superfluous. The occipital condyle is designed to allow dorso-ventral flexion, so that another mechanism to allow dorso-ventral flexion is not required.

The small size of microsaurs, most of which are under 30 cm in length (Carroll and Gaskill, 1978) may also influence the morphology of the occipito-vertebral articulation. The foramen magnum is larger relative to the skull width than in larger vertebrates. The exoccipitals are relatively more widely spaced in smaller animals due to the wider foramen magnum. This provides the opportunity for a wide condyle to evolve in response to functional demands. However, small size alone is insufficient to induce this morphology, since not all lepospondyls have straplike condyles.

There are within the microsaurs, cases of modification of the atlas-axis complex which require special mention. In Pantylus, the first cervical vertebra consists of an elongated centrum with a tall neural arch fused to it.

Anterior to this arch is another smaller accessory arch. This first cervical also bears two pairs of ribs, and is most likely the result of the fusion of the first two vertebrae. The resemblance to the atlas-axis complex of labyrinthodonts is coincidental, as this microsaur is neither early nor primitive. The specialized pattern in this genus is likely a modification for support due to its large size and comparatively very large head. The neural arches of the first cervical vertebrae of Microrater and Euryodus dalyae are fused to their centra, but are paired and do not meet dorsally, leaving the roof of the neural canal open. In both these animals the dorsal margin of the foramen magnum is notched, and this may well represent a specialization to prevent occlusion and reduce stretching and compression of the spinal cord during head flexion.

The occipital articulation in nectrideans is comparable to that of microsaurs. It is best known in Diploceraspis (Beerbower 1963), which is clearly specialized in the possession of broad tabular horns, but it is similar in other nectrideans as well. The articulating surface is wider than the first cervical centrum and comprises lateral condyles and a median depression for an odontoid process. It differs, however, in that the articular surface is not continuous; the lateral articular surfaces are distinct from the median articulation. The lateral surfaces are very slightly convex, and face slightly medially. The condyles are positioned at the ventral margin of the braincase.

The occipital surface of the first cervical vertebra comprises lateral shallow concave facets and a median spine. The lateral facets face slightly laterally, to match the angle of the occipital condyles. The neural arch is fused to the centrum, and in *Diploceraspis* extends anteriorly over the condyle to cover the spinal cord where it enters the foramen magnum. The neural arch of the first vertebra also extends posteriorly to articulate with the a zygantrum on the arch of the second vertebra. Accessory apophyses are also present dorsal to the postzygapophyses.

The pattern of the occipito-cervical articulation in nectrideans is clearly designed to restrict mobility of the head. The multiple articulations between first and second vertebrae prevent axial rotation, and prevent or greatly restrict vertical flexion. The broad occipital articulation and the slightly medial orientation of the condyles prevent axial rotation and lateral flexion. The forward extension of the arch over the spinal cord in *Diploceraspis* would limit the extent of dorsal flexion. The only movements of which the occipito-cervical joint of nectrideans were capable were slight lateral flexion between the first and second vertebrae, and slight vertical flexion between the occiput ant first vertebra. Other motion must have been accomplished through the combined action of more posterior vertebrae.

The restrictive pattern of the occipital condyle in nectrideans likely served to reduce oscillation of the head, in oreder to increase swimming efficiency (A. C. Milner, 1980). The reason for the greatly restrictive pattern in *Diploceraspis* is the large tabular horns, which extend posterolaterally from the back of the skull. It is believed that such nectrideans inhabited a benthic aquatic habitat (Beerbower, 1963). Axial rotation of the head would result in the horns being forced into the substrate. The ventral surface of the horns of *Diploceraspis* posterior to the occiput slope up and back at an angle of about 12° to allow the skull to be tilted up for feeding (Beerbower, 1963). Vertical flexion of the cranio-vertebral joint would not need to allow for more than this 12° limit. Lateral flexion is likewise limited, as strong lateral flexion would result in the horns being thrust into the animal's side.

It would seem that the occipital condyle is a primary constraining factor in the morphology of the atlas-axis complex. The structure of the braincase, including that of the occiput, is conservative, presumably reflecting historical constraints. The pattern of vertebral ossification is relatively plastic and responsive to selective pressures (Laerm, 1979; Panchen, 1977; Jarvik

1980), but the pattern of the atlas-axis complex is physically constrained by the nature of the occipital articulation. It represents a compromise between the plasticity of the column, to which it articulates posteriorly, and the conservative occiput, to which it articulates anteriorly.

The pattern of the "atlas-axis" complex of Paleozoic tetrapods is sufficiently conservative within each group that it is frequently used as a diagnostic character. It should be noted however that the conservative character is not the pattern of the first two vertebrae, but the pattern of the occipital condyles. There can be a great degree of variation in the patterns of the vertebrae, as can be seen in the anterior vertebrae of microsaurs (figure 18 F-I), in which the only major similarity is the occipital articulation.

The Atlas-Axis Complex and Tetrapod Diversity

The phylogenetic relationships of early tetrapods are the subject of much debate (Carroll 1988, 1991, 1992; Jarvik 1962, 1980; Panchen and Smithson, 1987, 1988). The intent of this discussion is not to construct a scheme of the specific relationships of tetrapods, but to examine the cranio-vertebral joint in the context of the tetrapod radiation. The most significant characteristics of the atlas-axis complex are those of the pattern of the articulation between the occiput and the first vertebra.

In the apsidospondylous lineages, beginning with the rhipidistian fish and leading to amniotes, we can see two major trends. The first is an increase in the degree of ossification of the vertebral elements, and the second is the progression towards increased axial rotation at the occipital joint. In Eusthenopteron the notochord is essentially unconstricted by the vertebrae and penetrates the otoccipital completely. The neural arches, though in close proximity, bear no zygapophyses. The intercentra are paired ventral crescents, and the pleurocentra are small paired dorsal elements. In Ichthyostega the notochord fully penetrates the otoccipital, but the vertebrae are more heavily ossified and the arches, at least in the trunk region, articulate through zygapophyses. The notochord of Acanthostega does not penetrate the otoccipital completely, and the first neural arch is slightly reduced in size. Greererpeton has more heavily ossified centra, which constrict the notochord slightly. The intercentra are ventral crescentic elements, formed by the fusion of paired elements at an early age. The pleurocentra are still paired dorsal elements, though they extend down considerably farther than in rhipidistians or Ichthyostega. The occiput bears a concave surface for the anterior terminus of the notochord, there is no ball and socket joint between the occiput and first centrum. The atlas arch is reduced and posteriorly directed, and the axis arch extends forward between the two halves of the atlas arch. Paired proatlas elements articulate with the atlas arch and the occiput. As argued in the previous section, this pattern is designed to allow axial rotation between atlas and occiput.

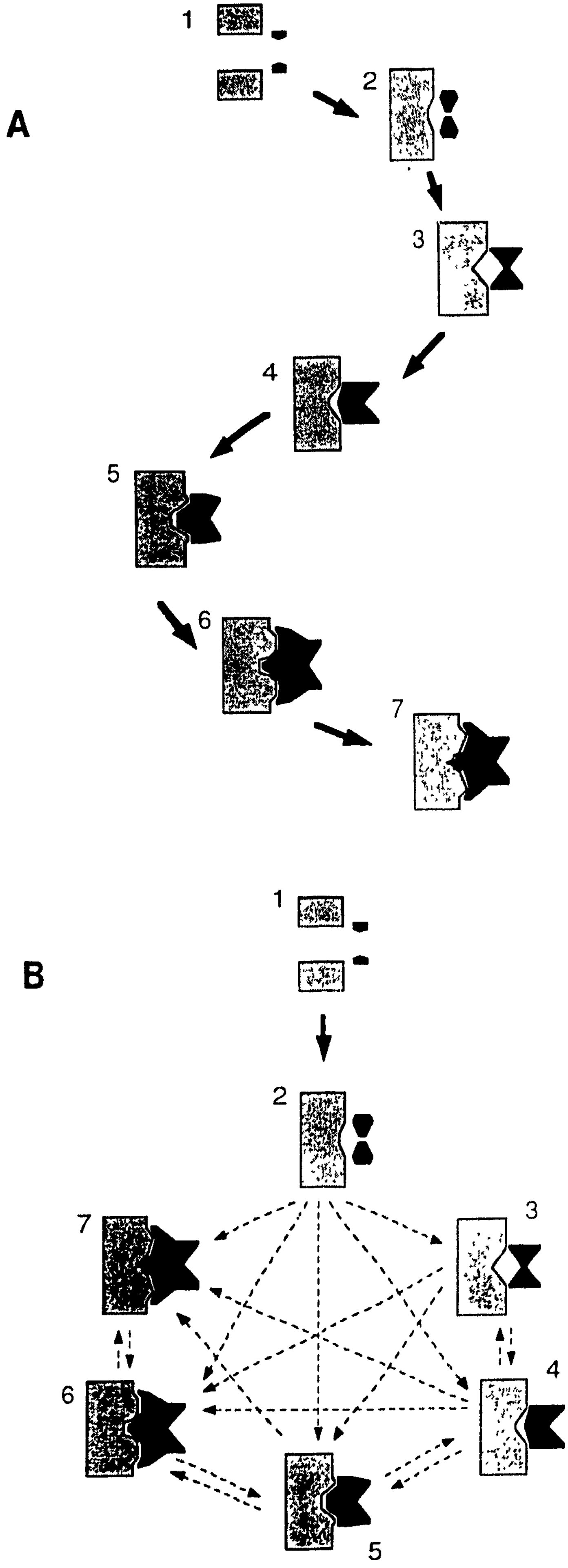
Primitive embolomeres, such as Proterogyrinus, show greater notochordal constriction than Greererpeton and further ventral development of the pleurocentra, which fuse at the ventral midline. The atlas-axis complex is essentially the same as that of Greererpeton, including the retention of paired pleurocentra. It differs by a further reduction of the atlas arch, and greater expansion of the axis arch in order to take over more of the atlas arch's role as a tension member. This further frees the atlas arch to improve axial rotation between atlas and occiput. In more advanced anthracosaurs, the joint between the atlas and occiput develops to better accommodate axial rotation. The Permian embolomere Archeria, for example, develops a fully cylindrical atlas intercentrum with a strongly convex anterior surface, forming a ball to fit the occipital socket.

The earliest amniotes are known from the middle Pennsylvanian, and their ancestry likely predates this time considerably. The anthracosaurs of this time had not yet evolved the cylindrical atlas centra of Archeria, but did have an atlas-axis complex which allowed for axial mobility between the atlas and occiput. Accompanying the increase in ossification of the vertebrae of early amniotes was the evolution of a ball and socket occipital articulation. Unlike Archeria, the occipital surface became convex. Whether the atlas intercentrum remained crescentic in order to accommodate the occipital condyle, or the condyle developed on the occiput because the atlas intercentrum was incomplete is uncertain. In either case, or both cases acting concurrently, the evolution of the occipital condyle in early amniotes presents a step which is different from that of Archeria, but performs a similar function.

In contrast to the labyrinthodonts and early amniotes, most lepospondyls seem to have non-axially mobile occipital joints, relying instead on the vertebral column to provide axial rotation. This suggests that the various groups of lepospondyls diverged from apsidospondylous tetrapods before the trend towards an axially mobile occipital articulation was well established. However, it may also be due to mechanical or developmental properties inherent to holospondylous centra.

Ignoring other characters, the patterns of the occipito-vertebral articulation in lepospondyls may be represented as a serial progression (Figure 19 A). The occipito-vertebral connection in aïstopods is notochordal, the conical occipital articular surface closely resembling the face of a vertebral centrum. The amount of notochordal tissue in the occipito-vertebral joint is reduced in adelogyrinids by an anterior process of the first centrum. In lysorophids the anterior process becomes more distinct, and lateral concavities are added for convex facets of the occiput contributed by the exoccipitals. In microsaurs the median process of the first vertebra is reduced, and the exoccipital facets are enlarged. And finally, in nectrideans, the median process of the first centrum is reduced to a spine and is separated from the lateral facets.

Figure 19. A schematic of the occipito-vertebral articulations of paleozoic tetrapods as models of an evolutionary sequence. In A, a linear progression, and B, a more realistic model. Dashed lines represent potential pathways. Groups represented are: 1, rhipidistians and Ichthyostega; 2, Carboniferous labyrinthodonts; 3, aïstopods; 4, adelogyrinids; 5, lysorophids; 6, microsaurs; 7, nectrideans. Shaded blocks represent the occiput, dark blocks represent the atlas centrum, shown in horizontal section.


A
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Alternative sequences may also be readily constructed. For example, lysorophids have reduced limbs, adelogyrinids are limbless but retain a pectoral girdle, aïstopods are without limbs or girdles. The above steps of aïstopod-adelogyrinid-lysorophid-microsaur may be reversed, the degeneration of the occipital articulation matching the degeneration of the limbs. Although these sequences are not the least bit parsimonious when other characteristics are considered, they are useful as models to demonstrate the steps that may have occurred to achieve each pattern.

The very different nature of the vertebrae in lepospondyls poses problems in that it is difficult to visualize the evolution of these elements from a labyrinthodont pattern. It is no easier to evolve these vertebral patterns from the level of Ichthyostega or rhipidistian fish, so that one need not reach that far back in tetrapod phylogeny to find a suitable ancestor.

Holospondyly has arisen separately within the actinopterygian fish, the amniotes and the amphibians. The morphology of lepospondyl vertebrae shows considerable variation between groups of lepospondyls, but a reasonable degree of consistency within these groups. It is plausible, if not most likely that holospondyly arose more than once within the lepospondyls, from separate apsidospodylous ancestors.

Part of the explanation for the difference in the shape of the vertebrae between lepospondyls and labyrinthodonts may lie in the explanation for lepospondyly outlined by Carroll (1989). Carroll points out that juvenile labyrinthodonts of small size have very poorly ossified vertebrae. If the lepospondyl condition were to evolve through precocious ossification of perichordal tissue, the normal (ie. ancestral) pattern of development of the vertebrae would be considerably disrupted. Furthermore, the mechanical properties of the vertebral column would be significantly different. The resultant vertebral pattern would likely bear little resemblance to its apsidospondylous predecessor.

The simplest lepospondyl occipito-vertebral joint, that of aïstopods, may be seen as evolving from an early labyrinthodont, due simply to the evolution of holospondylus centra. In both groups the connection is notochordal, and the articulating faces of both the atlas and occiput are concave. The major difference is simply that the first centrum of the aïstopod is a single element. Once holospondyly is achieved, the cranio-vertebral joint evolves according to the functional requirements of each lineage. In this way, each of the separate groups of lepospondyls may have evolved from distinct apsidospondylous ancestors, passing through one or more intermediate steps from the sequence described above (Figure 19 B).

The atlas-axis complex provides little evidence for establishing specific relationships between groups of Paleozoic tetrapods, and provides no good synapomorphy to link the lepospondyls through common ancestry. Most of the definable attributes of the atlas and axis in Paleozoic tetrapods are either shared primitive characters (such as a notochordal connection between occiput and atlas, and apsidospondylous vertebrae) or separately derived characters (such as holospondylous vertebrae, and a bony occipital condyle). It does however provide some useful, if not altogether conclusive, information on the adaptive diversity of Paleozoic tetrapods. By recognizing trends in the functional patterns, and establishing which morphological features are influenced by functional demand and which by different developmental factors, the role of the atlas-axis complex in the radiation of tetrapods may be better understood.

SUMMARY

The anterior portion of the vertebral column in Eusthenopteron is specialized in the possession of large blade-like supraneural spines separate from the neural arches, above arches 1, 3, and 5. The supraneurals act to bridge the epaxial myotomes of the right and left sides, and are positioned to allow rapid and powerful contraction of these muscles. The contraction of these muscles acts not only to raise the head, but also to depress the lower jaw by rotation about the ceratohyals by the forward swing of the quadrate. Jaw closure may be initiated by the contraction of the subcephalic muscles, which would induce a rearward swing of the quadrate. The similarity of the components of the head of Eusthenopteron and other osteolepiforms indicates a similar feeding mechanism, which in turn indicates a skeleto-muscular complex of similar function, if not exactly similar morphology, in the anterior most vertebrae. This skeleto-muscular complex evolved into the atlas-axis complex of the earliest tetrapods through a change in function from supplying rapid bursts of muscular contraction to the skull to more consistent support and control of head movement.

The occiput of tetrapods, consisting of the basioccipital and exoccipitals, is not formed by the addition of vertebral elements onto the braincase subsequent to the rhipidistian condition, but by a reduced ossification of the rhipidistian occiput. If these elements are serially homologous with the vertebrae, then their incorporation into the braincase occurred early in the evolution of gnathostomes. In some tetrapods without a bony condyle the occiput resembles the notochordal surfaces of the vertebrae. This is likely due to the ossification of notochordal tissue in a manner analogous to that of the vertebral centra without being homologous, as has been documented in actinopterygian fishes. The proatlas may well develop as a neural arch analog induced by mechanical stress on skeletogenous tissue between the first cervical vertebra and the occiput.

The atlas-axis complex, while providing support and controlling mobility of the head, represents a compromise between the functional demands of the relatively plastic vertebral column and the need to articulate with the more conservative occiput. The two main divergent trends in the mobility of the atlas-axis complex are for an increase in the axial mobility at the occipito-vertebral joint, and for a decrease in axial mobility in this joint. The latter occurs among the lepospondyls, but whether this is due primarily to divergence from apsidospondylous tetrapods before the trend towards axial mobility was well established, or to mechanical or developmental properties inherent to holospondylus vertebrae, is not known.

The fact that the occipito-vertebral articulation remains conservative in many lineages makes it an excellent diagnostic feature. However, the divergent nature of the atlas-axis complex, plus the numerous primitive characters and separately derived characters, makes it difficult to use as a basis for establishing specific relationships between different lineages.

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