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The cranial morphology and relationships of the aberrant Carboniferous amphibian *Spathicephalus mirus* Watson

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The skull of *Spathicephalus mirus* Watson, an amphibian from the Namurian, basal Upper Carboniferous, of Scotland is described. It shares with the Loxommatoidea a closed palate, palatal ornament and antorbital vacuities, and the family Spathicephalidae is recognized as the sister group of the Loxommataidae. A new diagnosis of the Loxommatoidea is presented together with one of the Spathicephalidae. An analysis of the functional morphology of the *Spathicephalus* skull suggests that it was incapable of rapid jaw closure required for catching fish. Instead it is proposed that *Spathicephalus* was a sluggish bottom-dwelling filter-feeder of small, soft invertebrates.

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ADDITIONAL KEY WORDS:—Carboniferous – Amphibia – anatomy – functional morphology – phylogeny.

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INTRODUCTION

Spathicephalus mirus was first described by Watson (1929) from material collected in the 1880s from the Namurian Limestone Coals at Loanhead, Midlothian. Knowledge of its anatomy was increased with the discovery by Stanley Wood in 1974 of fragmentary cranial remains in a richly fossiliferous bone bed at the Dora Open Cast site, near Cowdenbeath, Fife (Andrews *et al.*, 1977; Smithson, 1980a) in deposits contemporaneous with those at Loanhead. Known only from cranial material, *Spathicephalus* is one of the most unusual Carboniferous amphibians with a broad, flat, square-shaped skull and uniform dentition of delicate chisel-shaped teeth. Despite these aberrant features, Watson (1929) identified *Spathicephalus* as a loxommatid and included it in the superfamily Loxommatoidea (Romer, 1966; Loxommoideae Watson (1929)) along with three other genera, *Baphetes*, *Loxomma* and *Megelocephalus* from the Viséan and Westphalian of Europe and North America. This classification was generally accepted by subsequent authors but, following a major review of the Viséan and Westphalian taxa, (Beaumont (1977) divided the Loxommatoidea into two families. The Loxommatidae (Baphetidae of Milner & Lindsay, this volume) was retained for *Baphetes*, *Loxomma* and *Megalocephalus*, whilst *Spathicephalus* was placed in a new family, the Spathicephalidae. This classification is followed here.

The first aim of this paper is to present a detailed description of the skull of *Spathicephalus mirus*. Specimen drawings were prepared either from photographs or with the aid of a camera lucida. The restorations of the skull were based on a plasticine model reconstructed using data from the three principal specimens from Loanhead. The second aim is to analyse the jaw mechanism of *Spathicephalus* and present new interpretation of its feeding biology.

Abbreviations preceding specimen numbers refer to the following collections: BMNH, Department of Palaeontology, Natural History Museum, London; NMS, Department of Geology, National Museums of Scotland, Edinburgh; SM, Sedgwick Museum, Cambridge.

MATERIAL AND METHODS

The specimens used in the description of *Spathicephalus* are listed below.

From Rumbles Ironstone, called Loanhead Ironstone No. 2 by Traquair (1903) (see Andrews & Brand, 1991), Loanhead District, near Edinburgh, Lothian Region, Scotland.

- | | |
|-------------------|--|
| NMS G 1950.56.3. | Skull in palatal exposure, incomplete anteriorly. (Holotype). |
| NMS G 1950.56.4. | Ventral surface of incomplete skull, preserved in part as natural mould. |
| NMS G 1950.56.5. | Skull table and right cheek region, associated with part of right jaw ramus. |
| NMS G 1885.50.73. | Jaw fragment with teeth. |
| NMS G 1885.50.74. | Jaw fragment with teeth. |
| NMS G 1886.90.8. | Maxilla. |
| SM E19868. | Anterior part of paired jaw rami. |

From Dora Bone Bed, Dora Open Cast site, Cowdenbeath, Fife Region, Scotland (see Smithson 1985a,b).

BMNH R 10951. Anterior part of right jaw ramus.

NMS G 1993.56.5. Isolated frontal bones.

NMS G 1994.103.1. Anterior part of right jaw ramus.

The description of the skull of *Spathicephalus* is based largely on the three most complete specimens from the Loanhead district, NMS G 1950.56.3., NMS G 1950.56.4, and NMS G 1950.56.5. Watson (1929) referred to these specimens as A, B, and C respectively. All three are dorsoventrally compressed. NMS G 1950.56.3 and NMS G 1950.4 are exposed in ventral view: only in NMS G 1950.56.5 is both the dorsal and ventral surface of the skull exposed.

NMS G 1950.56.3 and NMS G 1950.56.4, are mounted in plaster. Measurements from the two skulls suggest that the anterior and posterior portions of NMS G 1950.56.3 have not been mounted correctly and the gap between the two parts is too wide (Fig. 1).

The specimens were prepared mechanically with dental mallet, mounted needles and an airbrasive machine. A solution of 'perspex' dissolved in chloroform was used to strengthen and repair breaks in specimens.

ABBREVIATIONS

a	angular	pal	palatine
b.p.	basal process	pf	postfrontal
basi	basioccipital	po	postorbital
bas.p	basipterygoid process	pp	postparietal
ch	choana	prf	prefrontal
cor	coronoid	prm	premaxilla
d	dentary	prsp	presplenial
ect	ectopterygoid	psp	postsplenial
f	frontal	psy. p	parasymphysial plate
j	jugal	pt	pterygoid
l	lacrimal	q	quadrate
l.l.c	lateral line canal	qj	quadratojugal
m	maxilla	sq	squamosal
n	nasal	st	supratemporal
occ	occiput	stap	stapes
ot. cap	otic capsule	sa	surangular
p	parietal	t	tabular
pa	parasphenoid	v	vomer

DESCRIPTION

Class Amphibia

Superfamily Loxommatoidea (Watson, 1929)

Diagnosis. Amphibians with well ossified skulls. No trace of lateral kinetic line. Broad squamosal–supratemporal suture; squamosal–tabular suture precluded by temporal

notch. Large antorbital fenestra surrounded by jugal, lacrimal and prefrontal. Lacrimal with distinct v-shaped notch in posterior edge. Palate closed, pterygoids sutured along midline. Quadrate ramus of pterygoid ornamented with irregular shaped pustules and ridges. Well-ossified braincase. Broad otic capsules securely attached to skull roof. No contact between occipital arch and postparietals. Long parasphenoid which contacts the occiput.

Family Spathicephalidae Beaumont, 1977

Diagnosis. Loxommatoids with broad, squarish skull outline. Skull length and breadth approximately equal; largest known is 220 mm long. Snout and cheek region greatly expanded. Orbits close to midline and far back in skull (three quarters of total skull length pre-orbital). Orbit margin extends forward to form a large antorbital vacuity (length of orbit plus antorbital vacuity $c.$ quarter of total skull length). Frontals enter orbit margin, preventing contact between prefrontal and postfrontal. Skull table extremely short. No intertemporal bone. Laterally expanded supratemporal forms anterior border of temporal ('otic') notch. Small, laterally expanded tabular with horns. Skull table and cheek firmly sutured. Premaxillary, maxillary and dentary teeth small, numerous and chisel-shaped. The vomer and parasymphysial plate bear a row of smaller teeth. No denticles on palatal bones or coronoids. Pterygoids sutured along midline and appear to be firmly united with basiptyergoid processes. No interptyergoid vacuities. Pterygoids, vomers and parasphenoid ornamented with fine ridges and pits. Otic region of braincase well ossified and firmly attached to skull roof. No post-temporal fossae. Broad parasphenoid with widely separated basiptyergoid processes. Short, narrow cultriform process. Robust, plate-like stapes.

Genus *Spathicephalus* Watson, 1929

Type species: *Spathicephalus mirus* Watson, 1929

Diagnosis. As for family.

Spathicephalus mirus Watson, 1929

Diagnosis. Spathicephalid with pustular ornament and well developed tabular horn.

Holotype. NMS G 1950.56.3 Skull in palatal exposure, incomplete anteriorly. Preservation includes posterior palate and braincase.

Type horizon and locality. Rumbles Ironstone, called Loanhead Ironstone No. 2 by Traquair (1903) (see Andrews & Brand, 1991), upper part of Limestone Coal Group, Namurian A, Upper Carboniferous, Loanhead district, near Edinburgh, Lothian Region, Scotland.

Distribution. Lothian and Fife Regions, Scotland.

Range. E₁ zone of Namurian A stage, Upper Carboniferous.

Remarks. A second species, *S. pereger* (Baird, 1962) has been described from the Upper Mississippian (lower Namurian of Europe) of Nova Scotia. The type specimen consists of the right half of a skull table and interorbital region, preserved as a natural mould. The pattern and shape of the bones are similar to those of the type species, but they differ in having reticulate dermal ornament of the type found in loxommatids, colosteids and most temnospondyls, rather than the pustular ornament of *S. mirus*.

General skull morphology

The skull of *Spathicephalus* is extremely broad and flat, and is quite unlike that of any other known Palaeozoic amphibian. It most closely resembles the skull of the aberrant temnospondyl *Sclerothorax hypselonotos* (Huene, 1932) from the Lower Triassic of Germany. The maximum length (premaxilla to quadrate) of the largest specimens NMS G 1950.56.3 (Fig. 1) and NMS G 1950.56.4 is 220 mm and the maximum width is approximately the same. The isolated frontals NMS G 1993.56.5 are from a similar sized skull. NMS G 1950.56.5 is somewhat smaller with an estimated maximum width of 160 mm. The snout is broad, flat and bluntly rounded. The ratio of width at the premaxillary–maxillary suture to that across the quadratojugals is 2:3.

All the material has been compressed post mortem, but the least flattened skull, NMS G 1950.56.5, is 21 mm high. In none of the specimens are the external nares preserved. The orbits lie close to the midline and far back in the skull restricting the extent of the skull table and promoting the development of long, broad bones in the pre-orbital region which makes up nearly three quarters of the length of the skull. The orbits face almost entirely dorsally and are barely visible in lateral view. The anterior extension of each orbit is gently curved, producing a long, bluntly crescent-shaped opening on either side of the skull roof. In outline they are quite different to the keyhole-shaped orbits of loxommatids (Beaumont, 1977).

The ornamentation of the dermal skull roofing bones in *S. mirus* is unlike that of most other Palaeozoic amphibians. The bones display a series of pustules and stout ridges, the exact reverse of the reticulate or ‘honeycomb’ ornament of colosteids, loxommatids and temnospondyls. The pustules radiate out from the ossification centres and form ridges along the zones of elongation. This type of ornament is also found in the skull of *Ichthyostega* (Jarvik, 1980) and in all plagiosaurs with the exception of *Plagiosternum* (Panchen, 1959) and is comparable with that found in some sarcopterygian fish, for example the osteolepiform *Eusthenopteron wangsji* (Jarvik, 1952) and the lungfish *Uronemus spendens* (T.R.S., pers. obs.)

In none of the skulls is there evidence of lateral line canal system, but a deep groove for the mandibular canal is present on the lower jaw specimens.

Dermal skull roof

The pattern of bones forming the skull roof is shown in Figures 2, 4 and 7 and restored in Figure 5. The anterior portion of the broad snout is formed from the premaxillae, which meet in a strongly interdigitating midline suture. Each premaxilla has a short postero-lateral maxillary contact as in other early tetrapods, and they are thus included in the general lateral skull expansion and are not confined to the tip of the snout. Paired internasal ossifications, present in the loxommatids (Beaumont, 1977) are absent in *Spathicephalus*. The nasal bones are exceptional only in their great expansion, being extremely broad anteriorly. They narrow considerably posteriorly where they suture with the frontal bones in the orbital region. A groove, possibly for the olfactory nerve or the dorsal attachment of the sphenethmoid, is visible on the ventral surface of the nasals in both NMS G 1950.56.3 and NMS G 1950.56.4.

The frontals narrow considerably in their mid-region where they form a narrow

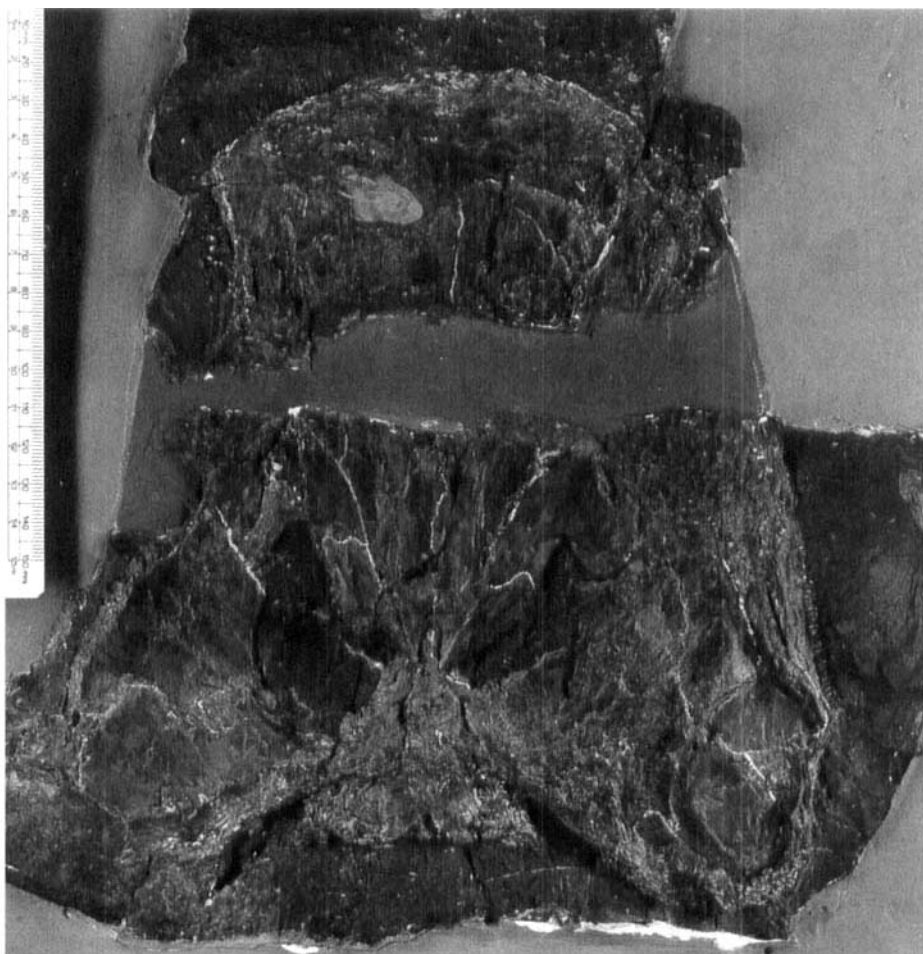


Figure 1. *Spathicephalus minus* Watson, holotype skull NMS G 1950.56.3, ventral view. ($\times 0.5$)

bar between the orbits. The mesial edge of this interorbital bar is thickened to form part of the orbital margin, broadly separating the small triangular prefrontal and the narrow postfrontal bones. Thus each orbit is surrounded by six bones: frontal, prefrontal, postfrontal, postorbital, jugal and lacrimal. Since there is no ingrowth of the jugal, the antero-lateral border of the orbit is not demarcated as in loxommatids and the vacuity is kidney-shaped.

Most of the sutures of the skull table are reasonably clear in NMS G 1950.56.5 and have been confirmed in part from a latex peel of the natural mould of this region in NMS G 1950.56.4. The structure is essentially similar to that of the *Spathicephalus pereger* (Baird, 1962). The temporal series consists only of a laterally expanded supratemporal, which forms the anterior border of the 'otic' or temporal notch and firmly unites the skull table and cheek region, and a small tabular. There is no intertemporal bone. The tabular has a small boss on its posterior similar to that present on the tabular colosteids (Smithson, 1982), and an extended postero-lateral process, pointing towards the quadrate, which resembles the tabular horn of

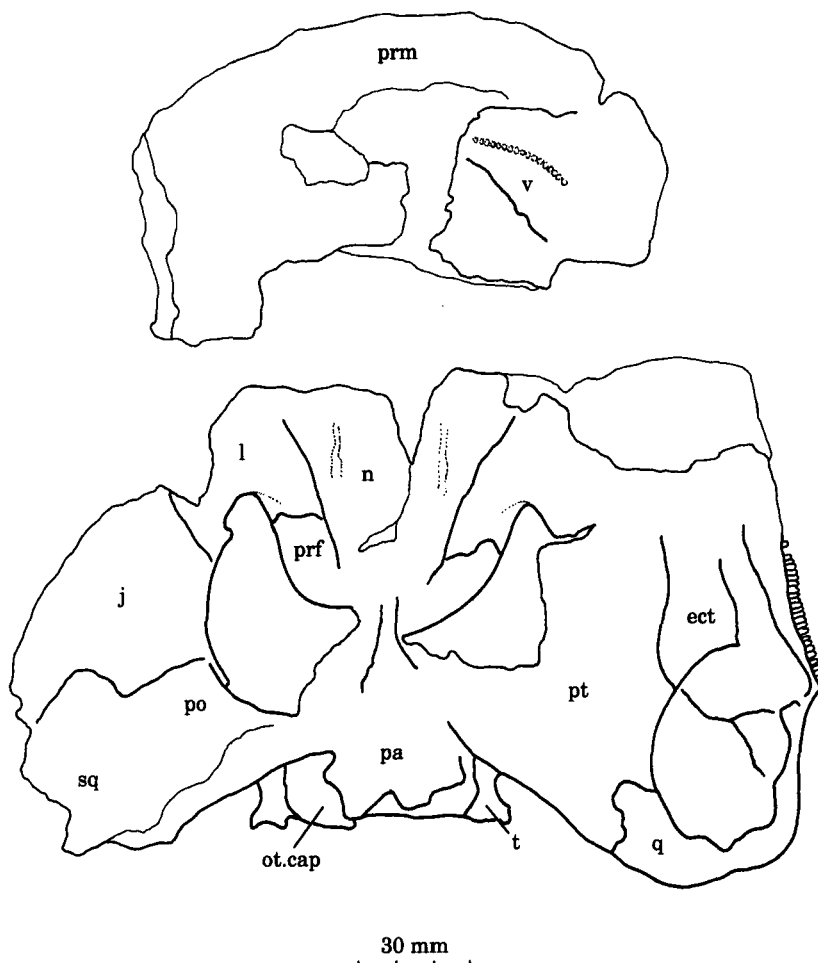


Figure 2. *Spathicephalus mirus* Watson, holotype skull NMS G 1950.56.3, ventral view ($\times 0.5$). For list of abbreviations, see p. 189.

embolomeres (Clack, 1987). This latter feature is far more pronounced in *S. mirus* than *S. pereger*.

Watson (1929) believed that the pineal foramen was absent in *S. mirus*, but a normal foramen is described by Baird (1962) in *S. pereger*. Clearing of the dorsal surface of NMS G 1950.56.5 revealed a normal, if rather small, pineal opening (diameter 2 mm) anteriorly placed in the midline suture between the parietal bones (Fig. 7) a feature confirmed from a latex peel of this region in NMS G 1950.56.4 (Fig. 4). The postparietals are similar in size to the parietals. They are firmly attached to the underlying braincase and there is no evidence of post-temporal fossae. Indeed, much of the dorsal surface is exposed behind the postparietals as in many anthracosaurs, e.g. *Eoherpeton* (Smithson, 1985b) and *Palaeoherpeton* (Panchen, 1964), such that it is the braincase that forms the posterior edge of the skull table rather than the postparietals.

Greatly expanded jugal and lacrimal bones form most of the lateral snout region in front of the orbits. Only part of the suture between these two bones is known

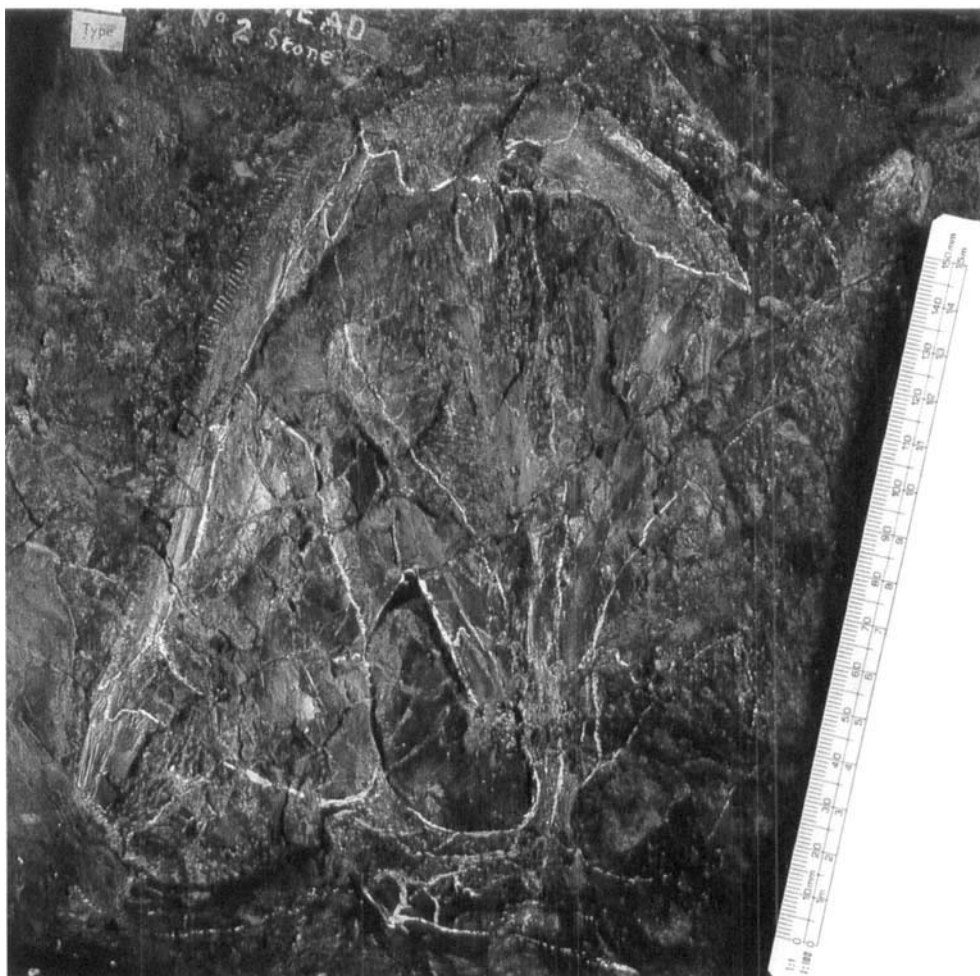


Figure 3. *Spathicephalus mirus* Watson, skull NMS G 1950.56.4, ventral view, palate and braincase missing ($\times 0.66$).

with certainty, but in restoration it has been continued to reach the maxilla as in other early tetrapods. The ventral surface of each bone is exposed in NMS 1950.56.3 and NMS G 1950.56.4. They lack the ventrally projecting shelf which unites the skull roof and palate in loxommatid genera (Beaumont, 1977) and thus there is no solid lateral wall to the antorbital vacuity.

The maxilla forms the lateral jaw margin and is a long thin ossification never exceeding 10 mm in width. Unlike most other early tetrapods there is no apparent increase in maxillary depth anteriorly. This is probably due to the uniformity of tooth size throughout the series. The posterior border of the maxilla contracts the quadratojugal, which is a long narrow bone, since the large squamosal fills most of the posterior cheek region. The quadratojugal appears to be firmly sutured to the quadrate.

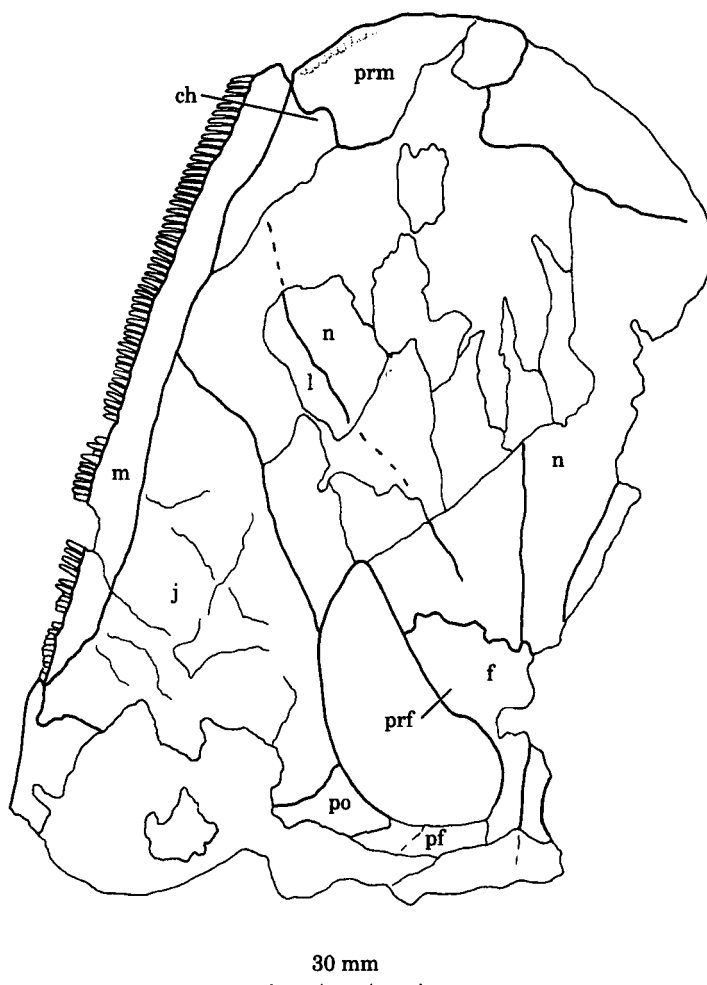


Figure 4. *Spathicephalus mirus* Watson, skull NMS G 1950.56.4, ventral view, palate and braincase missing ($\times 0.66$).

Palate

Together the three partial skull specimens from Loanhead give some indication of the structure of all elements of the palate, apart from the palatine. This information is presented in the tentative reconstruction (Fig. 6A). *Spathicephalus* has a closed palate, the basal articulation appears to be fused and the flat palatal bones form a fairly rigid structure. The choanae are elongate vacuities of some 20 mm in length, lying close to the lateral margin of the snout and as in other early tetrapods each is surrounded by the premaxilla, maxilla, vomer and palatine. There is no anterior palatal fenestra. The subtemporal fossae are relatively small.

The surfaces of the palatal bones are unusual. They lack denticles and instead bear irregularly shaped pustules and ridges, rather like the dermal ornament on a diminutive scale, but far less regular in its arrangement. Similar ornamentation is found on the quadrate ramus of the pterygoid of loxommatids but is unknown in other early tetrapods.

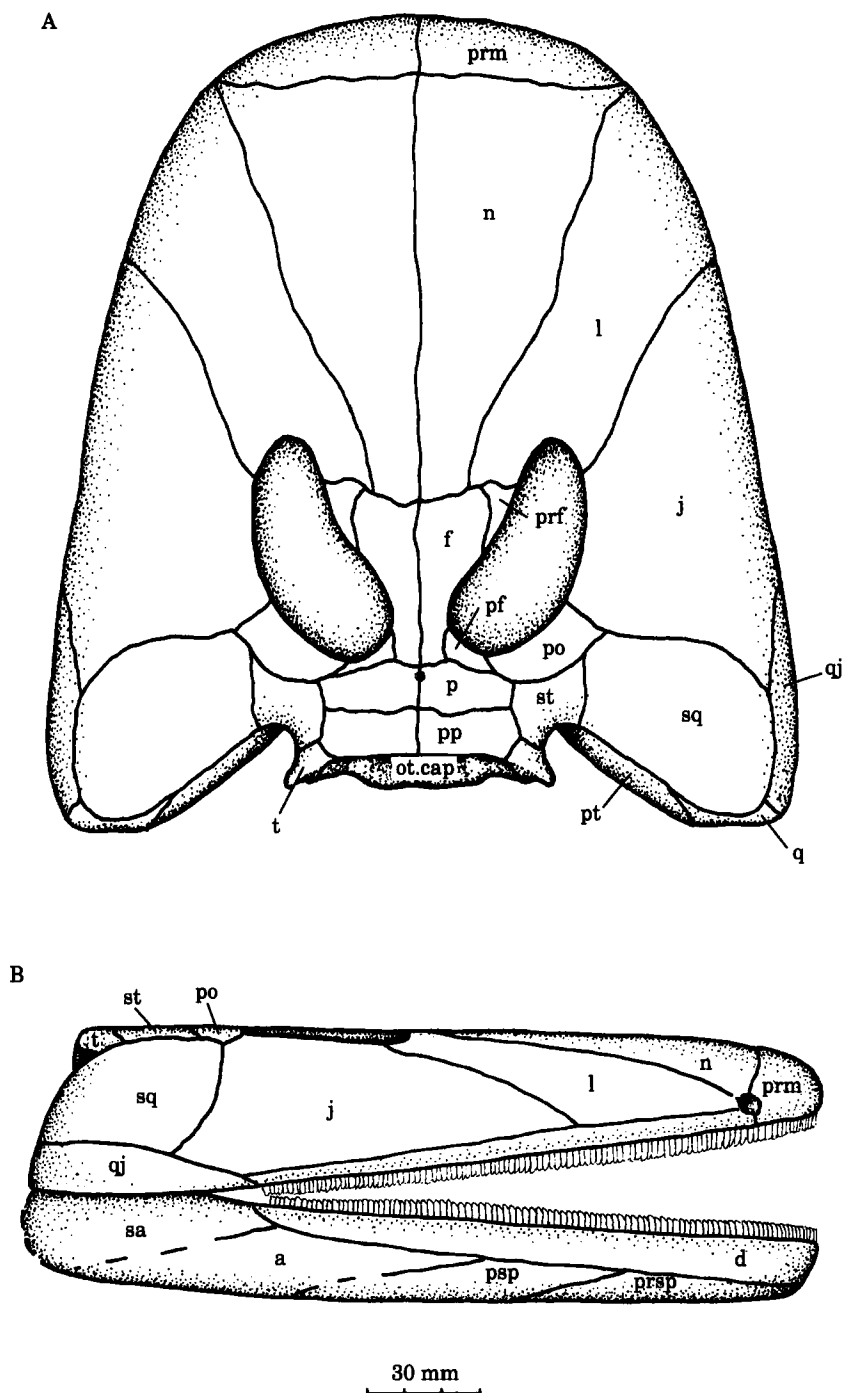


Figure 5. *Spathicephalus mirus* Watson, restoration of skull. A, dorsal view; B lateral view ($\times 0.5$).

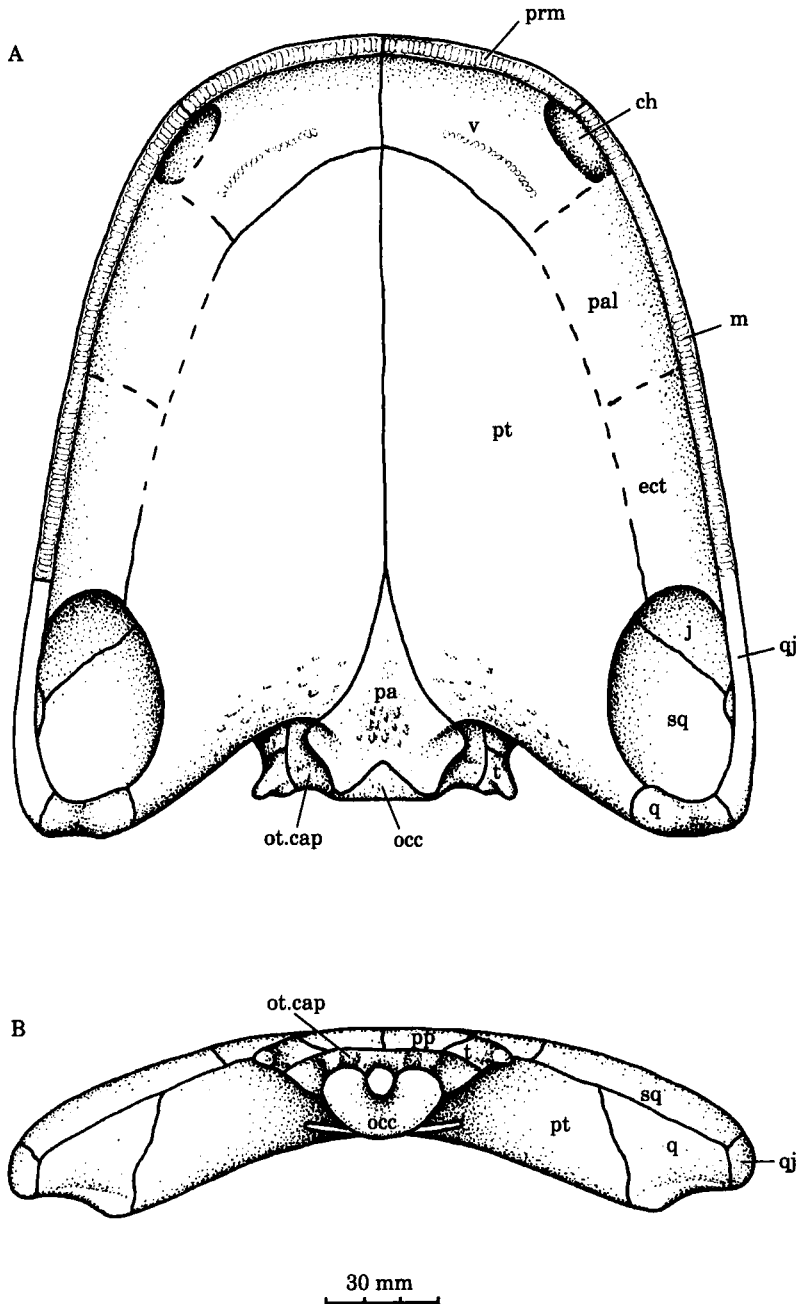


Figure 6. *Spathicephalus mirus* Watson, restoration of skull. A, ventral view; B, occipital view ($\times 0.5$).

The premaxillae are uncomplicated. They lack the ventral midline buttresses that occur in loxommatids and, apart from the tooth row, have little exposure on the palatal surface. They suture with the maxillae below the choanae. The maxillae form most of the lateral margin of the palate. Each extends as a tooth-bearing ridge of uniform width to the quadratojugal. This bone forms the lateral margin of the

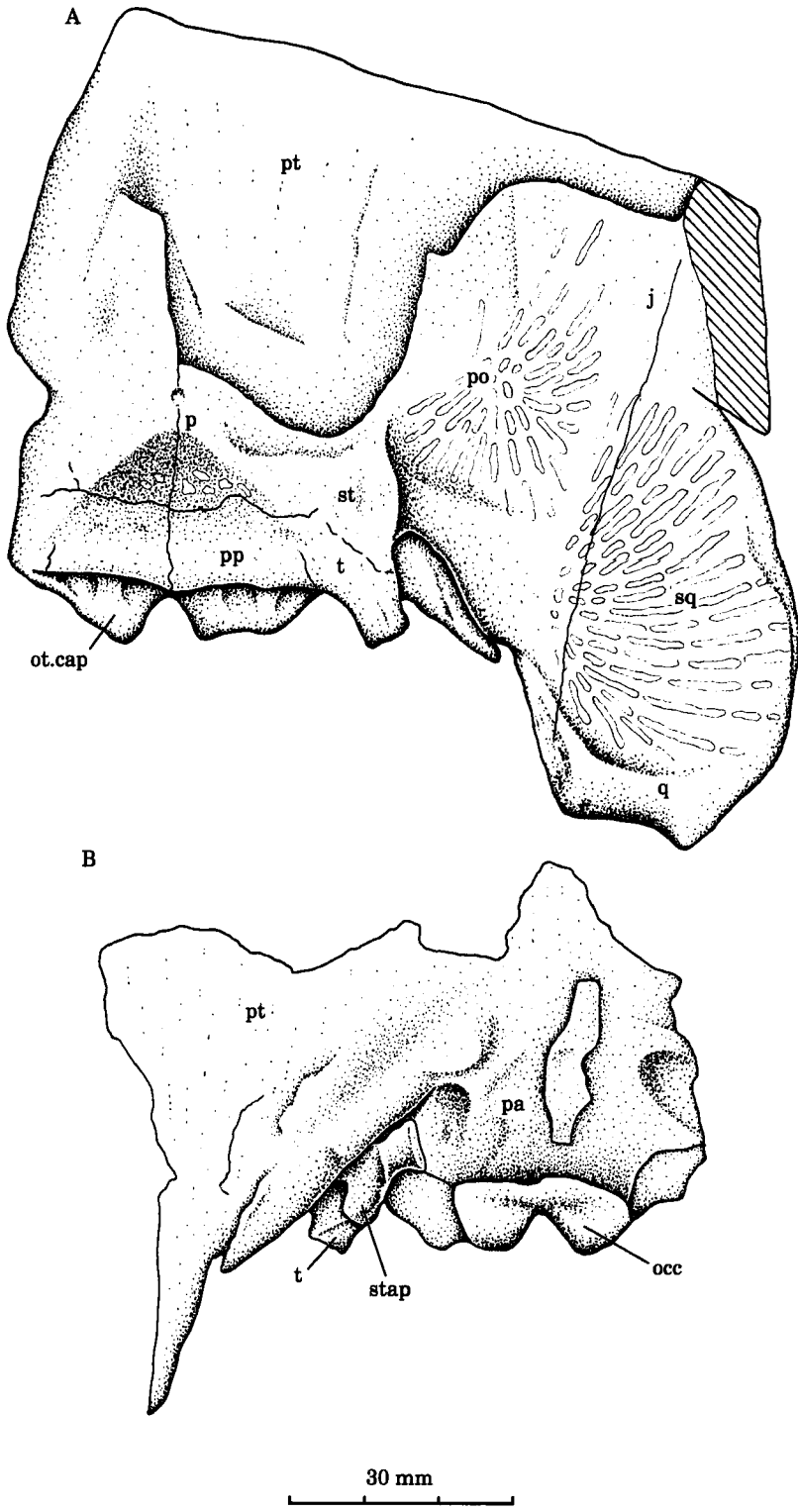


Figure 7. *Spathicephalus mirus* Watson, incomplete skull NMS G 1950.56.5. A, dorsal view; B, ventral view ($\times 1$). Broken bone hatched.

supratemporal fossa, sutures with the quadrate and contributes to the jaw articulation.

Part of the right vomer is preserved in NMS G 1950.56.3 the interdigitating suture with the ptergoid being clearly visible. The broken bases of a row of small teeth form an arc approximately parallel with that of the premaxilla midway between the edge of the choana and the pterygoid.

The palatines are missing in all specimens. However, part of the ectopterygoid is present in NMS G 1950.56.3. It is a long narrow bone which forms the anterior edge of the subtemporal fossa. The bone surface is much smoother than that of the other palatal elements although laterally it is badly eroded and small depressions along the edge of the ectopterygoid superficially resemble tooth sockets.

Large paired pterygoids form most of the area of the palate. Their structure is known incompletely from NMS G 1950.56.3 and from both dorsal and ventral exposure in NMS G 1950.56.5. The condition of the basal articulation differs from that of other early tetrapods in that the palate is apparently fixed in this region. On the palatal surface of NMS G 1950.56.5 the pterygoid and parasphenoid can be seen to suture around the rim of the basal process. The suture has been forced slightly apart by compression in NMS G 1950.56.3 to expose a continuous core of spongy bone formed presumably from the basisphenoid and the epipterygoid. Immediately in front of this region the pterygoids in NMS G 1950.56.5 are sutured. There is no evidence of interpterygoid vacuities.

Behind the basal articulation the quadrate ramus of the pterygoid extends posteriorly at an angle of 45° to the midline to contact the quadrate. Its lateral border forms the inner margin of the subtemporal fossa and dorso-mesially it sutures with the squamosal.

The available material of *Spathicephalus* provides little information on the structure of the palatoquadrate. The epipterygoid is either lost or compressed between the skull roof and palate. The palatal exposure of the quadrate in NMS G 1950.56.3 shows the articular surfaces very clearly. The rounded mesial articular face is extremely pronounced and forms a stout buttress which projects ventrally well below the lateral margin of the skull. Its surface is distinct from, rather than being continuous with, the lateral, strap-like articular face.

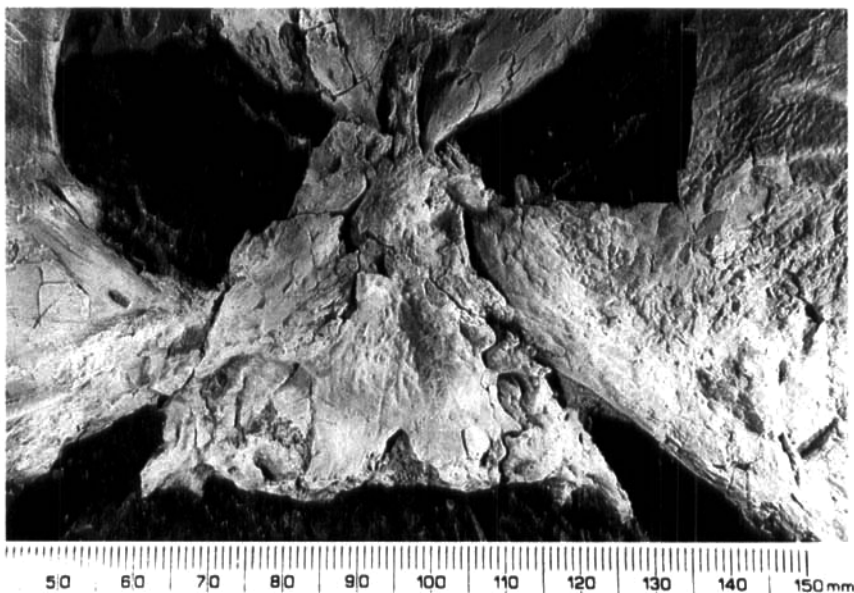
Parasphenoid and braincase

The otic region of the braincase is preserved in NMS G 1950.56.3 and NMS G 1950.56.5 (Fig. 7B, 8). In both specimens the bones forming the braincase have been crushed and the cavum cranii closed. Neither specimen is complete but together they provide sufficient data to allow reconstruction of the braincase within the palatal and occipital views of the skull (Fig. 6).

The otic-occipital region of the braincase of *Spathicephalus* closely resembles that of loxommatids (Beaumont, 1977) and anthracosaurs like *Archeria* (Holmes & Clack, 1988), *Eoherpeton* (Smithson, 1985b) and *Pholiderpeton* (Clack, 1987). It has broad, well ossified otic capsules, securely attached to the overlying bones of the skull roof, a broad parasphenoid which extends posteriorly to the level of the skull table, and a single element forming the occipital condyle which, unlike the condition in colosteids and temnospondyls (Smithson, 1982), makes no contact with the postparietals. There is no evidence of post-temporal fossae.

The parasphenoid is beautifully preserved in NMS G 1950.56.3. Most of its

A



B

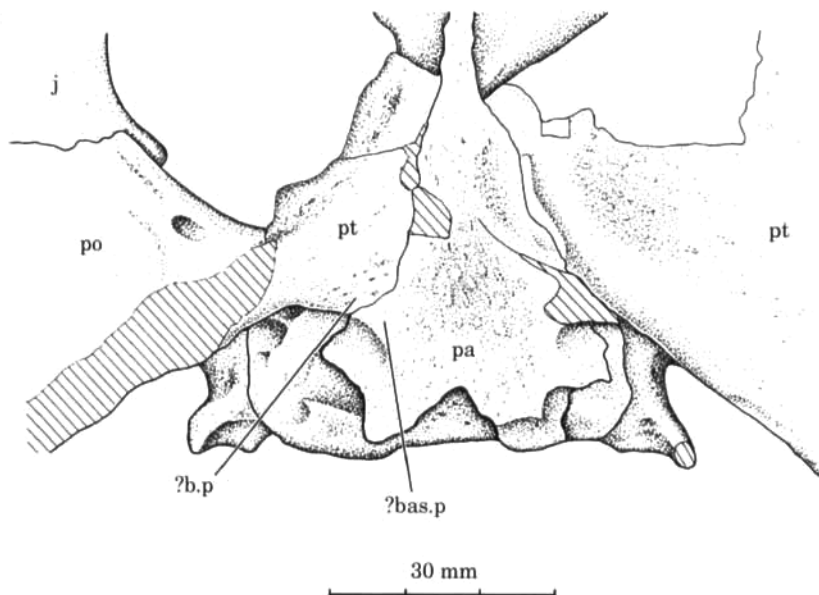


Figure 8. *Spathicephalus mirus* Watson, NMS G 1950.56.3. A, otico-occipital region of braincase, whitened with ammonium chloride; B, drawing of specimen ($\times 1$). Broken bone hatched.

ventral surface is ornamented with the same irregular pustules and ridges found on the bones of the palate. There are no denticles. The cultriform process is missing but the remaining portion of bone underlies the interorbital region and the skull table. It is a broad bone and reaches the maximum width of 34 mm at the level of the temporal notch. In this region it forms the floor of the fenestra ovalis. The bone

gently tapers anteriorly to a minimum width of 4 mm at its broken end. It probably extended forward above the pterygoids to form a cultriform process which supported the sphenethmoid region of the braincase. Posteriorly the parasphenoid is approximately w-shaped. In NMS G 1950.56.5 the medial portion is securely attached to the occiput. This has become detached and lost in NMS G 1950.56.3. However, on both specimens the lateral edge of the bone has nothing to attach to and there appears to be a large unossified area in the wall of the braincase directly behind the fenestra ovalis.

The basiptyergoid process is expanded laterally and ensheathed by the parasphenoid. In both specimens the region or the basal articulation is crushed and cannot be described with total confidence. However, there is evidence from each skull that the parasphenoid and pterygoid are sutured, as in Permian and Triassic temnospondyls (Milner, 1990) thus 'fixing' the palate and preventing movement on the basal process.

The otic capsules are well preserved in both specimens but little anatomical detail can be observed as they are concealed ventrally by the parasphenoid and quadrate rami of the pterygoids and dorsally by the bones of the skull roof. However, because of the truncated skull table they have unusual proportions; they are broad but very short. In NMS G 1950.56.3 they have a maximum width of 49 mm and estimated maximum length of 20 mm giving a ratio of 5:2. In NMS G 1950.56.5 the proportions were similar. This compares with a width to length ratio of 3:2 in *Eoherpeton* (Smithson, 1985b), and 4:3 in *Loxomma* and *Megalocephalus* (Beaumont, 1977). The capsules are firmly attached to the supratemporals, tabulars and postparietals. In NMS G 1950.56.5 the region of the braincase can be observed in both dorsal and posterior view, and there is no evidence of post-temporal fossae extending forward between the roof of the otic capsules and the tabulars and postparietals. Indeed, the posterior edge of the skull table is slightly emarginated above the capsules, as it is in antracosaur, which may account for the lack of post-temporal fossae (Panchen [in] Smithson, 1985b:327).

The occiput is preserved in NMS G 1950.56.5. It has been slightly displaced from its natural position following dorso-ventral crushing of the skull but appears to be largely intact. In posterior view it is a broad, crescent-shaped element, excavated medially to form a deeply concave articulating surface. Along its dorsal edge is a v-shaped notch marking the boundary of the foramen magnum. Sutures are absent and separate exoccipital and basioccipital bones cannot be distinguished.

Stapes

A right stapes is preserved in articulation with the braincase in NMS G 1950.56.5. (Fig. 7B). Post mortem compression of the skull apparently caused some rotation of the bone such that its dorsal surface rests against the underside of the tabular. In addition, the quadrate ramus of the pterygoid has been forced backwards concealing part of the ventral surface of the stapes. Despite this, the stapes appears well preserved although unfortunately it has been slightly damaged during preparation. The stapes of *Spathicephalus* closely resembles those of *Acanthostega* (Clack, 1989) and *Greerpeton* (Smithson, 1982). It is expanded proximally to form a large foot plate which sits firmly within the fenestra ovalis. Behind this, the bone is slightly constricted and is bisected by a prominent ridge which extends antero-posteriorly to separate

the foot plate from the broad, flattened distal region. It is likely that in its natural orientation within the skull this distal portion rested against the quadrate ramus of the pterygoid as it does in *Greererpeton*. The edge of the distal plate is unfinished and probably continued in cartilage. Unfortunately, one of the characteristic features of the stapes of early tetrapods, the stapedia foramen, is concealed in this specimen by surrounding bones of the skull.

Lower jaw

The only associated lower jaw material is on the same block as the skull NMS G 1950.56.5. Parts of the dentary, angular and postsplenial are preserved. The jaw itself was evidently large and shallow with a maximum depth of 22 mm in this specimen. Its lateral face bears the ridges and pustular ornament present on other dermal bones of this species. The close-set spatulate teeth are identical to those in the upper jaw (see 'Dentition' below).

Three isolated specimens provide information on the anterior region of the lower jaw. One specimen from Loanhead, SM E19868, shows the symphyseal region of both jaw rami preserved from the mesial surface. The other two from the Dora Bone Bed, BMNH R. 10951 (Fig. 9) and NMS G 1994.103.1 are the anterior ends of two different right jaw rami. Each has been fully prepared from the matrix.

In *Spathicephalus* the symphyseal region is u-shaped, mirroring the skull in outline. The dentaries and presplenials appear to be firmly united at the symphysis and it is unlikely that any movement was possible around this region. However, it is clear from both BMNH R. 10951 and NMS G 1994.1 that the symphysis is undeveloped and lacks the thickening or elaborate rugosities observed in the lower jaws of many early tetrapods, e.g. *Greererpeton* (Smithson, 1982), *Megalocephalus* (Beaumont, 1977) and *Pholiderpeton* (Clack, 1987; Panchen, 1972).

The dentary is unremarkable. Externally it bears a delicate ornament of fine ridges and grooves which develop into slightly coarser pits just below the tooth row. It has a straight uncomplicated suture with the presplenial. This bone carries the mandibular lateral line canal. For most of its length it is carried in an open groove, but anteriorly this is bridged to produce a series of pits. The external surface of the presplenial has the characteristic pustular ornament and internally it is pierced by a number of small foramina. Between the dentary and presplenial on the dorsal surface of the jaw are two bones. The most anterior of these is a parasymphysial plate, behind which is the anterior coronoid. The parasymphysial plate (adsymphysial plate of Godfrey & Holmes (1989)) is a long, narrow triangular-shaped bone and is particularly well preserved in BMNH R. 10951 (Fig. 9A, B). It has a simple straight suture with the presplenial and a more elaborate interdigitating suture with the dentary. Along its medial edge it bears a tooth row (see Dentition below) which extends posteriorly for approximately three quarters of the length of the bone. The extent of the tooth row is largely obscured in dorsal view but is very clear in mesial view. The long narrow anterior coronoid is featureless apart from a fine ornamentation of ridges and grooves. In no specimen is the prearticular preserved.

Dentition

The dentition of *Spathicephalus* is one of the most important characters which distinguishes it from the majority of other early tetrapods. It also provides an easily

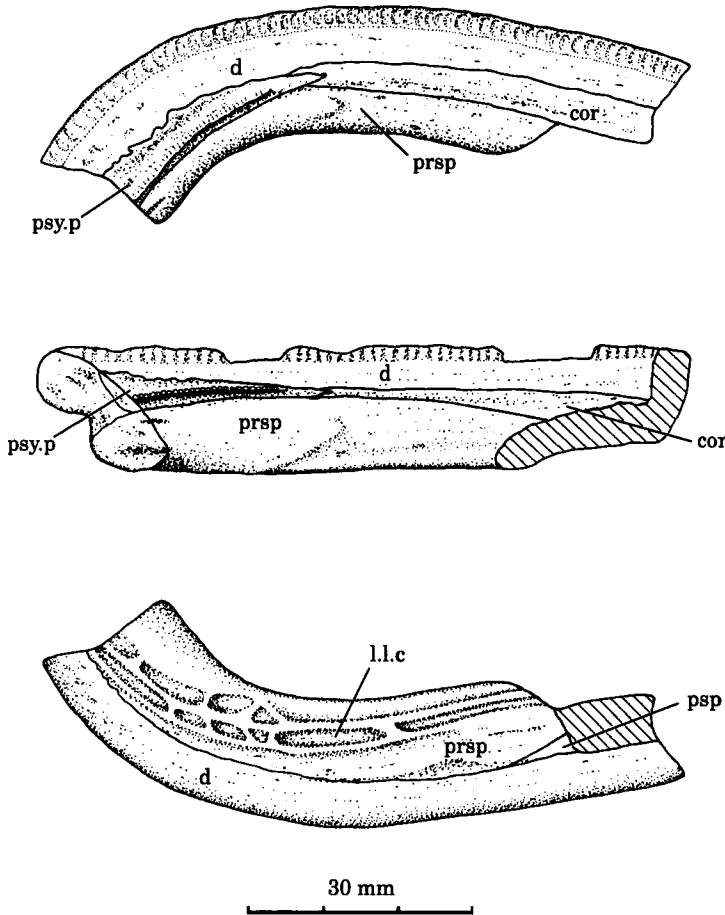


Figure 9. *Spathicephalus mirus* Watson. Anterior part of right jaw ramus BMNH R. 10951. A, dorsal view, B, mesial view, C, ventral view ($\times 1$). Broken bone hatched.

recognized feature by which to identify fragmentary cranial remains. The teeth are small, chisel-shaped and extremely numerous. They most closely resemble those of the Permian embolomere *Archeria* (Holmes, 1989) but are also superficially similar to the teeth of adelogyrinids from the Viséan and Namurian of Scotland (Smithson, 1980a, Andrews & Carroll, 1991). The marginal teeth form a continuous band around the anterior and lateral skull margins, while those of the vomer and parasymphysial plate apparently formed a second band inside and parallel to the first. There are no palatal tusks.

All the premaxillary teeth are broken in the available specimens of *Spathicephalus* but in NMS G 1950.56.4 the bases of the teeth are preserved with spaces for approximately 32. In the same skull, the right maxilla is essentially complete (Fig. 10). Approximately 95 teeth are present. All are closely packed, of equal size and apparently none is missing, apart from where part of the maxilla was lost during collection of the specimen. Thus, the tooth row presents an almost continuous 'biting' surface (see below: mode of life of *Spathicephalus*) with few, if any, replacement pits. On the right vomer of NMS G 1950.56.3, a row of 20 or more closely packed

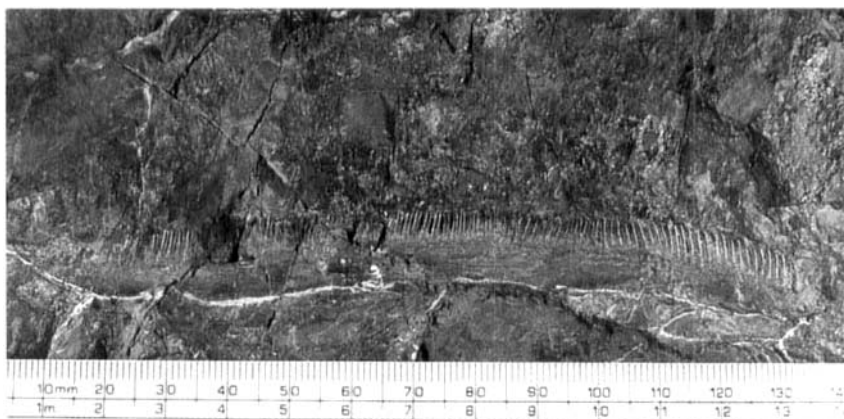


Figure 10. *Spathicephalus mirus* Watson, NMS G 1950.56.4, right maxilla ($\times 0.75$).

tooth bases run parallel with the premaxillary tooth row. The maximum diameter of the tooth bases is 1.0 mm and is significantly smaller than that of marginal teeth in the same skull which measures 3.0 mm. It is not known whether teeth were present on the palatines, but none is present on the ectopterygoid.

In none of the lower jaw specimens is a complete dentary preserved and the total number of marginal teeth is unknown. However, comparing the dentition of NMS G 1950.56.4 and NMS G 1950.56.5 the teeth in the upper and lower jaws are of a similar size and we estimate that the dentary would have had spaces for 110–120 teeth. The symphyseal region of the lower jaw of *Spathicephalus* is known in three specimens and in the two from the Dora Bone Bed the parasymphysial plate is preserved (Fig. 9A). In both BMNH R. 10951 and NMS G 1994.103.1 a row of small teeth lines the mesial edge of the bone immediately behind the symphysis. There are spaces for 28 teeth and all but one is represented in the jaw. All were broken just above their base prior to preservation. The orientation of the tooth bases indicates that intact teeth would have pointed mesially towards the opposite jaw ramus rather than dorsally towards the palate. This does not appear to be an artefact of preservation: the symphysis of BMNH R. 10951 is uncrushed and the relationship between the parasymphysial plate and surrounding bones is undisturbed. This mesial orientation of teeth on the parasymphysial plate is not unique. In the unnamed jaw from Parrsboro, Nova Scotia (Godfrey & Holmes, 1989), in which the parasymphysial plate was recognised for the first time in tetrapods, the teeth also point mesially.

There is no evidence of teeth or denticles on the coronoids of *Spathicephalus*.

DISCUSSION

Mode of life of Spathicephalus

The jaw mechanism and feeding biology of a variety of large early tetrapods have been discussed in recent years e.g. anthracosaurs (Panchen, 1964, 1970, 1972, 1977),

Crassigyrinus (Panchen, 1985) and loxommatids (Beaumont, 1977). All were considered to be active fish-eating predators with relatively large heavy jaws which closed rapidly against water pressure using the kinetic inertial system described by Olson (1962). All these early tetrapods had elaborate kinetic mechanisms in the skull and palate, or vacuities in the palate or skull roof to facilitate jaw closure and accommodate contracting muscles. In contrast, *Spathicephalus* had a non-kinetic skull, with an apparently fixed basal articulation, a closed palate and relatively small antorbital vacuities. This, together with its highly specialized dentition, suggests that *Spathicephalus* had evolved a mode of life significantly different from that of other early tetrapods.

Romer (1947) suggested that *Spathicephalus* was essentially a bottom-dwelling form, with piscivorous habits and Baird (1962) agreed with this interpretation. The Triassic plagiosaurs are believed to have occupied such a niche (Panchen, 1959). In a typical plagiosaur, e.g. *Plagiosuchus*, the subtemporal fossae are large, stretching over two-thirds of the skull length and a piscivorous habit was apparently possible because of the strong adductor musculature. Since the plagiosaur skull is extremely flat, the depressor mandibulae muscles must have worked at a mechanical disadvantage, making rapid opening of the mouth unlikely. It is thought that these forms lay with the lower jaw on the substrate, the anterior position of the jaw articulation allowing the skull to be raised to provide a wide gap and that the extensive adductor muscles would effect a powerful, rapid snap to secure the prey.

By comparison, *Spathicephalus* is ill-adapted for such a mode of life. The subtemporal fossae are small, being confined to the posterior quarter of the skull, and in front of the adductor muscles extended a broad, flat plate-like palate. Even taking into account a synchronized lowering of the hyoid, the problem of resistance of water would be great, were the jaw to snap shut from a wide open position. Skull structure indicates that the pterygoideus musculature was not highly developed, unlike the condition in loxommatids (Beaumont, 1977), and that the external adductor muscles would be acting at a mechanical disadvantage if the jaws were wide open. The latter would be most effective, i.e. at right angles to a line joining the jaw joint and its area of insertion, when the jaw was almost closed. In any case the adductor muscles were comparatively small and could have exerted little pressure at the front of the jaws and in the absence of pointed teeth or palatal denticles it seems unlikely that the animal could maintain a firm grip on a living fish. Furthermore, the jaw articulation of *Spathicephalus*, although far forward, was still behind the plane of the occipital condyle and extensive jaw opening would involve slight raising of the body and bending of the neck region (Watson, 1951). Thus the animal is most unlikely to have spent long periods with its mouth open waiting to trap fishes as suggested by Romer (1947) and Baird (1962).

The most likely mode of life is that of a sluggish bottom-dwelling form, but the nature of the teeth casts doubt on a fish-eating habit. In their structure, number and arrangement the teeth of *Spathicephalus* contrast markedly with those of a piscivorous early tetrapod, such as *Megalocephalus*, which has sharp lanceolate teeth and stout palatal tusks for dealing with its prey (Beaumont, 1977). *Spathicephalus* with its rows of small, blunt closely-packed teeth has a skull structure which is very well adapted as a food-filtering mechanism and small soft invertebrates would seem to be a most likely source of food.

The long, broad antorbital region of *Spathicephalus* may have accommodated large nasal capsules and olfaction may have been important in the location of food. Eyes

were apparently directed dorsally and may also have been involved in prey detection. It is probable that food was procured in a manner similar to that found in large flat-headed turtles, e.g. *Chelys*. It is presumed that when close to the prey the animal slowly opened its jaws a little by contracting the depressor mandibulae muscles. If the hyoid was then suddenly lowered the resultant rush of water into the buccal cavity would carry small prey with it. The jaws would only need to be slightly open, and, were this the case, the adductor musculature would be at its greatest mechanical advantage and could effect jaw closure. If the hyoid were raised when the jaws were virtually closed, then presumably water would be forced out of the mouth, but the parallel rows of teeth would be instrumental in preventing the loss of any food material that had been engulfed. Such a system of food capture would not require extensive development of pterygoideus, external adductor or depressor mandibulae muscles and it would seem that *Spathicephalus* with its relatively weak jaw musculature is well adapted for such a mode of life.

It has been noted earlier that the antorbital vacuity in *Spathicephalus* is smaller and different in structure to that found in the Loxommatidae, where it is believed to have allowed bulging of a large pterygoideous muscle mass in relation to a kinetic inertial system of jaw closure (Beaumont, 1977). Similarly, were the pterygoideous solely attached to the dorsal surface of the anterior palate in this species, it would be at its greatest mechanical advantage were the jaws to be wide open, which is assumed to be a rare occurrence. In some archosaurs, e.g. *Stagonolepis* (Walker, 1961), parts of this muscle mass are thought to originate around an antorbital vacuity and it is worth noting that any fibres of the pterygoideous that inserted on the sphenethmoid region of the braincase or the small antorbital vacuity in *Spathicephalus* would increase the mechanical advantage and enhance the efficiency of jaw closure in the suggested mode of feeding.

Relationships of Spathicephalus

The genus *Spathicephalus* is currently represented by two species: *S. mirus*, Watson (1929) from the Namurian of Scotland and *S. pereger* Baird (1962) from the Namurian of Nova Scotia. Together they form the monotypic family Spathicephalidae. Recently, however, Lebedev has suggested that *Doragnathus woodi*, (Smithson, 1980b) is "possibly a juvenile *Spathicephalus*" (in Lebedev & Clack, 1993: 731) and that *Doragnathus* is "probably synonymous with *Spathicephalus*" (in Ahlberg *et al.*, 1994: 310).

Doragnathus was originally erected to name a large number of jaw specimens from Viséan and Namurian localities in Scotland (Smithson, 1980b, 1985a). Most of this material was collected from the Dora Bone Bed and is represented by incomplete pieces of lower jaw, premaxillae and maxillae. No complete or partially complete skull is known. The lower jaw is unremarkable with the normal arrangement of dermal bones. The external bones are ornamented with the characteristic pits and ridges of early tetrapods, and the Meckelian foramina on the internal jaw surface are small. Posteriorly there is a short retroarticular process. The diagnostic feature of *Doragnathus* is its dentition. It has large numbers of small, closely packed, sharply pointed marginal teeth with a strong lingual curve (Smithson, 1980b: fig. 3). In addition, the coronoid series and the parasymphysial plate bears a single row of short needle-like teeth running parallel to the row on the dentary.

Superficially the marginal teeth of *Doragnathus* closely resemble those of *Spathicephalus*

mirus. In both taxa there are large numbers of small, closely packed teeth. However, those of *Spathicephalus* are clearly chisel-shaped whilst those of *Doragnathus* are sharply pointed and strongly curved. Lebedev (in Ahlberg *et al.*, 1994) has suggested that this difference in tooth morphology is size related, the *Doragnathus* jaws representing juveniles of *Spathicephalus*. However, this is refuted by NMS G 1885.50.74, a small *Spathicephalus* jaw containing 26 teeth, of similar size to those described from *Doragnathus* but having the same chisel-shape as those in larger specimens.

The dentitions of *Spathicephalus* and *Doragnathus* also differ in the arrangement of teeth on the parasymphysial plate and coronoid series. In *Spathicephalus* there is a row of small teeth on the parasymphysial plate but none on the coronoids, whilst in *Doragnathus* there is a continuous row of teeth along the inner edge of the jaw, from the anterior edge of the parasymphysial plate to the posterior margin of the coronoid series. Thus it seems to us highly improbable that *Spathicephalus mirus* and *Doragnathus woodi* are synonymous.

In the Introduction we acknowledged Beaumont's (1977) division of the Loxommatoidea into two families, the Spathicephalidae and Loxommatidae. Although *Spathicephalus* shares little with the loxommatids they have in common the following apomorphies that characterize the Loxommatoidea: closed palate with midline pterygoid suture, palatal ornament and antorbital vacuities. Thus the Spathicephalidae and Loxommatidae are sister-groups. The broader relationships of the loxommatooids will not be considered here. The description of *Spathicephalus* has unfortunately provided little new data with which to test current hypotheses (see Smithson, 1982, 1985b; Milner *et al.*, 1986; Carroll, 1988; Panchen & Smithson, 1988; Ahlberg & Milner, 1994; Lebedev & Coates, 1995). However, it is anticipated that the complete description of the loxommatid postcranium from the Upper Carboniferous of Lancashire, England, (Milner & Lindsay, 1989; and this volume) will generate new data with which to determine the relationships of loxommatooids.

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