30 mm

Figure 6. *Eoherpeton watsoni* Panchen, holotype skull RSM GY 1950.56.1, dorsal view. Natural size.
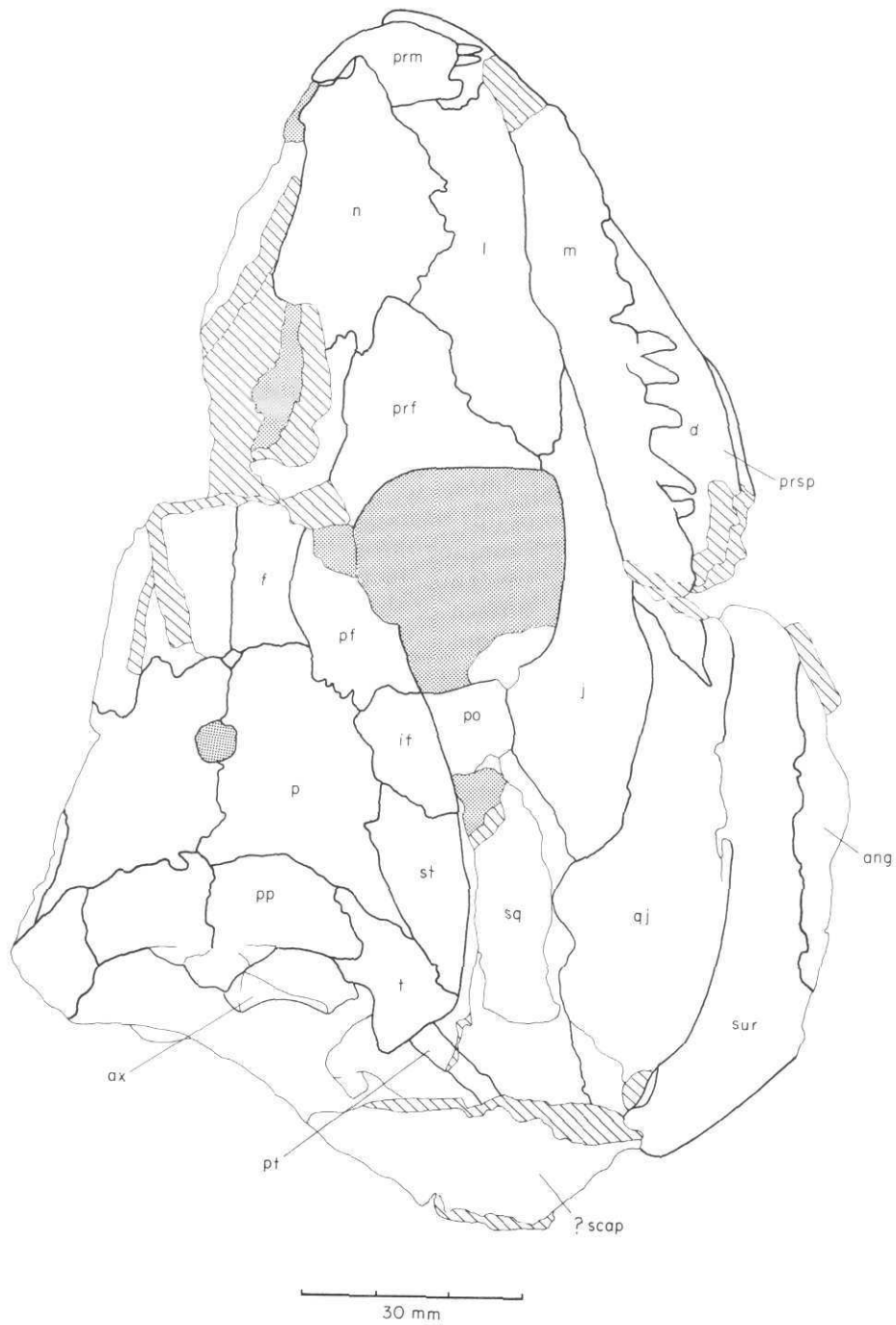
Figure 7. *Eoherpeton watsoni* Panchen, holotype skull, RSM GY 1950.56.1, dorsal view. Natural size. Broken bone hatched, matrix mechanical stipple.
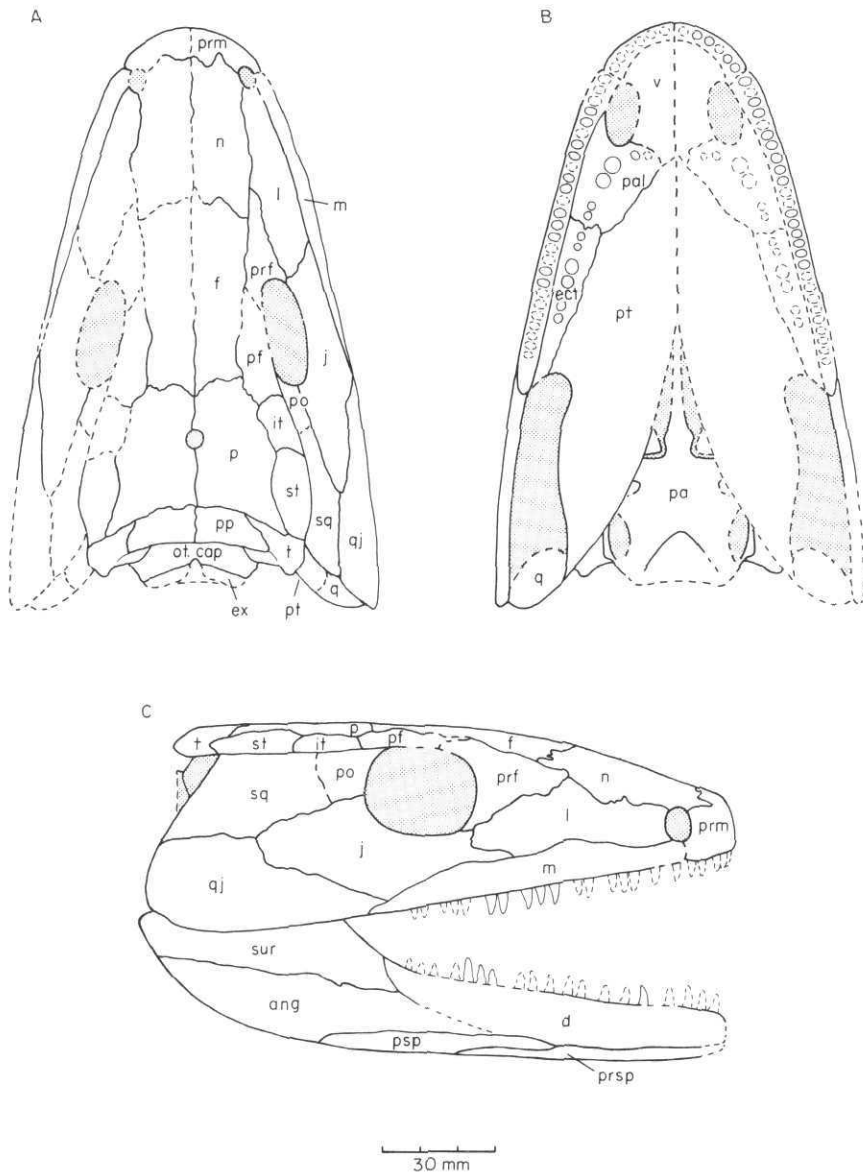
Figure 8. *Eoherpeton watsoni* Panchen, composite outline restoration of skull (× 0.5). A, Dorsal view; B, ventral view; C, lateral view.

has been proposed as a feature of early captorhinomorphs and pelycosaurs (Parrington, 1955; Hotton, 1959), and a similar hypothesis may be applicable to *Eoherpeton*. However, the presence of the tabular tuberosity suggests that this was not the case. A direct or ligamentous connection between the tabular and dorsal surface of the palatoquadrate would reduce the size of the middle ear cavity and possibly interrupt the connection between a stapes and tympanum (Fig. 9A). But, more importantly, if present, the m. depressor mandibulae probably hugged the posterior border of the skull as it extended down to the lower jaw
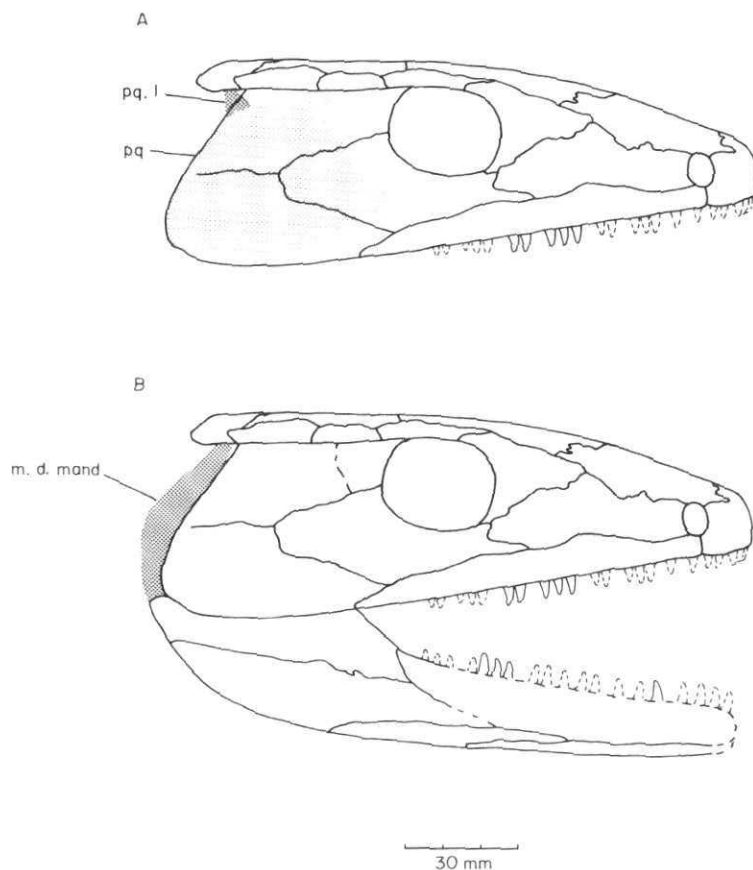
Figure 9. *Eoherpeton watsoni* Panchen. A, Outline restoration of skull, lateral view, showing possible position of palatoquadrate ligament (×0.5). Outline of palatoquadrate after *Palaeoherpeton* (Panchen, 1964: fig 5); B, outline restoration of skull, lateral view, showing possible position of m. depressor mandibulae (×0.5).

(Fig. 9B), in a manner similar to that proposed by Reisz (1981: 66) for the early diapsid *Petrolacosaurus kansensis* Lane. Consequently, as there appears to be no otic notch in *Eoherpeton*, there was no place for a tympanum. A groove on the posterior edge of the squamosal of *Eoherpeton* was interpreted by Panchen (1975: 588) as forming part of the border of an otic notch, but it more probably marks the course of m. depressor mandibulae across the back of the skull. A similar groove is present on the squamosal of *Gephyrostegus bohemicus* (A. C. Milner & A. R. Milner, personal communication) and *Proterogyrinus* (Holmes, 1984). Thus, there seems little reason to believe that a tympanum was present in *Eoherpeton*. The significance of this conclusion is discussed below 'Relationships of anthracosaurs'.

Parasphenoid and braincase

The braincase in the holotype of *Eoherpeton* is disrupted and incomplete, and much of its anatomy is obscured by the surrounding bones of the skull
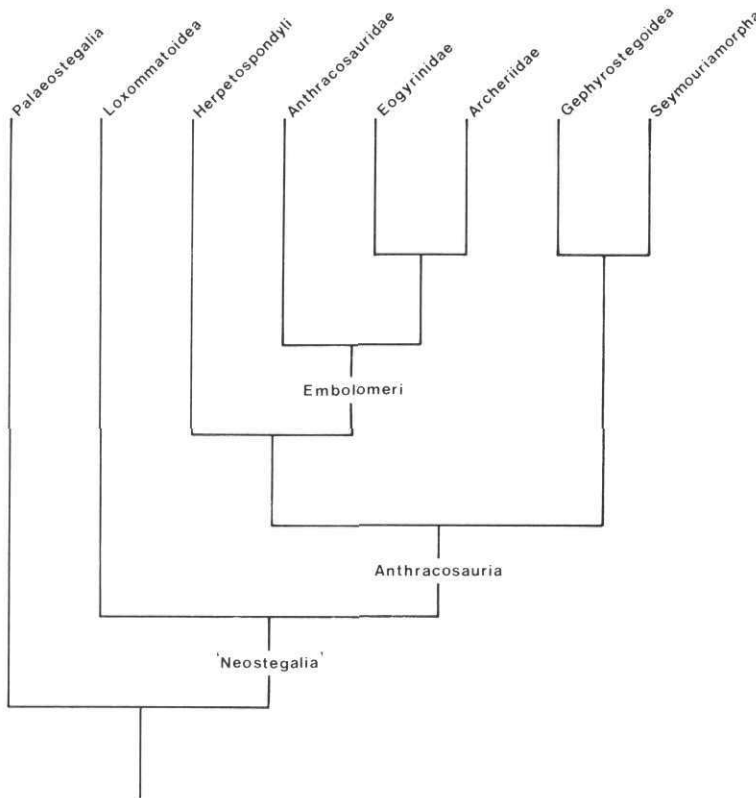
Figure 31. A phylogeny of the Batrachosauria. After Panchen (1980).

skull-roof patterns of anthracosaurs and cotylosaurs". *However, only in anthracosaurs and seymouriamorphs did a connection develop between the tabular and parietal on a skull table including the intertemporal.* Thus characterized, this is a derived condition among primitive tetrapods and is here considered to be an autapomorphy of the Anthracosauria, uniting embolomeres, gephyrostegids, herpetospondyls and seymouriamorphs as a monophyletic group. In other tetrapods which exhibit a tabular–parietal suture, at least one bone in the temporal series is absent. If these forms had originally passed through a stage in which the intertemporal bone was present, its subsequent loss may have led to a change in the relative position of the remaining bones, and account for the development of a tabular–parietal suture (see Panchen, 1975: 612–613). In anthracosaurs the intertemporal bone is retained and the tabular–parietal suture almost certainly developed as the result of differential growth of the tabular and parietal bones (Parrington, 1956).

In his attempt to demonstrate how 'cotylosaurs' and 'reptiles' were "in no way related to any known labyrinthodont, least of all to any anthracosaur" (Heaton, 1980: 515), Heaton noted that "perhaps the most significant character separating batrachosaurs and their presumed descendants from other Palaeozoic tetrapods was the structure of the braincase" (Heaton, 1980: 511). He listed a number of similarities which he considered were unique to batrachosaurs. These included a **Y**- or **V**-shaped sphenethmoid, an unossified

15

groups of equal rank (Fig. 34). However, in my formal classification I have not erected a new infraorder to embrace the Eoherpetontidae. In the past few years a number of different schemes of anthracosaur interrelationships have been proposed with accompanying new terminologies, many of which have since been abandoned: for example Schizomeri and Diplomeri (Romer, 1964, 1966—see Panchen, 1970, 1975), Batrachosauria (Panchen, 1970, 1975—see Panchen, 1980), and possibly Herpetospondyli (Panchen, 1975, 1980—see above). Until a more definite statement can be made regarding the relationships of *Eoherpeton* I do not intend to erect a new infraorder which may be redundant within a year or so. Similarly, I have chosen not to include the Gephyrostegidae in a separate infraorder. Inclusion of the genera which constitute the family Gephyrostegidae, *Gephyrostegus*, *Eusauropleura* and probably *Bruktererpeton fiebigi* (Boy & Bandel,
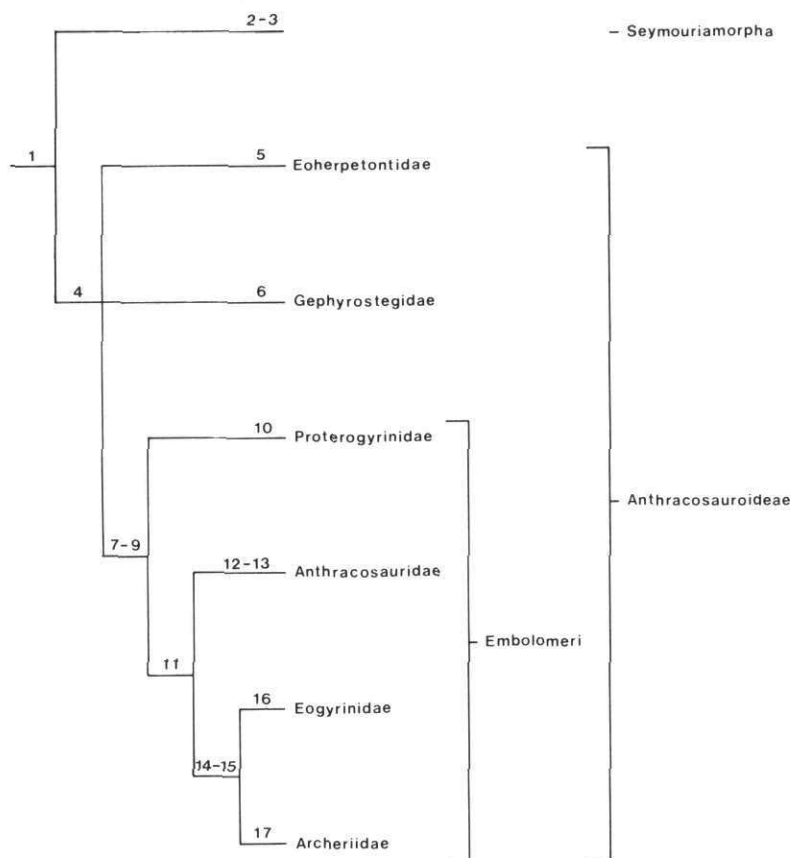

Figure 34. A phylogeny of the Anthracosauria. Numbered characters refer to the following synapomorphies: 1, tabular–parietal suture on a primitive skull table; 2, squamosal–intertemporal suture; 3, lateral otic tube; 4, emargination of skull table, post-temporal fossae lost; 5, accessory rib articulations on transverse processes; 6, frontals included in orbit margins; 7, enlarged Meckelian fenestrae; 8, oblique glenoid of scapulocoracoid; 9, 32 or more presacral vertebrae; 10, sutural ridges along the midline sutures of the parietals and postparietals, and along the transverse parietal–postparietal suture; 11, tuskless vomers; 12, loss of skull-table cheek kinetism; 13, confluent Meckelian fenestrae; 14, 40 presacral vertebrae; 15, long prefrontal jugal suture excluding lacrimal from orbit; 16, ?deep descending flange of quadrate ramus of pterygoid; 17, ?chisel-shaped marginal teeth.

1973) in a distinct infraorder merely serves to balance the classification and conveys no additional information as to the relationships of the family.

The taxonomic results of this discussion can now be summarized in the following classification.

> Order   Anthracosauria
> Suborder   Anthracosauroideae
> Infraorder   Embolomeri
> Family   Proterogyrinidae
>   Anthracosauridae
>   Eogyrinidae
>   Archeriidae
> Infraorder   unspecified
> Family   Gephyrostegidae
> Infraorder   unspecified
> Family   Eoherpetontidae
> Suborder   Seymouriamorpha
> Family   Discosauriscidae
>   Kotlassiidae
>   Seymouriidae

Relationships of anthracosaurs

Until recently the generally accepted view of the interrelationships of Amphibia was that developed by Romer (1945, 1947, 1950, 1966). In the third edition of his *Vertebrate Paleontology* (Romer, 1966) the class Amphibia included three subclasses: Labyrinthodontia, Lepospondyli and Lissamphibia. The Labyrinthodontia embraced the orders Anthracosauria, Temnospondyli and Ichthyostegalia, while the Lepospondyli included the orders Aïstopoda, Microsauria and Nectridea. The living groups Anura, Apoda and Urodela comprised the Lissamphibia. However, during the last 15 years, and in particular since 1975, an increasing number of authors have begun to suspect that the three major amphibian groups are artificial (Brough & Brough, 1967; Thomson & Bossy, 1970; Carroll & Currie, 1975; Bossy, 1976; Panchen, 1977a, 1980; Gaffney, 1979; Carroll & Holmes, 1980; A. C. Milner, 1980; Gardiner, 1982, 1983; Smithson, 1982). The characters which in the past have been used to define the three groups are now either considered to be primitive for all tetrapods, for example compound vertebrae, labyrinthodont teeth and the absence of an otic notch, or are suspected of being acquired convergently, for example holospondylous lepospondyl vertebrae and pedicellate teeth, and the immediate relationships of the constituent orders are now disputed.

The relationships of anthracosaurs were recently discussed by Panchen (1980) following a preliminary description of a new specimen of the primitive amphibian *Crassigyrinus* from Cowdenbeath. He noted that while *Crassigyrinus* lacked the characteristic anthracosaur pattern of bones on the skull table, it exhibited a number of features which indicated close relationship with the Anthracosauria, for example tabular horns, distinct otic notches and ventrally complete pleurocentra (Panchen, 1980: 343), and he suggested that the suborders Palaeostegalia (*Crassigyrinus*: Panchen, 1973) and Anthracosauria

should be included in the order Batrachosauria. He also proposed that the loxommatids should be removed from the Temnospondyli (see also Smithson, 1982) and tentatively suggested that they may be immediately related to anthracosaurs. Although this suggestion was not incorporated within his formal classification he indicated in a cladogram (Fig. 31) that the Loxommatoidea may be the plesiomorphic sister-group of anthracosaurs, together forming the 'Neostegalia', which in turn was the sister-group of the Palaeostegalia. However, in the review Panchen did not consider the broader relationships of the Batrachosauria save to note (Panchen, 1980: 343) "that Batrachosauria, not Anthracosauria, is the collateral group of, and equal in rank to, the taxon Temnospondyli".
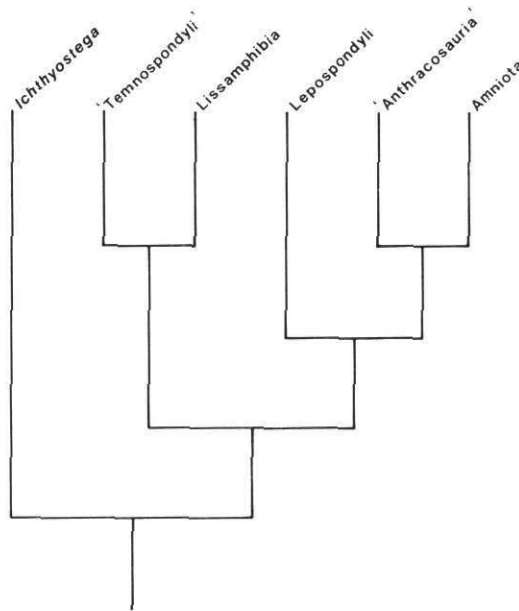

Figure 35. A phylogeny of the Amphibia. After Gaffney (1979).

The intrinsic relationships of Amphibia were briefly considered by Gaffney (1979) in a discussion of tetrapod monophyly. He accepted the traditional view that anthracosaurs were immediately related to reptiles (*contra* Panchen, 1970, 1972b, 1975, 1980—see below) and on the basis of the tabular–parietal contact and narrow vomers between the choanae he suggested that 'leopspondyls', anthracosaurs and amniotes constituted a monophyletic group (Fig. 35). However, the relationship is inconsistent with recent studies which have demonstrated that the order Lepospondyli is almost certainly polyphyletic (Thomson & Bossy, 1970; Bossy, 1976; A. C. Milner, 1980; Gardiner, 1982, 1983; Smithson, 1982) and the validity of the characters used to establish a relationship between 'lepospondyls' anthracosaurs and amniotes is therefore questionable. Subsequently, Gardiner (1982) presented a rather unorthodox scheme (Fig. 36) in which both the anthracosaurs and microsaurs were considered to be amniotes. The aïstopods and nectridea were thought to be

sister-groups, and the group which they comprise was thought to be immediately related to the three extant groups Apoda, Anura and Urodela (Lissamphibia). This grouping was referred to as the 'Division Amphibia' (Gardiner, 1982: 228) and was said to be the sister-group of the 'Division Amniota'. However, Gardiner's scheme was based on a series of characters which are considered by many authors to be primitive for all tetrapods, for example diplospondylous vertebrate (Panchen, 1977a), pentadactyl manus (Smithson, 1982), tripartite atlas (Panchen, 1972b) labyrinthodont teeth (Rosen *et al.*, 1981), and a stapes with enlarged base plate and stapedial foramen, which extends to the quadrate (Smithson & Thomson, 1982; Smithson, 1982). Consequently Gardiner's scheme of relationship is questionable and most of his groupings are probably artificial.

More recently, Gardiner (1983) modified these views following a re-examination of the structure of vertebrae in gnathostomes. He no longer considers Aïstopoda and Nectridea to be immediately related and proposes that the Nectridea alone are the sister-group of the Lissamphibia (Gardiner, 1983: fig. 15). However, as in his earlier scheme the characters used to support this relationship are either (1) present in other taxa and may have arisen
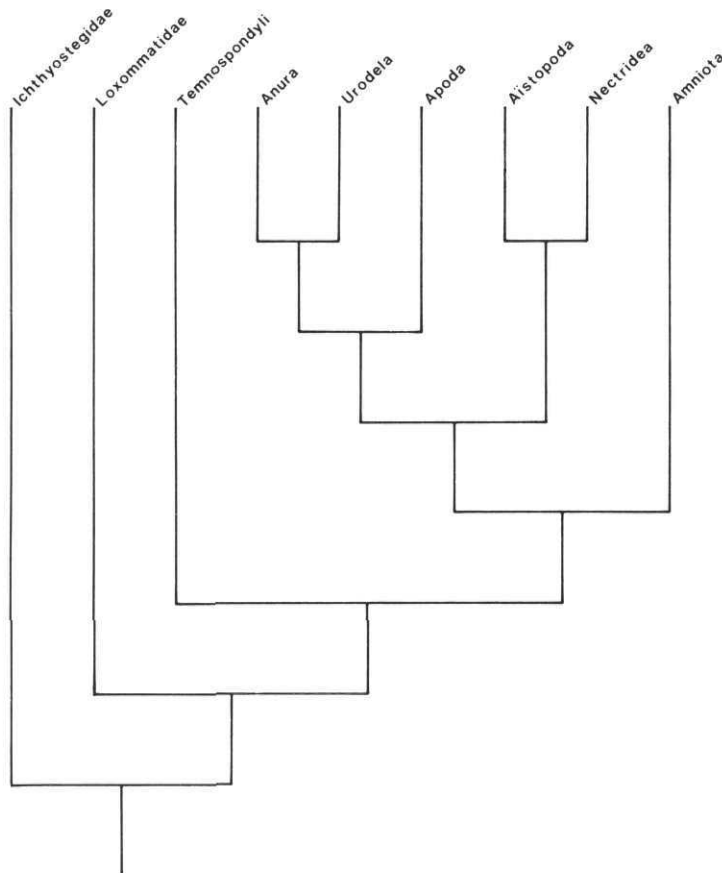

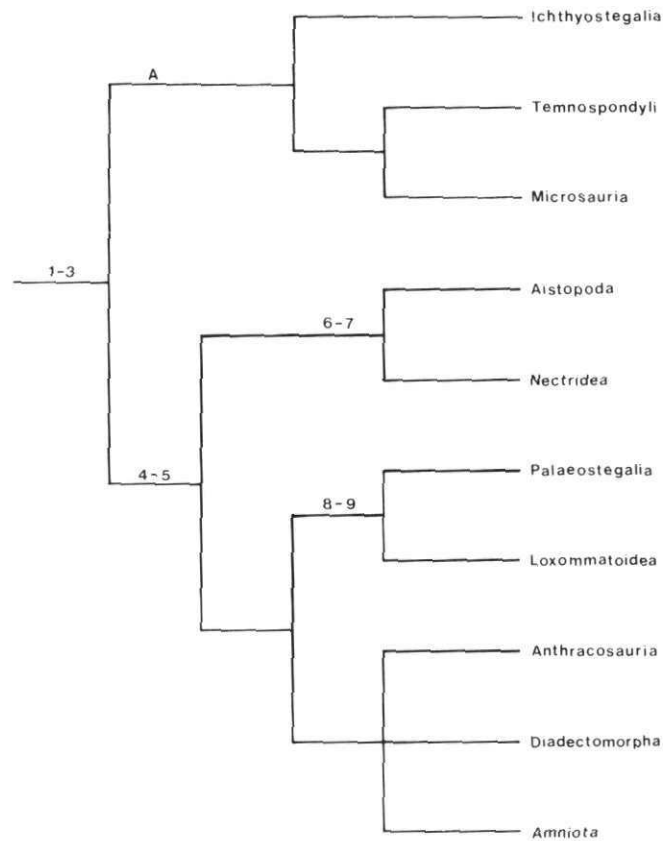Figure 36. A phylogeny of the Amphibia. After Gardiner (1982).

Figure 40. A phylogeny of the Amphibia. Numbered characters refer to following synapomorphies: 1, jugal quadratojugal suture; 2, carpus, tarsus and dactyly; 3, sacrum; 4, ventral otic fissure eliminated, cranial kinesis retained; 5, 'peg and socket' basal articulation mobile; 6, neural arch pedicels perforated by spinal nerves; 7, extra articulations above zygapophyses; 8, lanceolate teeth; 9, series of dentary tusks; A, see Fig. 37.

relationship between *Crassigyrinus*, loxommatids, anthracosaurs, diadectomorphs and amniotes is paraphyletic and parallels the problem of reptiles within the Amniota. While it is possible to diagnose Aves and Mammalia by autapomorphous characters, and individual groups within the Reptilia, for example Crocodilia and Pterosauria, the Reptilia itself cannot be diagnosed as a monophyletic group. A similar problem is evident on the other side of the dichotomy in that while microsaurs and temnospondyls share a number of derived characters, and microsaurs have a number of autapomorphies which characterize them as a monophyletic group, the temnospondyls cannot be adequately diagnosed.

In both cases the inability to diagnose the groups as monophyletic may stem from a paucity of characters: the postcranial skeleton of loxommatids is largely unknown and that of *Crassigyrinus* is presently being studied by Dr A. L. Panchen at Newcastle. In temnospondyls the difficulty lies in distinguishing characters which are common to the group as a whole from those which have developed within the many taxa which constitute the order. Most of our

ABBREVIATIONS USED IN FIGURES

ang	angular	pq. l	palatoquadrate ligament
art	articular	pra	prearticular
at	atlas neural arch	prf	prefrontal
ax	axis neural arch	prm	premaxilla
b. p	basal process of epipterygoid	prsp	presplenial
basi	basioccipital	psp	postsplenial
bas. p	basipterygoid process	pt	pterygoid
c. p	cultriform process	q	quadrate
cor	coronoid	qj	quadratojugal
d	dentary	r. pit	retractor pit
d. s	dorsum sellae	rad	radial condyle
ect	ectopterygoid	ret. p	retroarticular process
ectc	ectepicondyle	ri. h	humeral ridge
entc	entepicondyle	sn. c	supraneural canal
ex	exoccipital	scap	scapulocoracoid
f	frontal	scc	channel for semicircular canal
f. o	fenestra ovalis	sq	squamosal
fc. cap	facet for capitulum	st	supratemporal
fc. ex	facet on opisthotic for exoccipital	sur	surangular
fib	fibial condyle	supa. b	supraacetabular buttress
h. conc	humeral concavity	supa. n	supraacetabular notch
h. conv	humeral convexity	supc. f	supracoracoid foramen
il. b	iliac blade	supg. f	supraglenoid foramen
in. but	infraglenoid buttress	t	tabular
int. car. art	groove marking course of internal carotid artery	t. tub	tabular tuberosity
		tib	tibial condyle
intcon. g	intercondylar groove	tr. l	transverse line of the ilium
intcon. r	intercondylar ridge	ul	ulnar condyle
it	intertemporal	v	vomer
j	jugal	m. brach	position of brachialis muscle
l	lacrimal	m. corbrach	position of coracobrachialis muscle
m	maxilla		
Meck. fen	Meckelian fenestra	m. d. mand	position of depressor mandibulae muscle
n	nasal		
ob. f	obturator foramen	m. delt	position of deltoideus muscle
ot. cap	otic capsule	m. ischio	position of ischiotrochantericus muscle
p	parietal		
p-il. p	post-iliac process	m. lat. dor	position of latissimus dorsi muscle
pa	parasphenoid		
pal	palatine	m. pect	position of pectoralis muscle
pf	postfrontal	m. subcor	position of subcoracobrachialis muscle
po	postorbital		
pp	postparietal	m. sup	position of supinator muscle
pq	palatoquadrate	m. supracor	position of supracoracoideus muscle