A review of the lower actinopterygian phylogeny

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A review of lower actinopterygian phylogeny has led us to the conclusion that the Cladistia are the sister group of Recent actinopterygians (Actinopteri) and that the extinct Palaeonisciformes are a paraphyletic group, comprising stem-group actinopterygians (e.g. *Cheirolepis*), stem-group actinopterans (e.g. *Moythomasia*) and relatives of higher actinopterans such as *Pteronisculus*. Our analysis further concluded that the Acipenseriformes formed a clade together with *Saurichthys* and *Birgeria*, which was most parsimoniously resolved when the Acipenseriformes and *Saurichthys* were sister groups. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, **144**, 511–525.

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INTRODUCTION

Phylogenetic relationships amongst primitive actinopterygians have been the subject of several studies in recent years. Most of these have concentrated on time-restricted assemblages (Schultze, 1992; Lund, 2000; Poplin & Lund, 2000) or on numerous taxa of assumed very basal actinopterygians (Cloutier & Arratia, 2004). The sequence of phylogenetic events within the lower actinopterygians, up to the origin of the neopterygians, has been investigated by Gardiner & Schaeffer (1989) and by Coates (1999). In order to produce a more concise analysis, we have concentrated here on a hypothetical character transformation based on 14 taxa and 38 characters confined in a sequence framed by *Cheirolepis* and the neopterygians. Our analysis used heuristic search in PAUP v. 3.1, with characters unordered and optimized using ACCTRAN (accelerated transformation).

To produce diagnostic information for the optimal tree, we chose the apomorphy output list. This option summarizes state changes for each branch of the tree, and specifies which characters change their state from one condition to another – either node to taxon or node to node. Character states are listed for each change along with the consistency index (CI).

On the basis of this information, we have produced a normal PAUP-generated tree, as shown in Figure 1. The character state changes are noted both on the tree and elsewhere in the text by character numbers followed by the state change in brackets.

COMMENTS ON INTERNODAL CHARACTER CHANGES

The hypothetical internal character state changes have been ordered into a transformation sequence based on the synapomorphy and apomorphy lists (Appendix 1). Reconstructed states for the internodes proceed from outgroup A to internode J–K. CI values for each state change range from 1.000 to 0.330; they are included to indicate their relevant significance.

State changes between the hypothetical outgroup and node A are also related to *Cheirolepis*. Changes between internodes A–B and B–C are diagnostic of node C (*Mimia*). This indicates that preselected optimization has forced these states to the earliest possible node. The position of the crown group *Polypterus* (Cladistia) between nodes A and C is related to particular states involving *Cheirolepis* and *Mimia*.
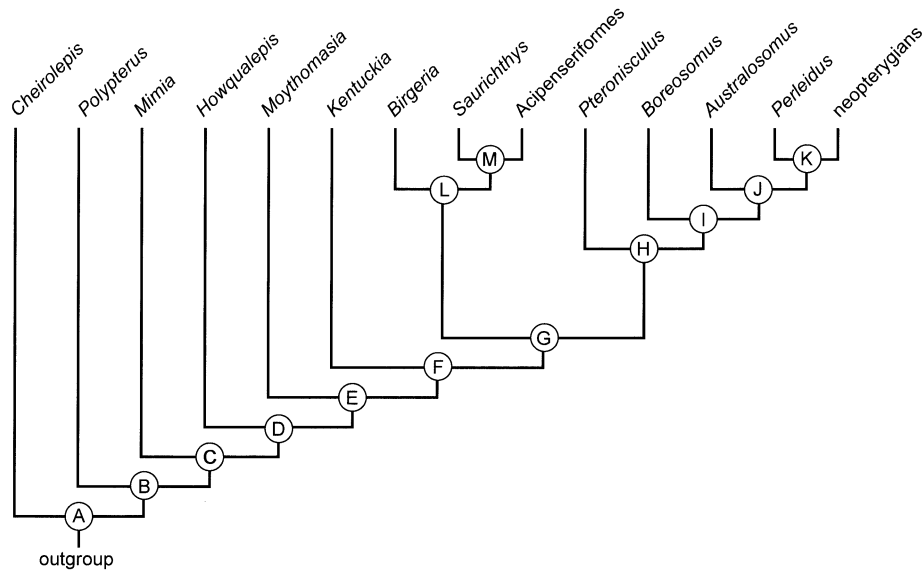
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Figure 1. Most parsimonious tree showing lettered nodes. The character transformations are given as follows. Those related to transformations along the internal branches are given in the first paragraph, those leading to the terminal taxa in the second. Against each lettered node the character number is given, followed by the character state transformation in parentheses. This is followed by the consistency index (CI) of that character in square parentheses. Synapomorphic (or autapomorphic in the case of terminal taxa) character states are preceded by asterisks. The nature of the character state change is indicated by the arrows. Double stemmed arrows indicate unambiguous character state changes, meaning that the particular change will occur under any optimization (e.g. ACCTRAN, as used here, or DELTRAN). Single stemmed arrows mean ambiguous optimization (i.e. the optimization may change if different assumptions of optimization are invoked).

Transformations along internodes

Outgroup → **Node A**: 24 (0 ⇒ 1) [0.500], *36 (0 ⇒ 1) [1.000], *37 (0 ⇒ 1) [1.000], *38 (0 ⇒ 1) [1.000]. **Node B**: *15 (0 ⇒ 1) [1.000], *20 (0 → 1) [1.000], 35 (0 ⇒ 1) [0.667]. Node C: *5 (0 ⇒ 1) [1.000], *30 (0 ⇒ 1) [1.000]. **Node D**: *10 (0 ⇒ 1) [1.000]. **Node E**: *16 (0 ⇒ 1) [1.000], 27 (0 → 1) [0.500]. **Node F**: *6 (0 → 1) [1.000], 8 (0 ⇒ 1) [0.750], *10 (1 ⇒ 2) [1.000], 23 (0 ⇒ 2) [0.400]. **Node G**: *4 (0 ⇒ 1) [1.000], *5 (1 ⇒ 2) [1.000], *6 (1 ⇒ 2) [1.000], 12 (0 ⇒ 1) [0.600], 14 (0 ⇒ 1) [0.500], 18 (0 → 3) [0.800], 24 (1 ⇒ 0) [0.500], 29 (0 → 1) [0.667]. **Node H**: 21 (0 ⇒ 1) [0.800], *25 (0 ⇒ 1) [1.000], 34 (0 ⇒ 1) [0.333]. **Node I**: *11 (0 → 1) [1.000], *20 (1 ⇒ 2) [1.000], *26 (0 → 1) [1.000]. **Node J**: *2 (0 ⇒ 1) [1.000], *3 (0 ⇒ 1) [1.000], 18 (3 → 2) [0.800], 32 (0 → 1) [0.750]. **Node K**: 1 (0 → 1) [0.667], 8 (1 ⇒ 2) [0.750], *11 (1 → 3) [1.000], *17 (1 ⇒ 0) [1.000], 19 (0 ⇒ 3) [1.000], 22 (0 ⇒ 2) [0.667], 29 (1 ⇒ 2) [0.667], *31 (0 ⇒ 1) [1.000]. **Node L**: 1 (0 ⇒ 1) [0.667], 8 (1 ⇒ 3) [0.750], *10 (2 → 3) [1.000], *11 (0 → 4) [1.000], 12 (1 → 2) [0.600], *19 (0 ⇒ 4) [1.000], 22 (0 → 1) [0.667], 35 (1 ⇒ 2) [0.667]. **Node M**: *7(0 ⇒ 1) [1.000], 9 (0 ⇒ 2) [0.667], *20 (1 → 4) [1.000], 23 (2 → 0) [0.400], 29 (1 → 0) [0.667].

Transformations leading to terminal taxa

Node B to *Polypterus*: *4 (0 ⇒ 2) [1.000], 8 (0 ⇒ 3) [0.750] 9 (0 ⇒ 1) [0.667], *10 (0 ⇒ 4) [1.000], *11 (0 ⇒ 6) [1.000], 12 (0 ⇒ 3) [0.600], *17 (1 → 4) [1.000], 18 (0 ⇒ 1) [0.800], *20 (1 ⇒ 6) [1.000], 21 (0 ⇒ 4) [0.800], *28 (0 ⇒ 2) [1.000], 32 (0 ⇒ 3) [0.750], 33 (0 ⇒ 3) [0.600]. **Node D to *Howqualepis***: *19 (0 ⇒ 1) [1.000]. **Node E to *Moythomasia***: 33 (0 ⇒ 1) [0.600], 34 (0 ⇒ 1) [0.333]. **Node F to *Kentuckia***: 27 (1 → 0) [0.500]. **Node H to *Pteronisculus***: 18 (3 ⇒ 0) [0.800], *19 (0 ⇒ 2) [1.000], 23 (2 → 1) [0.400]. **Node I to *Boreosomus***: *11 (1 → 2) [1.000], 14 (1 ⇒ 0) [0.500], 35 (1 ⇒ 0) [0.667]. **Node J to *Australosomus***: 12 (1 ⇒ 0) [0.600], 23 (2 → 0) [0.400], 33 (0 ⇒ 1) [0.600], 34 (1 ⇒ 0) [0.333]. **Node K to *Perleidus***: 23 (2 → 1) [0.400]. **Node K to neopterygians**: 1 (1 ⇒ 2) [0.667], 9 (0 ⇒ 1) [0.667], *13 (0 ⇒ 1) [1.000], 18 (2 ⇒ 4) [0.800], *20 (2 ⇒ 3) [1.000], 21 (1 ⇒ 2) [0.800], *28 (0 ⇒ 1) [1.000], 32 (1 → 0) [0.750], 33 (0 ⇒ 2) [0.600]. **Node L to *Birgeria***: *11 (4 → 5) [1.000], *17 (1 ⇒ 3) [1.000], 21 (0 ⇒ 2) [0.800], 33 (0 ⇒ 1) [0.600]. **Node M to *Saurichthys***: *17 (1 ⇒ 2) [1.000], 22 (1 → 0) [1.000], 32 (0 ⇒ 2) [0.750]. **Node M to Acipenseriformes**: *6 (2 ⇒ 3) [1.000], 12 (2 → 0) [0.600], *19 (4 ⇒ 5) [1.000], *20 (4 → 5) [1.000], 21 (0 ⇒ 3) [0.800], *26 (0 ⇒ 2) [1.000].

Internode C–D records the presence of an incipient ascending process, 10 (0–1), on the parasphenoid (CI = 1.000). Although not recorded, we should note the presence in *Moythomasia* of a robust ascending process with a spiracular groove. Internode D–E involves contact of the nasal and intertemporal and the presence of a supra-angular (first occurrence). Both have a CI of 1.000. The terminal taxon for node E is *Moythomasia*. Internode E–F, relates to terminal taxon *Kentuckia* which features a paired posterior myodome and an ascending process that reaches the spiracle (in both, CI = 1.000). The parasphenoid terminates anterior to the ventral otic fissure (CI = 0.600).

Internode F–G is of particular interest because the terminal taxon for node G (plus node L) is the crown group Acipenseriformes, which separates the stem actinopterans from the stem neopterygians. Two characters with a CI of 1.000 represent the F–G internode. These are the spiracular canal in the otic wall, 4 (0–1), and the lateral cranial canal which is confluent with the fossa Bridgei, 5 (1–2). The states for internodes G–L and L–M are listed in Appendix 2.

Internode G–H includes only one state with a CI of 1.000: the presence of an antopercular bone, 25 (0–1), as in *Pteronisculus, Boreosomus, Australosomus, Perleidus* and neopterygians. One other state of the basipterygoid process is composed of both endoskeletal and dermal components: 12 (0–1) (CI = 0.750). Internode H–I involves two states with a CI of 1.000 that are related to *Boreosomus*. The carotid arteries enter the braincase above the parasphenoid and pass through the ascending process, 11 (0–1); the maxillary blade is lobate and the preopercular is trilobate, 20 (0–2).

Two states with a CI of 1.000 at internode I–J anticipate the neopterygian condition: the presence of a subtemporal, 2 (0–1), and a dilatator fossa, 3 (0–1). Another state tied to node J (and *Australosomus*) is the fusion of the intertemporal and the supratemporal to form the dermopterotic, 17 (0–1). This fusion occurred independently in *Polypterus* and in the clade Acipenseriformes and *Birgeria* and *Saurichthys*.

Recorded states for internode J–K (CI = 1.000) include only incipient neopterygian ones: a carotid notch in the parasphenoid behind the ascending process, 11 (1–3), a keystone shaped dermosphenotic, 18 (0–4), premaxilla and antorbital separated and premaxilla with dorsal process, 19 (0–3), rectangular supraorbitals between nasal bone and dermosphenotic 22 (0–2), and median rays and radials equal. It should be noted that the single state here related to *Perleidus*, suborbitals, 23(0–2), only has a CI of 0.400. The numerous supraorbital bones between the nasal bone and the dermosphenotic are either irregular (22–1) (e.g. *Palaeoniscum, Scanilepis, 'Elonichthys canbalis', Birgeria*) or regular (22–2) (e.g. *Perleidus, Cleithrolepis, Peripeltopleurus, Luganoia, Acentrophorus*). The

supraorbitals may be few in number, as in *Acipenser, Polyodon, Stichopterus, Pholidophorus* and *Elops*, or far more numerous, as in *Meridensia, Luganoia* and *Elonichthys serratus*. Their absence in the pholidopleurids, or the presence of one supraorbital (adnasal) in the redfieldiforms, have limited systematic value.

To recapitulate, we have endeavoured to provide a hypothetical, internodal character state transformation sequence, based on selected lower actinopterygians, that terminates in the higher taxon Neopterygia. The cladogram by Coates (1999; fig. 9C) has more taxa but resembles this one in that *Acipenser* is a sister group to *Saurichthys* and *Birgeria* (Coates, 1999: 454). It differs in having several groups anchored to his node H (*Pteronisculus, Boreosomus, Woodichthys, Kansasiella, Mesopoma*).

CHARACTER RESUMÉ

The characters and character states are discussed below in the same order as in the character list. The purpose of this resumé is to provide background information for the topics covered in the analysis section, although there may be some factual duplication. A few characters, such as the pineal foramen, have been omitted here because of limited distribution and variation. Character and state selection is obviously pivotal to the entire analysis, although the process is necessarily highly subjective when dealing with a paraphyletic group such as the lower actinopterygians. We have used multistate characters in order to elucidate the dermal bone patterns associated with the neurocranium and the various arterial configurations associated with the parasphenoid and to interpret the relationship of the maxilla with the preopercular (see Table 1).

1. Post-temporal fossa: (0) absent; (1) rudimentary; (2) well developed.
The trunk musculature in some lower actinopterygians is inserted in shallow depressions on the posterior face of the occiput (viz. *Mimia*; Gardiner, 1984: figs 1, 2). There is no true post-temporal fossa in *Polypterus, Mimia, Pteronisculus, Boreosomus* or the neopterygian *Lepisosteus*. However, an incipient fossa is present in sturgeons, *Birgeria, Saurichthys, Australosomus* and *Perleidus*. A deep post-temporal fossa is characteristic of many neopterygians.

2. Sub-temporal fossa: (0) absent; (1) present.
A subtemporal fossa or depression for the origin of the dorsal hyoid constrictor muscle is absent in *Polypterus*, Acipenseriformes, *Mimia, Moythomasia,*

Table 1. Data matrix: (1) post-temporal fossa; (2) sub-temporal fossa; (3) dilatator fossa; (4) spiracle; (5) lateral cranial canal; (6) anterior myodome; (7) craniospinal process; (8) parasphenoid; (9) occipital vertebral fusion; (10) ascending process; (11) carotids; (12) basipterygoid process; (13) symplectic; (14) ceratohyal; (15) acrodin; (16) intertemporal–supratemporal; (17) dermopterotic; (18) dermosphenotic; (19) rostral–premax. antorbital; (20) maxilla–pop.; (21) infraorbitals; (22) supraorbitals; (23) suborbitals

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cheirolepis	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Acipenseriformes	1	0	0	1	2	3	1	3	2	3	4	0	0	1	1	?	1	3	5	5	3	1	0
Australosomus	0	1	1	1	2	2	?	1	0	2	1	2	0	1	1	?	1	2	0	0	1	0	0
Birgeria	1	0	0	1	2	2	0	3	0	3	5	2	0	1	1	?	3	3	4	4	2	1	2
Boreosomus	0	0	0	1	2	2	0	1	?	2	2	1	0	0	1	1	?	?	0	2	1	0	2
Howqualepsis	0	0	0	0	?	0	0	0	?	1	0	0	0	0	1	0	?	0	1	1	0	0	0
Kentuckia	0	0	0	0	1	1	0	1	?	2	0	0	0	0	1	1	?	0	0	0	?	0	?
Mimia	0	0	0	0	1	0	0	0	?	0	0	0	0	0	1	0	?	0	0	0	0	0	0
Moythomasia	0	0	0	0	1	0	0	0	?	1	0	0	0	0	1	1	?	0	0	0	0	0	0
Neopterygian	2	1	1	1	2	2	0	2	1	2	3	1	1	1	1	?	0	4	3	3	2	2	2
Perleidus	1	1	1	1	2	2	0	2	0	2	3	1	0	1	1	?	0	2	3	2	1	2	1
Polypterus	0	0	0	2	0	0	0	3	1	4	6	3	0	0	1	?	4	1	0	6	4	0	0
Pteronisculus	0	0	0	1	2	2	0	1	?	2	0	1	0	1	1	1	?	0	2	1	1	0	1
Saurichthys	1	0	0	1	2	2	1	3	2	3	4	2	0	1	1	?	2	3	4	4	0	0	0

Table 1. (*Continued*) Outgroup comprising *Acanthodes + Eusthenopteron:* (24) dermohyal; (25) antopercular; (26) quadratojugal; (27) supra-angular; (28) caronoid process; (29) suspensorium; (30) pectoral girdle; (31) median fins; (32) caudal fin; (33) neural spines; (34) fringing fulcra; (35) squamation; (36) dentary canal; (37) pelvic plate; (38) presupra–cleithrum

	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cheirolepis	1	0	0	0	0	0	0	0	0	0	0	0	1	?	1
Acipenseriformes	0	0	2	1	0	0	1	0	0	0	0	2	1	1	1
Australosomus	0	1	1	1	0	1	1	0	1	1	0	1	1	1	1
Birgeria	0	0	1	1	0	1	1	0	0	1	0	2	1	1	1
Boreosomus	0	1	1	?	0	1	1	0	0	0	1	1	1	1	1
Howqualepsis	1	0	0	?	0	0	?	0	0	0	0	1	1	1	1
Kentuckia	1	0	0	0	0	0	?	0	0	0	0	1	1	1	1
Mimia	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1
Moythomasia	1	0	0	1	0	0	1	0	0	1	1	1	1	1	1
Neopterygian	0	1	1	1	1	2	1	1	1	2	1	1	1	1	1
Perleidus	0	1	1	1	0	2	1	1	1	0	1	1	1	1	1
Polypterus	1	0	0	0	2	0	0	0	3	3	0	1	1	1	1
Pteronisculus	0	1	0	1	0	1	1	0	0	0	1	1	1	1	1
Saurichthys	0	0	1	1	0	0	1	0	2	0	0	2	1	1	1

Pteronisculus, Saurichthys, Boreosomus and *Birgeria*. There is, however, a rudimentary fossa in *Australosomus* and *Perleidus*. A subtemporal fossa is found in extinct neopterygians, but is absent in *Amia* and *Lepisosteus*.

3. Dilatator fossa: (0) absent; (1) present.
In *Polypterus*, *Mimia* and other lower actinopterygians the constrictor dorsalis muscle (levator arcus palatini + dilator operculi) originates on the pos-

torbital process and inserts on the hyomandibula. A dilatator fossa or depression for the attachment of the hyoid constrictor is present in *Australosomus*, *Perleidus* and neopterygians.

4. Spiracular canal: (0) in groove; (1) enclosed in canal; (2) canal absent.
The uniquely enlarged spiracle in *Polypterus* is anterior to the ascending process and is not enclosed in a

canal, but lies alongside the braincase. In *Mimia* and *Moythomasia* the spiracular canal occupies a spiracular groove that lies lateral to the fossa Bridgei in more advanced actinopterygians. A bone-enclosed spiracular canal and sense organ represent a synapomorphy for actinopterygians above the level of *Moythomasia*. It occurs in more advanced taxa, including for instance *Pteronisculus* and neopterygians. Among extinct taxa the spiracular canal has a connection with the fossa Bridgei in *Pteronisculus*, *Boreosomus* and *Australosomus*. Within the Acipenseriformes and the neopterygians a spiracular recess, the fossa Bridgei, contains a blind-ending spiracular diverticulum which penetrates the postorbital process. In these fishes, the recess is confluent with the fossa Bridgei as it is in *Perleidus, Saurichthys, Birgeria* and neopterygians. The ascending process of the parasphenoid in all these fishes reaches or enters the spiracular canal.

5. Lateral cranial canal and fossa Bridgei: (0) absent; (1) independent chamber in otic wall; (2) partly overlaid by and confluent with fossa Bridgei.

The lateral cranial canal (including connections with the cranial cavity), is a space between the posterior and anterior semicircular canals where the supratemporal branch of the glossopharyngeal nerve enters the canal laterally. Posteriorly, the lateral cranial canal connects with the cranial cavity by a large foramen. The canal is not developed in *Polypterus* or *Australosomus*, which may represent the primitive condition. There is, however, a large lateral cranial canal in *Mimia*, *Moythomasia*, Acipenseriformes and neopterygians. In extant Acipenseriformes, *Lepisosteus* and *Amia* there is a haemopoietic organ in the lateral cranial canal, dorsal to the medulla.

Another space in the otic region called the fossa Bridgei is apparently absent in the primitive actinopterygians *Polypterus*, *Mimia* and *Moythomasia*. It is diffusely developed in *Kentuckia*, but better defined in *Kansasiella*. In *Boreosomus*, however, the fossa Bridgei lies above the lateral cranial canal; it may communicate posteriorly with the cranial cavity by way of the lateral cranial canal, as in *Polyodon* and *Pteronisculus*. In *Acipenser* the lateral cranial canal and the fossa Bridgei are confluent, while the lateral cranial canal no longer connects with the cranial cavity. This must be another derived condition. Furthermore, the lateral cranial canal communicates with the cranial cavity posteriorly through a loop of the posterior semicircular canal in *Mimia, Moythomasia, Kansasiella, Kentuckia, Boreosomus*, and *Polyodon*. *Perleidus* has an anterior opening into the cranial cavity, while some neopterygians have both anterior and posterior openings. Information on the distribution of

these spaces and their interrelationships in the extinct actinopterygians is limited and the rôle of homoplasy is unknown.

6. Posterior myodome: (0) absent; (1) paired; (2) median; (3) lost.

Posterior myodomes only occur in more advanced lower actinopterygians and neopterygians. They are not present in *Polypterus, Mimia, Moythomasia* or Acipenseriformes. Uniquely in *Polypterus*, three of the recti muscles have their origin on the basisphenoid pillar, while the fourth (internal rectus) takes its origin anterior to the optic foramen. Development of the myodome is associated with the backward growth of the external rectus muscle onto the parasphenoid immediately below and lateral to the pituitary. In *Kentuckia* the myodome is represented by small paired depressions lateral to the pituitary vein and foramen, and ventral to the abducens canal. In more derived actinopterygians, as in *Pteronisculus* and neopterygians, the myodome is unpaired. In *Birgeria*, Stensiö (1921) and Nielsen (1942–49) reported an unpaired myodome.

7. Craniospinal process: (0) absent or poorly developed; (1) present.

The craniospinal process which develops as a lateral protrusion of the occipital arch takes the form of an acutely rounded, dorsolateral prominence immediately posterolateral to the vagal foramen. Patterson (1975: fig. 55) has noted that the intercallar bone in the pholodophorids developed in a lateral process of the occipital arch, posterodorsal to the vagal foramen in much the same manner as the craniospinal process of *Acipenser*. However, in Acipenseriformes and *Saurichthys* the craniospinal process is a greatly enlarged, with a rather lobate flange, well posterior to the vagal foramen. In *Birgeria* a small process lies immediately above the vagal foramen.

8. Parasphenoid: (0) terminates at ventral otic fissure; (1) terminates at otic fissure which lies more posteriorly than in Devonian actinopterygians; (2) extends across otic fissure; (3) extends to basioccipital.

The parasphenoid is a membrane bone that develops in the oral epithelium and is closely applied to the ventral surface of the neurocranium. In primitive extinct lower actinopterygians the parasphenoid extends from the premaxilla–vomer area to the base of the ascending process. The oral surface is usually covered with a toothed plate of varying size, which is pierced by the foramen for the bucco-hypophysial canal. This condition is found in *Cheirolepis, Mimia* and *Moytho-*

masia. The dorsal aortae passed forward beneath the neurocranium and at the posterior margin of the parasphenoid, at the level of the basipterygoid process, gave rise to the internal carotid arteries, which passed up into the endocranium via the parabasal canals.

Elongation of the posterior part of the parasphenoid behind the ascending process and towards the cranial fissure occurs in *Pteronisculus* and *Boreosomus*. The parasphenoid terminates at the ventral otic fissure. However, in the post-Devonian actinopterygians and *Kentuckia*, this lies more posteriorly. Extension across the ventral cranial fissure occurs in *Perleidus* and in the neopterygian *Watsonulus*, but in neither does the parasphenoid reach the occiput. In all extant neopterygians, however, it reaches the occiput and this is considered to be derived.

The parasphenoid also reaches the occiput in at least seven lower actinopterygians. The genera involved are *Polypterus*, the only living fish with an aortic canal. This canal is long and bifurcates anteriorly to give rise to the lateral dorsal aortae. In *Pteronisculus* and *Boreosomus* the canal is also long and bifurcates anteriorly, as in *Polypterus*. Paired openings in the floor of the canal are presumed to have transmitted the second efferent arteries while there is always a dorsolaterally directed canal for the occipital artery, much as in the pholidophorids. In *Australosomus*, however, the aortic canal is short, as in leptolepids and parasemionotids. In the remaining six lower actinopterygian genera, however, the parasphenoid has grown back beneath the dorsal aortae, rather than above it as in *Polypterus*. These include Acipenseriformes, *Saurichthys, Birgeria, Errolichthys, Amphicentrum* and *Bobasatrania*. The parasphenoid of *Saurichthys, Birgeria* and Acipenseriformes has a median ridge posteriorly and is deeply notched for the dorsal aorta.

In *Pholidophorus* the parasphenoid just reaches the anterior half of the basioccipital. As in *Saurichthys* and the Acipenseriformes, where there has been an incorporation of multiple vertebrae into the occipital region, the parasphenoid extends beneath that region.

9. Occipital vertebral fusion: (0) no fusion; (1) minor fusion; (2) multiple occipital-vertebral fusion.
In both *Polypterus* and the neopterygians there has been some vertebral incorporation into the occipital region. However, only in *Saurichthys* and Acipenseriformes has there been an incorporation of multiple vertebrae into the occipital region (Bemis & Forey, 2001). Both the Acipenseriformes and *Saurichthys* have exceedingly long occipital regions, said to be the longest in the actinopterygians. In *Scaphirhynchus* up to six neural arches are incorporated.

10. Ascending process of the parasphenoid: (0) confined between basipterygoid process and incisure; (1) terminates below spiracular canal; (2) meets mouth of spiracular canal; (3) overlaps part of orbitotemporal and otic regions; (4) fused to otic region; not related to spiracle.
The primitive form of the actinopterygian parasphenoid is as in *Cheirolepis* and *Mimia*, with a short, relatively broad tooth plate that extends to the ventral otic fissure. The ascending process of the parasphenoid is short and does not extend across the oticosphenoid fissure onto the lateral commissure. This type of parasphenoid is similar to that found in primitive sarcopterygians; the base of the ascending process crosses the oticosphenoid fissure in *Moythomasia* and *Kentuckia*. This slender ascending process extends dorsally to the lateral commissure and terminates at the level of the jugular canal, developed in relation to the spiracular diverticulum. In more advanced actinopterygians such as *Pteronisculus* and *Boreosomus*, the ascending process approaches or enters the lower opening of the spiracular canal. In *Polypterus*, the spiracle is unconstricted, the ascending process is uniquely large, complicated by the invasion of membrane bone and unlike that in any other actinopterygian.

In Acipenseriformes, *Saurichthys* and *Birgeria* the area immediately behind the ascending process has increased in breadth and has expanded to cover a major part of the wall of the otic and orbitotemporal regions, and supports the endoskeletal articulation of the first infrapharyngobranchial. It also covers the canal for the jugular vein, the hyomandibularis facilis and almost reaches the exit of the IXth cranial nerve.

11. Parasphenoid–carotid relationship: (0) carotids notch the posterior margin of the parasphenoid as they pass up into the braincase; (1) carotids pass into the braincase above parasphenoid; (2) carotids pass through base of ascending process; (3) carotids notch parasphenoid behind ascending process; (4) carotids pass through stem of parasphenoid behind ascending process; (5) carotids pass beneath parasphenoid; (6) parasphenoid covers entire arterial system.
Primitively, neither the internal carotids nor the efferent pseudobranchials passed through the parasphenoid. Instead, both notched its posterior margin. The backward growth of the parasphenoid has a marked effect on the course of the internal carotids and associated arteries. At least four different topographies can be recognized. In *Polypterus* the posterior part of the parasphenoid not only encloses the carotid arteries, but is also below the entire dorsal arterial system. This pattern is unique among osteichthyans. In recent Acipenseriformes the posterior part of the

parasphenoid, as well as the ascending processes, are above or lateral to the carotid arteries. In *Saurichthys, Chondrosteus* and *Gyrosteus* there is a large paired foramen in the underside of the parasphenoid, beneath the posterior margin of the ascending process, which is assumed to have transmitted the common carotids. This pattern favours regarding *Saurichthys* as the sister group of the Acipenseriformes.

In *Birgeria* the only evidence of the aortic–carotid circulation is the shallow aortic notch which appears to direct the aorta away from the ventral surface. Thus we deduced the condition was as in *Acipenser*. In *Pteronisculus, Perleidus* and some neopterygians (*Lepisosteus, Amia*) the efferent pseudobranchial and internal carotid arteries pass through notches in the lateral edges of the parasphenoid, but in *Boreosomus* the internal carotid arteries passed through foramina in the base of the ascending process, as in pholidophorids and leptolepids.

12. *Basipterygoid process:* (0) endoskeletal; (1) endoskeletal with dermal component; (2) lost; (3) entirely dermal.

Primitively, the actinopterygian skull possessed a well-developed endoskeletal basipterygoid process, which developed as a lateral projection of the polar cartilage between the trabecula and parachordals, as in *Acipenser*. In stem-group neopterygians the basipterygoid process acquired support from the parasphenoid. Thus a mostly or entirely dermal basipterygoid process is present in *Boreosomus, Pteronisculus* and *Perleidus*. In *Polypterus* (see above), *Birgeria, Saurichthys, Australosomus, Amia* and almost all teleosts the endoskeletal basipterygoid process has been reduced or lost and in teleosts it is replaced by a massive dermal process. In summary, the presence or absence of a dermal component in extinct taxa may be difficult to distinguish, but a general trend from endoskeletal to dermal is evident, as the dermal basipterygoid process seems to reinforce the ventral wall of the myodome in the neopterygians.

In summary, the variation in the amounts of endoskeletal vs. dermal bone plus loss of the process seems haphazard above the *Mimia–Moythomasia* level and therefore presents a problem in meaningful scoring.

13. *Symplectic and jaw joint:* (0) absent; (1) present.

The symplectic bone is absent in the lower actinopterygians and the jaw joint is composed entirely of the quadrate and articular. This opinion (Patterson, 1973: fig. 23) has been further supported by an acid-prepared specimen of *Perleidus* which shows no articular surface for a symplectic (no perichondral bone) on the articular bone behind that for the quadrate.

The interhyal articulates directly with the ceratohyal, and apparently has no contact with the articular. In the neopterygians the symplectic developed as a new ossification in the hyoid arch anterior to the interhyal. It served in the primitive neopterygians and in the teleosts as a brace along the posteroventral border of the quadrate. In the halecostomes and the pycnodonts it elongated and formed a second jaw joint with the articular behind the original articular quadrate one. This interpretation gets around an awkward explanation for a switch from a sequential double jaw articulation in the lower actinopterygians to a serial one in the neopterygians as proposed by Olsen (1984). One final problem has been a confusion between the interhyal with a posterior ceratohyal, as in *Polypterus* (Jollie, 1984), and the interhyal with the symplectic in *Acipenser* (De Beer, 1937). All these matters have been discussed and clarified by Patterson (1982) and Gardiner, Maisey & Littlewood (1996).

14. *Ceratohyal:* (0) single ossification or cartilage; (1) two ossifications or cartilages.

Cladistians and basal actinopterygians have a single ceratohyal whereas Acipenseriformes and neopterygians have two ossifications or cartilages in the hyoid bar. *Eusthenopteron* has two ossifications in the hyoid bar, but one of these is more parsimoniously interpreted as an interhyal (See Patterson, 1982: fig. 1).

15. *Acrodin:* (0) absent; (1) present.

Although a tooth cap composed of acrodin has not been found in *Cheirolepis* (Patterson, 1982), and is not clearly defined in *Howqualepis*, the study by Meinke (1982) on the histochemistry of the tooth cap matrix in *Polypterus* suggests an ectodermal–mesodermal interaction for acrodin formation that must date well back in actinopterygian history. However, although acrodin is present in the Gogo genera it is only clearly visible on large teeth. Acrodin is absent in pachycormids and some teleosts.

16/17. *Intertemporal–supratemporal–dermopterotic*

In the primitive lower actinopterygians (e.g. *Mimia, Howqualepis*) the intertemporal is smaller than the supratemporal, and the former does not reach the nasal. *Moythomasia* has a nasal–intertemporal contact as in other taxa in which the intertemporal is a separate element. In *Watsonichthys* and related taxa (Gardiner, 1963) the nasal is in contact with a single bone called the dermopterotic. Whether or not the dermopterotic represents only the supratemporal or a fusion with the intertemporal cannot be determined

from fossil specimens. However, there is evidence in *Polypterus* (Pehrson, 1922, 1958; Jollie, 1984) that two ossification centres are involved in the development of the dermopterotic (which here also may fuse with the parietal). These centres are presumed to represent the anlagen of the intertemporal and supratemporal.

Grande & Bemis (1991) have noted that some adult specimens of *Polyodon* have separate intertemporals and supratemporals (their fig. 7) while others have a single bone in that position which must be dermopterotic (their fig. 13A). Also, Jollie (1980: fig. 10) has figured a skull roof of *Acipenser* with two ossifications on one side and a single on the other that is certainly the dermopterotic. Although this evidence is not proof of fusion in the early actinopterygians, it does favour fusion over loss of the intertemporal. In any case, we believe that the best compromise is to call the single ossification the dermopterotic, which is present in *Polypterus*, actinopterans and neopterygians. We resolved the problem by treating the presence of an intertemporal and supratemporal as one character and the presence of a dermopterotic as another. Finally, the dermopterotic is spatially separated from the nasal bone in *Birgeria, Cosmoptychius, Perleidus* and all other taxa with supraorbitals.

16. Intertemporal–supratemporal: (0) intertemporal smaller than supratemporal, no nasal bone contact; (1) intertemporal in contact with nasal bone.

17. Dermopterotic: (0) intertemporal and supratemporal fused as the dermopterotic, in contact with the nasal bone; (1) not in contact with nasal bone; (2) dermopterotics meet behind parietals; (3) elongated frontals meet extrascapulars and separate dermopterotics from parietals; (4) dermopterotics meet, parietals absent.

18. Dermosphenotic: (0) broadly arcuate, in contact with nasal and intertemporal and supratemporal; (1) fused to sphenotic; (2) fused to frontal; (3) separated from nasal by frontal, or nasal absent; (4) keystone shaped, separated from nasal by supraorbitals.
The dermosphenotic can be readily identified by the curve in its infraorbital canal before it enters an infraorbital bone. The dermosphenotic lies dorsolaterally or anteriorly to the spiracle. It is basically arcuate in shape, in contact anteriorly with the nasal bone and posteriorly to an upper infraorbital. In Devonian taxa it has a posterior extension that presumably developed independently in a few later taxa such as *Mesopoma*. In *Cheirolepis, Howqualepis* and *Stegotrachelus*

this extension reaches the dermohyal. It maintains contact with the nasal except for spatial separation in *Boreosomus, Ptycholepis, Saurichthys* and the Acipenseriformes. In *Birgeria, Palaeoniscum* and *Cosmoptychius*, plus several other taxa with an oblique suspensorium, the nasal and the dermosphenotic are separated by a series of irregular, partly overlapping supraorbitals. Advanced stem-group neopterygians, with the possible exception of the pholidopleuriforms, have a row of rectangular supraorbitals between the nasal and the keystone-shaped dermosphenotic. This same rectangular pattern is present in the generalized neopterygians. According to our cladistic analysis, the lower actinopterygian taxa with irregular and regular supraorbitals evolved independently.

19. Premaxilla–antorbital–rostral: (0) opposite premaxilla–antorbitals meet below rostral; (1) opposite premaxilla–antorbitals separated by rostral; (2) premaxilla and antorbitals separated; (3) premaxilla and antorbitals separated, premaxilla with dorsal process; (4) opposite premaxillae fused below antorbitals and rostral commissure passes into the premaxilla; (5) premaxilla and antorbitals absent.
In the upper jaw margin of lower actinopterygians there is a single bone which bears replacement teeth and usually the junction of the supraorbital and infraorbital canals in the position of the premaxilla plus antorbital of the neopterygians. The probability that this element represents a fusion of two ossification centres is based mostly on fossil evidence, plus some ontogenetic evidence from *Polypterus*. According to Pehrson (1958), the premaxilla is defined by the 24 mm stage. Jollie (1984) notes that it fuses with three 'rostral' canal tubes which are situated below the nasal capsule. These ossifications around the infraorbital canal are figured by Pehrson (1947: 422), in which they are labelled as antorbital anlagen.

Bartsch (pers. comm.), has noted that in *Polypterus* the dentigerous anlaga and three canalicular ossifications fuse to form a rostro-premaxilla, or in our terminology a premaxilla–antorbital. We favour Pehrson's interpretation mainly because the antorbital, whether fused with the premaxilla or separate in the adult, carries a tripartite configuration of three sensory canals – the infraorbital, supraorbital and rostral commissure. This pattern is evident in the adult *Polypterus*, as figured by Jollie (1984: fig. 7). The unique aspect of the proposed premaxilla–antorbital in this taxon is its extension on to the anterior border of the orbit (Jollie, 1984: fig. 147B and specimens).

In many lower actinopterygians there may be 'rostral' components fused into this complex ossification, the opposites (pmx/Ant), however, usually meet below a separate median rostral with a well defined commis-

sure. In taxa which have this element excluded by the maxilla from the jaw margin (e.g. *Australichthys*; Gardiner, 1969), teeth are absent and it is tempting to suppose that only the antorbital may be represented!

A fused premaxilla–antorbital is proposed as the primitive actinopterygian condition as it is the prevalent one for most lower actinopterygians. However, both *Pteronisculus* and *Birgeria* (Nielsen, 1942) have separate premaxillae, but without the dorsal process. In any case, this evidence indicates that nonfusion may have occurred at least three times independently: in the Acipenseriformes, in *Pteronisculus*, and in the neopterygians. In the latter the premaxilla always has a dorsal process. It should also be emphasized that the tripartite canal pattern, along with topology, consistently identifies the antorbital component in the extinct taxa, whether fused or separated. In pholodophorids premaxillae, antorbitals and also lateral dermethmoids are present. Uniquely in *Saurichthys* and *Birgeria*, the premaxillae are fused below the antorbitals and the rostral commissure passes into the premaxilla.

20. Maxilla–preopercular relationship: (0) maxilla gently curved, without distinct blade; preopercular curved and of uniform width; (1) maxillary blade rectangular, with posteroventral lobe; preopercular boomerang-shaped, conforming to maxilla; (2) maxillary blade essentially lobate but with reduced posteroventral lobe; preopercular trilobate with nearly vertical axis; (3) maxilla free with ethmoid articulation, separated from sickle-shaped preopercular; (4) maxilla with lobate blade; preopercular boomerang-shaped; (5) maxilla replaced by dermopalatine; preopercular represented by a chain of ossicles; (6) maxilla with superimposed infraorbital canal; dorsal arm of preopercular greatly expanded.

In the generalized lower actinopterygians the boomerang-like peropercular conforms to the shape of the posterodorsal margin of the maxillary blade. In taxa with an increasingly more vertical suspensorium (which occurred in more than one lineage) the blade became reduced in length, the posteroventral flange was reduced, the blade shortened and rounded, while the preoperculum became more trilobate. These pattern variations, related to the angle of the suspensorium, are characteristic of most post-Devonian taxa, including the deep bodied taxa. With the freeing of the maxilla from the cheek, as in *Luganoia*, the maxilla developed an ethmoid articulation.

21. Infraorbitals: (0) two elements, lacrymal and jugal; (1) three elements, including the postorbital; (2) more than three; (3) reduced to ossicles; (4) separate lacrymal plus ossicles fused to maxilla.
A majority of the taxa, including the Devonian, have two infraorbitals, the lachrymal and the jugal. The

primitive neopterygians plus the halecostomes have three or more, but the number is not constant. Among the lower actinopterygians, some taxa have an additional element, usually called the postorbital, as in *Pteronisculus, Palaeoniscum, Amblypterus, Gonatodus, Aeduella* and peltopleurids. Further increase in number is evident in *Birgeria* and the perleidiform *Meridensia*. In *Polypterus* the infraorbital canal appears to run through the maxilla behind the lachrymal (Pehrson, 1947: fig. 16).

22. Supraorbitals: (0) absent; (1) series of two or more irregular elements between nasal and dermosphenotic; (2) series of rectangular bones between nasal and dermosphenotic.
Excepting a single anamestic bone (adnasal) below the nasal and in front of the dermosphenotic in *Cheirolepis* and the redfieldiiforms, we have found no evidence that supraorbitals are primitively present in actinopterygians. *Palaeoniscum*, several 'species' of *Elonichthys, Cosmolepis, Scanilepis, Birgeria* and possibly *Evenkia* have a row of irregular and partly overlapping supraorbitals between the nasal bone and the keystone-shaped dermosphenotic. The oblique suspensorium, fused premaxilla–antorbital, rectangular maxillary blade, boomerang-shaped preoperculum and heterocercal caudal fin place these taxa below other more derived stem group neopterygians, which also have supraorbitals. The perleidiforms (*sensu lato*), including the cleithrolepids, peltopleurids and the enigmatic genus *Luganoia* have an even, rectangular series of supraorbitals (double in *Luganoia*), again between the nasal and the keystone-shaped dermosphenotic. This same rectangular pattern is present in generalized neopterygians such as *Acentrophorus*, and stem teleosts.

Supraorbitals have not been found in the pholidopleurids, which are otherwise putative stem neopterygians. Our evidence thus indicates that the supraorbitals, as in *Palaeoniscum* and in *Perleidus* plus neopterygians, appeared independently. Jakovlev (1977) has restored the acipenseriform genus *Stichopterus* with two regular supraorbitals (five in a second figure). In neopterygians there are usually three regular supraorbitals in sequence, while in *Polyodon* the soc runs through a series of ossicles or individual primordia. However, according to Jollie (1980) and Jarvik (1980) there are two supraorbitals in *Acipenser,* one of which fuses with the posterior nasal.

23. Suborbitals and spiraculars: (0) absent; (1) one to three; (2) multiple.
On the basis of our parsimony trees, suborbitals are first noticed in *Pteronisculus*. They are present in

varying number, usually one to three, in the primitive neopterygians. Their absence in Devonian taxa is regarded as primitive, but presence or absence in later lower actinopterans is an independent phenomenon.

The so-called spiraculars have an interesting distribution. According to our survey, they occur only in taxa with an inverted, triangular, preopercular with the broadest side on the dorsal border. These taxa are *Polypterus* and *Perleidus*. In the former, the spiracular bones extend in series from behind the postorbital bone to the dermohyal (see Jollie, 1984: 477). They are fewer in *Perleidus*, extending from the suborbital to the opercular. They are not clearly evident in the other perleidiforms, or in the other groups of stem neopterygians. They are absent in the neopterygians.

24. Dermohyal: (0) absent; (1) present.
The key to the identification of the dermohyal is its relationship to the hyomandibular. In *Polypterus, Mimia* and *Moythomasia* (Gardiner, 1984), it is a small dermal ossification firmly fused to the hyomandibula above the foramen for the hyomandibular canal. In *Howqualepis* it is a somewhat elongated wedge fused to a groove on the posterodorsal surface of the hyomandibula. A bone in a similar position is evident in *Pteronisculus* and *Boreosomus*, but here it is unattached (Nielsen, 1942 and specimens) and is presumed to be an antopercular – not a dermohyal. In most of the stem neopterygians the small triangular bone at the top of the contact between the preopercular and the opercular is often mistakenly called a dermohyal, but it is an antopercular. It is present in *Lepisosteus*.

25. Antopercular: (0) absent; (1) present.
This bone is frequently confused with the dermohyal, which occupies a similar position between the opercular and preopercular. In *Pteronisculus magna* there may be two or three partially overlapping plates (Nielsen, 1942: fig. 30) of which the most anterior sits over the head of the hyomandibula. In *Boreosomus* (Nielsen, 1942: figs 69, 72) and *Australosomus* and other *Pteronisculus* species there is but one antopercular which overlaps the anterior margin of the opercular, as does the posterior of the three bones in *P. magna*.

It is clear that in the majority of stem-group neopterygians the antopercular is well removed from the head of the hyomandibula (viz. *Tarrasius, Haplolepis*, redfieldids, pholidopleurids, ptycholepids, perleidids).

26. Quadratojugal: (0) plate-like, lateral to quadrate, may abut maxilla; (1) braces quadrate; (2) attached to dermopalatine.
In primitive actinopterygians such as *Mimia* and *Moythomasia*, the quadratojugal is fixed to the lower end of the preopercular and overlies the quadrate. It is covered in part or completely by the preopercular, and in part by the maxilla. Its pit line is innervated by a branch of mandibular VII, which also innervates the sensory canal and pit lines of the preopercular. Aside from the Devonian genera mentioned above, an exposed quadratojugal has been observed only in *Pteronisculus* and possibly in the perleidiform *Pseudobeconia*.

Patterson (1973: 250) has identified the quadratojugal in the neopterygians *Dapedium, Lepidotes* and *Lepisosteus* as a splint-like bone which retained its contact with the preopercular and quadrate in spite of the separation of the maxilla and the preopercular. In *Pholidophorus germanicus* (his fig. 7) the probable quadratojugal is partly fused to the posteroventral edge of the quadrate, and in more advanced teleosts it is presumably reduced to the posterior process of the quadrate.

In summary, although the quadratojugal is rarely seen in the lower actinopterygians, it must have persisted, although considerably modified, into the neopterygians. A separate ossification anterior to the preopercular in *Polypterus* has been identified as the quadratojugal, but this remains problematical. Patterson (1973: 249) also lists this bone as present in *Saurichthys, Acipenser, Cheirolepis, Australosomus* and *Birgeria*, some haplolepids and *Canobius*. In Acipenseriformes it is fused to the dermopalatine.

27. Supra-angular: (0) absent; (1) present.
The supra-angular is attached to the outer face of the angular, dentary and prearticular (not to be confused with the surangular which is part of the splenial series in the sarcopterygians). It is absent in *Cheirolepis, Mimia* and *Polypterus*, but is present in *Howqualepis*, *Moythomasia, Pteronisculus, Saurichthys, Birgeria* and other lower actinopterygians including *Chondrosteus*. Among the neopterygians it occurs in generalized taxa such as *Hulettia* and in other halecostomes. It is also present in the pholidophorids and leptolepids (*sensu lato*) but not in the teleosts (*sensu stricto*). In all taxa with this bone, it forms part of the lateral wall of the adductor fossa and in the nonteleost neopterygians also part of the coronoid process.

28. Coronoid process: (0) absent; (1) from supra-angular and dentary; (2) from prearticular.
This structure is an elevation of the lateral wall of the adductor fossa of the mandible in the neopterygians anterior to the jaw articulation. It includes part of the dentary and the supra-angular. This process is absent in lower actinopterygians. *Luganoia* has a free maxilla

with an ethmoid process and a very slight elevation suggestive of a coronoid (Patterson, 1973: 296). There is an apparent correlation between the elevation of the process and enlargement and subdivision of the adductor mandibulae. Although the process in *Polypterus* is formed entirely by the prearticular, the adductor musculature is similarly elaborated.

29. Suspensorium angle: (0) acute, 30–50°, hyoid facet directed posteroventrally; (1) moderately acute, 60–90°; (2) vertical, 80–90°, hyoid facet horizontal.
The suspensorium of the primitive actinopterygians has been characterized as oblique, in contrast with its more or less vertical orientation in many stem neopterygians. The obliquity of the suspensorium may be gauged by estimating the size of the angle formed by the intersection of a line drawn from the centre of the hyomandibular facet to the jaw articulation and from there anteriorly along the greatest length of the maxilla. The centre of the facet may be estimated by inspection of the dorsal border of the maxilla. The axis along the maxilla will be more or less parallel to its ventral border excluding any posterior flange. Although there is a general trend toward verticality in the *Cheirolepis*–neopterygian sequence, there are also numerous examples of extinct taxa that independently approached a vertical orientation.

30. Pectoral fin: (0) girdle tripartite, marginal rays embrace propterygium; (1) propterygial canal present.
The first pectoral radial of the actinopterygians is modified into a propterygium, which is enclosed by two or more lepidotrichia, except in *Polypterus*. The propterygium is perforated by a canal for nerves and blood vessels, which is absent in *Cheirolepis* and *Polypterus*. Primitively in actinopterygians there is an elongate, branched or jointed metapterygium, as in *Mimia, Moythomasia, Acipenser, Pteronisculus* and *Palaeoniscum*. The condition in *Cheirolepis* is unclear, but there are up to five basal elements. In *Lepisosteus* and teleosts the metapterygium is unbranched, while *Amia* and *Pachycormus* retain the plesiomorphic condition.

31. Median fin: (0) rays more numerous than radials; (1) rays and radials equal.
In the primitive actinopterygians the fin rays are considerably more numerous than their radial supports. The radials in *Mimia, Moythomasia* and *Pteronisculus* are variously fused into plates as indicated by notches and openings. With the exception of *Australosomus*, the lepidotrichia and the radials are equal in number in the stem neopterygians (perleidids, *Luganoia*) and neopterygians.

32. Caudal fin: (0) heterocercal; (1) heterocercal, upper caudal rays elongated; (2) diphycercal; (3) modified heterocercal.
The heterocercal tail is generally present in lower actinopterygians with an oblique suspensorium. The caudal fin pattern of *Polypterus* is best described as modified heterocercal as it is confluent with the last dorsal finlet (Bartsch & Gamballa, 1992). The hemiheterocercal condition with a reduced caudal lobe and elongated dorsal fin-rays is present in all stem neopterygians but with variation in the length of the lobe. In the perleidid *Meridensia* and in the pholidopleurid *Pholidopleurus*, the caudal fin is almost homocercal. In the generalized neopterygians (e.g. *Acentrophorus* Gill, 1923) the caudal fin is homocercal. In the neopterygian *Hulettia* (Schaeffer & Patterson, 1984), for which the caudal skeleton is known in detail, it is externally hemiheterocercal, but with longer dorsal fin rays. However, epaxial rays are absent and the haemal spines supporting the caudal rays are essentially unmodified.

It should be noted that epaxial fin rays and their epural supports must have developed numerous times independently, as in *Saurichthys* and various groups of neopterygians. Epurals are numerous in the lower actinopterygians, with 15 in *Pteronisculus* and 30 in *Acipenser*. The number of epurals drops in the primitive neopterygians to around seven.

33. Neural spines: (0) paired; (1) caudal spines median; (2) all spines median; (3) median, but membrane bone.
The history of neural spines in the actinopterygians represents an interesting interplay in developmental plasticity. In the primitive lower actinopterygians such as *Cheirolepis* and *Mimia*, the neural spines are paired, reflecting the paired basidorsal components of the axial skeleton. However, in *Moythomasia, Australosomus, Birgeria, Hulettia* and *Amia* the neural spines are unpaired (fused) in the caudal region, while in *Lepisosteus* they are paired. Median neural spines are characteristic of the halecostomes and the teleosts. Finally, *Polypterus* also has median neural spines, but like its vertebrae these are formed from membrane bone, suggesting independent origin. Scoring this character obviously presents problems.

34. Fringing fulcra and fulcral scales: (0) absent; (1) present.
The presence of dorsal and ventral basal fulcral scales anterior to the caudal fin represents an actinopterygian synapomorphy. *Cheirolepis* has one median, dorsal fulcral scale followed by a series of paired basal fulcra along the caudal lobe. Dorsal and ventral median fulcra are present in almost all other lower

actinopterygians, including *Mimia, Moythomasia* and *Acipenser*. In *Pteronisculus, Watsonichthyes, Amphicentrum, Boreosomus, Palaeoniscum, Perleidus, Hulettia* and the neopterygian *Lepisosteus*, the dorsal basal fulcra give way to fringing fulcra that extend along the border of the dorsal fin. Basal and fringing fulcra persisted in the macrosemiids, halecomorphs (except *Amia*) and some teleosts. Fringing fulcra are paired, leaf-like structures attached to the leading fin-rays.

35. Squamation: (0) complete, but no inversion in caudal area; (1) complete, but with caudal inversion; (2) reduced squamation, restricted mainly to dorsal caudal lobe and lateral line.

Primitively, actinopterygians possessed a complete body scaling with or without a caudal inversion. In many Acipenseriformes and in *Saurichthys* this scaling is reduced to the lateral line and one or two dorsal and ventral rows.

   In *Birgeria* the scaling is restricted to the dorsal caudal area, while the lateral line scales are tubular and widely separated from each other, just as they are in *Peipiaosteus*. The Polydontidae are characterized by a covering of noninterlocking microctenoid scales, although they still possess a series of tubular, widely separated lateral line scales.

36. Dentary: (0) canal absent; (1) with enclosed mandibular canal.

In actinopterygians alone among gnathostomes the mandibular sensory canal passes through the dentary. The canal is missing in sturgeons, while in *Polyodon* it is short and superficial and does not penetrate the dentary.

37. Pelvic plate: (0) pelvic fin with one series of radials; (1) pelvic fin with two series of radials.

The actinopterygian pelvic girdle appears to have incorporated the metapterygial skeleton of the fin (von Davidoff, 1880; Rosen *et al.* 1981). Whether or not this is the case, the pelvic endoskeleton of *Polypterus* closely resembles that of other actinopterygians in the possession of two series of radials.

38. Presupracleithrum: (0) absent (1) present.
Patterson (1982) has pointed out that the posterior postspiracular in *Polypterus* lies anterior to the supracleithrum in precisely the same place as the presupracleithrum of actinopterans (See also Nybelin, 1976). The possession of a supracleithrum is an actinopterygian character.

REFERENCES

Bartsch B, Gamballa S. 1992. On the anatomy and development of the vertebral column and pterygiophores in *Polypterus senegalus* (Cuvier, 1829) (Pisces, Polypteriformes). *Zoological Jahrbuch von Anatomie* **122:** 497–529.

de Beer GR. 1937. *The development of the vertebrate skull.* Oxford: Oxford University Press.

Bemis WE, Forey PL. 2001. Occipital structure and the posterior limit of the skull in actinopterygians. In: Ahlberg P, ed. *Major events in early vertebrate evolution.* London: Taylor & Francis, 350–369.

Cloutier R, Arratia G. 2004. Early diversification of actinopterygians. In: Arratia G, Wilson MVH, Cloutier R, eds. *Recent advances in the origin and early radiation of vertebrates.* München: Dr Friedrich Pfeil, 21–270.

Coates MI. 1999. Endocranial preservation of a Carboniferous actinopterygian from Lancashire, UK and the interrelationships of primitive actinopterygians. *Philosophical Transactions of the Royal Society of London, B* **354:** 435–462.

von Davidoff M. 1880. Beiträge zur vergleichenden Anatomie der hinteren Gliedmassen der Fische, ii Ganoidei Holostei. *Morphologische Jarbuch* **6:** 435–468.

Gardiner BG. 1963. Certain palaeoniscoid fishes and the evolution of the actinopterygian snout. *Bulletin of the British Museum of Natural History, London (Geology)* **8:** 255–325.

Gardiner BG. 1969. New palaeoniscoid fish from the Witteberg series of South Africa. *Zoological Journal of the Linnean Society* **48:** 423–452.

Gardiner BG. 1984. The relationships of the palaeoniscoid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bulletin of the British Museum of Natural History (Geology)* **37** (4)**:** 173–428.

Gardiner BG, Maisey JG, Littlewood DT. 1996. Interrelationships of basal neopterygians. In: Stiassny LJ, Parenti LR, Johnson GD, eds. *Interrelationships of fishes.* London: Academic Press, 117–146.

Gardiner BG, Schaeffer B. 1989. Interrelationships of lower actinopterygian fishes. *Zoological Journal of the Linnean Society* **97:** 135–187.

Gill EL. 1923. The Permian fishes of the genus *Acentrophorus*. *Proceedings of the Zoological Society of London* **23:** 19–40.

Grande L, Bemis WE. 1991. Osteology and phylogenetic relationships of fossil and Recent paddle fishes (Polydontidae) with comments on the interrelationships of Acipenseriformes. *Journal of Vertebrate Paleontology* **11** (Suppl. 1)**:** 1–121.

Jakovlev VN. 1977. Phylogensis of Acipenseriformes. In: Menner VV, eds. *Essays on phylogeny and systematics of fossil fishes and agnathans.* Moscow: USSR Academy of Sciences, 116–143 [in Russian].

Jarvik E. 1980. *Basic structure and evolution of vertebrates*, Vol. 1. London: Academic Press.

Jollie M. 1980. Development of the head and pectoral girdle skeleton and scales in *Acipenser*. *Copeia*: 226–249.

Jollie M. 1984. Development of the cranial and pectoral girdle bones of *Lepisosteus*, with a note on scales. *Copeia*: 476–502.

Lund R. 2000. The new actinopterygian order Guildayichthyiformes from the Lower Carboniferous of Montana (USA). *Geodiversitas* **22:** 171–206.

Meinke DK. 1982. A light and scanning electron microscope study of microstructure, growth and development of the dermal skeleton of *Polypterus* (Pisces: Actinopterygii). *Journal of Zoology, London* **197:** 355–382.

Nielsen E. 1942–49. Studies on Triassic fishes from East Greenland. I. *Glaucolepis* and *Boreosomus*. *Meddelser øm Grønland* **138:** 1–403 (1942). II. *Australosomus* and *Birgeria*. *Meddelser øm Grønland* **146:** 1–309 (1949).

Nybelin O. 1976. On the so-called postspiracular bones in crossopterygians, brachiopterygians and actinopterygians. *Acta Regiae Societatia Scientiarn et Littarum Gotheburgensia. Zoologica* **10:** 1–31.

Olsen PE. 1984. The skull and pectoral girdle of the parasemionotid fish *Watsonulus eugnathoides* from the Early Triassic Sakamena Group of Madagascar, with comments on the relationships of the holostean fishes. *Journal of Vertebrate Paleontology* **4:** 481–499.

Patterson C. 1973. Interrelationships of hosteans. In: Greenwood PH, Miles RS, Patterson C, eds. *Interrelationships of fishes*. London: Academic Press, 233–305.

Patterson C. 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London, B* **269:** 275–579.

Patterson C. 1982. Morphology and interrelationships of primitive actinopterygian fishes. *American Zoologist* **22:** 241–259.

Pehrson T. 1922. Some points in the development of telestomian fishes. *Acta Zoologica, Stockholm* **3:** 1–63.

Pehrson T. 1947. Some new interpretations of the skull in *Polypterus*. *Acta Zoologica, Stockholm* **28:** 399–455.

Pehrson T. 1958. The early ontogeny of the sensory lines and the dermal skull of *Polypterus*. *Acta Zoologica, Stockholm* **39:** 241–258.

Poplin C, Lund R. 2000. Two deep-bodied palaeoniscoid actinopterygians from Bear Gulch (Montana, USA, Lower Carboniferous). *Journal of Vertebrate Paleontology* **20:** 428–449.

Rosen DE, Forey PL, Gardiner BG, Patterson C. 1981. Lungfishes, tertrapods, paleontology, and plesiomorphy. *Bulletin of the American Museum of Natural History* **167** (4)**:** 163–275.

Schaeffer B, Patterson C. 1984. Jurassic fishes from western USA, with comments on Jurassic fish distribution. *American Museum Novitates* **2796:** 1–86.

Schultze H-P. 1992. Early Devonian actinopterygians (Osteichthyes, Pisces) from Siberia. *Academia* **1:** 233–242.

Stensiö EA. 1921. *Triassic Fishes from Spitzbergen*, I. Vienna: Adolf Holzhausen.

APPENDIX 1

Internodal change list A–K (excluding G–L, L–M). Note that character state changes between the hypothetical outgroup and node A may be ambiguous; however, these changes fit *Cheirolepis*. Whatever optimization is used, the character change is always the same. Changes between nodes A–B and B–C require special comment. First, all of these state changes are diagnostic of *Mimia*, which indicates that preselected optimization has forced all these character states to the earliest possible nodes, A–B. The position of *Polypterus* between nodes A and C is related to particular states at A and C as listed. Note also irregular supraorbitals (*Palaeoniscum*, *Cosmolepis*, *Birgeria*), bone pattern of oblique suspensorium plus dermpterotic. Compare with *Perleidus*, etc. Absent in *Australosomus*, peltopleurids

Internode	CI	Number	Change	Description of transformed state
Outgroup A	0.500	24	0–1	Dermohyal fused to hyomandibular
	1.000	36	0–1	Dentary with sensory canal
	1.000	37	0–1	Pelvic plate with two series of radials
	1.000	38	0–1	Presupracleithrum present
A–B	1.000	15	0–1	Acrodin tooth caps
	1.000	20	0–1	Maxillary blade rectangular; preopercular boomerang shaped
	0.667	35	0–1	Squamation complete with caudal reversion
	1.000	37	0–1	Pelvic plate with two series of radials
B–C	1.000	5	0–1	Lateral cranial canal (chamber) in otic wall
	1.000	30	0–1	Pectoral propterygium with canal
C–D	1.000	10	0–1	Presence of ascending process of parasphenoid which does not reach spiracular opening
D–E	1.000	16	0–1	Elongation of intertemporal bone to meet nasal
	0.500	27	0–1	Supra-angular present
E–F	1.000	6	0–1	Presence of paired posterior myodome
	0.750	8	0–1	Parasphenoid terminates anterior to ventral otic fissure
	1.000	10	1–2	Ascending process to spiracle

APPENDIX 1 *Continued*

Internode	CI	Number	Change	Description of transformed state
F–G	1.000	4	0–1	Spiracle enclosed in otic wall
	1.000	5	1–2	Lateral cranial canal confluent with fossa bridgei
	1.000	6	1–2	Median posterior myodome
	0.500	14	0–1	Ceratohyal in two units
	0.800	18	0–3	Dermosphenotic in contact with frontal
	0.500	24	1–0	Dermohyal not fused to hyomandibular
G–H	0.600	12	0–1	Basipterygoid endoskeleton plus dermal
	0.800	21	0–1	Infraorbitals three, including postorbital
	0.400	23	0–1	Suborbitals one to three
	1.000	25	0–1	Antopercular present
	0.667	29	0–1	Suspensorium moderate
	0.330	34	0–1	Fringing fulcra
H–I	1.000	11	0–1	Carotids pass into braincase above parasphenoid
	1.000	20	1–2	Maxillary blade lobate; preopercular trilobate
	0.400	23	1–2	Suborbitals one to three
	1.000	26	0–1	Quadratojugal braces quadrate
I–J	1.000	2	0–1	Subtemporal fossa present
	1.000	3	0–1	Dilatator fossa present
	0.800	18	3–2	Dermosphenotic fused to frontal
	0.750	32	0–1	Caudal upper rays elongated, heterocercal
J–K	0.667	1	0–1	Post-temporal fossa rudimentary
	0.750	8	1–2	Parasphenoid extends across ventral otic fissure
	1.000	11	1–3	Carotids notch parasphenoid behind ascending process
	1.000	17	1–0	Intertemporal and supratemporal fused as dermosphenotic
	1.000	19	0–3	Premaxilla and antorbital separate; premaxilla with dorsal process
	0.667	22	0–2	Supraorbitals rectangular between nasal and dermosphenotic
	0.667	29	1–2	Suspensorium vertical
	1.000	31	0–1	Median rays and radials equal
K–Neopterygian	0.667	1	1–2	Post-temporal fossa present
	0.750	8	1–2	Parasphenoid extends to basioccipital
	0.667	9	0–1	Occipital vertebral fusion minor
	1.000	11	1–3	Carotids notch parasphenoid behind ascending process
	1.000	13	0–1	Symplectic present
	0.800	18	2–4	Dermosphenotic keystone-shaped, separated from nasal by supraorbitals
	1.000	17	1–0	Dermopterotics not in contact with nasal bone
	1.000	19	0–3	Premaxilla and antorbitals separated; premaxilla with dorsal process
	1.000	20	2–3	Maxilla free, preopercular sickle-shaped
	0.800	21	0–2	Infraorbitals
	0.667	22	0–2	Preopercular trilobate with nearly vertical axis
	1.000	28	0–1	Coronoid process from suprangular plus dentary
	0.667	29	1–2	Suspensorium vertical; hyoid facet horizontal
	1.000	31	0–1	Rays and radials equal
	0.750	32	0–1	Caudal fin
	0.600	33	0–2	All neural spines median

Remarks about supraorbitals for all taxa with dermopterotic:

1. One 'adnasal' found in redfieldiids.

2. Variable number, irregular, and partly overlapping, in *'Elonichthys'*. Suspensorium oblique but dermopterotic present in *Coccolepis, Palaeoniscum, Scanilepis, Birgeria Saurichthys* and Acipenseriformes.

3. Regular, rectangular in series with dermosphenotic in perleidiforms and neopterygians. Not canal-related but is series with dermosphenotic.

4. Absent in *Australosomus*. Variable in peltopleurids. Double rows in *Luganoia* but see Patterson (1973: 297).

APPENDIX 2

INTERNODAL CHANGE LIST GL, LM

The Acipenseriformes, particularly certain Jurassic forms have a dual role in the construction of our cladogram. First, they represent a crown group intercalated between the stem actinopterygians and stem neopterygians. Second, together with *Birgeria* and *Saurichthys* they form a clade. This node L is supported by eight character changes, three of which are synapomorphies. The synapomorphies are characters 10, 11 and 19.

Character 10 concerns the ascending process of the parasphenoid (state 3) where the area immediately posterior to the ascending process has expanded to cover a major part of the wall of the orbitotemporal and otic regions of the braincase. It covers the canal for the jugular vein and hyomandibularis facilis and all but reaches the exit of IXth cranial nerve. In Recent Acipenseriformes and in *Birgeria* it also supports the endoskeletal articulation of the first infrapharyngobranchial. Character 11 concerns the nature of the passage of the carotid arteries (state 4). In *Saurichthys*, *Chondrosteus* and *Gyrosteus* the carotid foramen pierces the parasphenoid adjacent to the point of articulation of the first infrapharyngobranchial. Finally, character 19: the premaxilla–antorbital–rostral (state 4). The primitive condition of this character is for the opposite premaxilla/antorbital to meet below the rostral. In this instance, the opposite premaxillae are fused below the antorbitals and the rostral commissure passes into the premaxilla. Several other homoplasious character states support the group-ing Acipenseriformes, *Birgeria*, *Saurichthys*. These include character 8 (the posterior growth of the parasphenoid which extends to the basioccipital – state 3). This is also seen in *Polypterus* and stem teleosts; in the former, however, it has done so above the arterial system rather than below it as in *Polypterus*.

Additional support for node L is afforded by the appearance of the dermopterotic, which in our analysis has arisen three times: once in *Polypterus*, again in the group Acipenseriformes, *Birgeria* and *Saurichthys* and once again in neopterygians. Lastly, support is afforded by character 35 (state 2) which identifies the reduced squamation. In Acipenseriformes and in *Saurichthys* the scaling is reduced to the lateral line and one or two dorsal and ventral rows. In *Birgeria* and *Peipiaosteus* it is restricted to the dorsal caudal area and to the lateral lines where the scales are tubular and widely separated from one another.

The clade Acipenseriformes + *Birgeria* + *Saurichthys* can be resolved in three ways:

1. ((Acipenseriformes, *Saurichthys*) *Birgeria*)

Two synapomorphies support this grouping: characters 7 and 20. Character 7 (state 1), the presence of a craniospinal process, is characteristic of *Saurichthys* and Acipenseriformes and takes the form of an acutely rounded, dorsolateral prominence behind the vagal foramen. Character 20 (state 4) concerns the maxilla/preopercular relationship. Primitively, the maxilla is gently curved without a distinct blade and with a curved preopercular of uniform width. The derived condition is for the maxilla to have a lobate blade and the preopercular to be boomerang-shaped. Additional support for this grouping is provided by characters 9, 23 and 29. Character 9 relates to multiple vertebrae which have been incorporated into the occiput. Both *Acipenser* and *Saurichthys* have exceedingly long occipital regions in which several vertebrae have been condensed into the occipital region. In both *Polypterus* and neopterygians there has, however, been some vertebral incorporation into the occipital region (character 9, state 2). Characters 23 and 29 concern loss and change in features: the loss or absence of suborbitals in Acipenseriformes and *Saurichthys* (character 23, state 0), while the suspensorium angle, unlike that of *Birgeria*, typifies the primitive condition (character 29, state 0). Support for this grouping also comes from Character 11, the passage of the carotid arteries. As noted above in *Saurichthys* and the acipenseriforms *Gyrosteus* and *Chrondrosteus*, they pass through the stem of the parasphenoid. This we regard as the plesiomorphic condition. In Recent Acipenseriformes, *Peipiaosteus* and *Birgeria* the carotid artery does not pierce the parasphenoid; we regard this as derived within Acipenseriformes. Therefore we have coded Acipenseriformes as having state 4.

2. ((Acipenseriformes, *Birgeria*) *Saurichthys*)

One character (no. 22) supports this grouping: the supraorbitals, comprising two or more elements between the nasal and the dermosphenotic. Two in *Acipenser* and *Polyodon* and possibly *Stichopterus*, multiple in *Birgeria* (state 1), absent in *Saurichthys*.

3. ((Acipenseriformes (*Birgeria*, *Saurichthys*))

A single synapomorphy supports this grouping: character 19 (state 4) – the fusion of the two premaxillae in *Bigeria* and *Saurichthys*. Additional support comes from the loss of the basipterygoid process in both *Birgeria* and *Saurichthys*. A parallel loss also occurs in *Australosomus*. In *Acipenser* the basipterygoid process is entirely endoskeletal, a feature that we regard as primitive for actinopterygians.

We conclude from this analysis that *Saurichthys* and the Acipenseriformes are sister groups, as this grouping has the most character support. Within this three-taxon clade *Birgeria* is their sister group.