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A NEW FIND OF *TREMATOSUCHUS* (AMPHIBIA, TEMNOSPONDYLI) FROM THE *CYNOGNATHUS* ZONE OF SOUTH AFRICA

by

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ABSTRACT

Some aspects of the cranial morphology of *Trematosuchus sobeyi*, a temnospondylous trematosaurid amphibian from the South African *Cynognathus* Zone, are described in detail for the first time from a new fossil find referred to this form. The new specimen is similar in size to that of the Holotype of *Trematosuchus sobeyi* but differs in the more moderate elongation of the snout. Apart from the presence of the septomaxilla, the validity of the genus *Trematosuchus* is reconfirmed *inter alia* by its much larger size and the position of the supraorbital sensory groove alongside the lachrymal margin rather than crossing this bone. This last characteristic differentiates *Trematosuchus* from all other trematosauroids.

T. sobeyi is of particular importance since it represents the only purely freshwater Gondwanan form closely comparable to the European *Trematosaurus*. The presence of *T. sobeyi* in the lowermost strata of the *Cynognathus* Zone in South Africa, in association with some other forms related to the Upper Olenekian (Middle Buntsandstein) tetrapod assemblage of Europe, indicates that these strata belong to the Scythian in contrast to the higher strata of the *Cynognathus* Zone which are Anisian.

KEYWORDS: Trematosauridae, Biostratigraphy, *Cynognathus* Zone.

INTRODUCTION

Trematosauroid amphibians, characterised by their wedge-shaped skullsand paired anterior palatal vacuities, comprise one of the most common groups of Triassic temnospondyls. They stem from the family Benthosuchidae (Shishkin 1968, 1980; Getmanov 1989) which also gave rise to other more advancedlineages such as the Heylerosauridae (Shishkin 1980) and the poorly known Yarengiidae (Shishkin 1964; Novikov 1990).

The Benthosuchidae are recorded only from the early Lower Triassic (Induan – Lower Olenekian) of eastern Europe and northeastern Asia (Shishkin & Lozovsky 1979). Heylerosauridae are endemic to the Euroamerican province; they appear in the upper Lower Triassic (Upper Olenekian) and become very common in the Anisian (Morales 1987; Ochev & Shishkin 1989; Shishkin & Ochev 1993; Milner 1990). The Yarengiidae are known only from eastern Europe (Upper Olenekian). In contrast, members of the family Trematosauridae are recorded from all the continents except for South America and Antarctica.

The majority of trematosaurids come from the Lower Triassic. Middle Triassic finds reported from North Africa, India (Lehman 1971; Chatterjee & Hotton 1986; Welles 1993) and Canada (Baird 1986) are rare and poorly known. The Upper Triassic trematosaurids are known from a single find from western Europe (Hellrung 1987).

A number of transitional forms from the Lower Olenekian of eastern Europe suggest that Trematosauridae can be derived from the Laurasian Benthosuchidae (Shishkin 1968, 1980; Getmanov 1989). The Trematosauridae are one of only a few amphibian groups which succeeded in spreading to the nearshore habitats as seen from their particular abundance in the coastal marine facies of the Lower Olenekian of Spitsbergen and also in Madagascar.

Trematosaurids are most common in Europe and rare in the Gondwanan continents which may suggest that they dispersed fromLaurasia to the south, most probably via the coastal or borderland routes (Lehman 1979; Cosgriff 1984). This idea is complicated by the fact that most of the Gondwanan trematosaurid finds belong to the specialized needle-snouted forms, which first appeared in both hemispheres in the lowermost Lower Triassic (Induan), i.e. before the typical benthosuchid – derived trematosaurids which are first recorded in the Lower Olenekian (as exemplified by the Spitsbergen assemblage). The earliest Indian long-snouted forms are known from the Panchet Series of India (*Gonioglyptus*, *Panchetosaurus*; Tripathi 1969), the marine Prionolobus Beds of the Salt Range in Pakistan (*Halobatrachus kokeni*; Huene 1920; Hammer 1987) and from the Vokhmian horizon of the Cis-Urals (undescribed form; Shishkin & Ochev 1993). This seems to reinforce the suggestion that theassemblage of forms currently termed Trematosauridae may well prove to be diphyletic in origin (cf. Bystrow and Efremov 1940 p 143; Shishkin 1964). The subdivision of the Trematosauridae into two (or three) subfamilies has been suggested by Efremov (1933) Säve-Söderberg (1935), Hammer (1987) and Welles (1993).

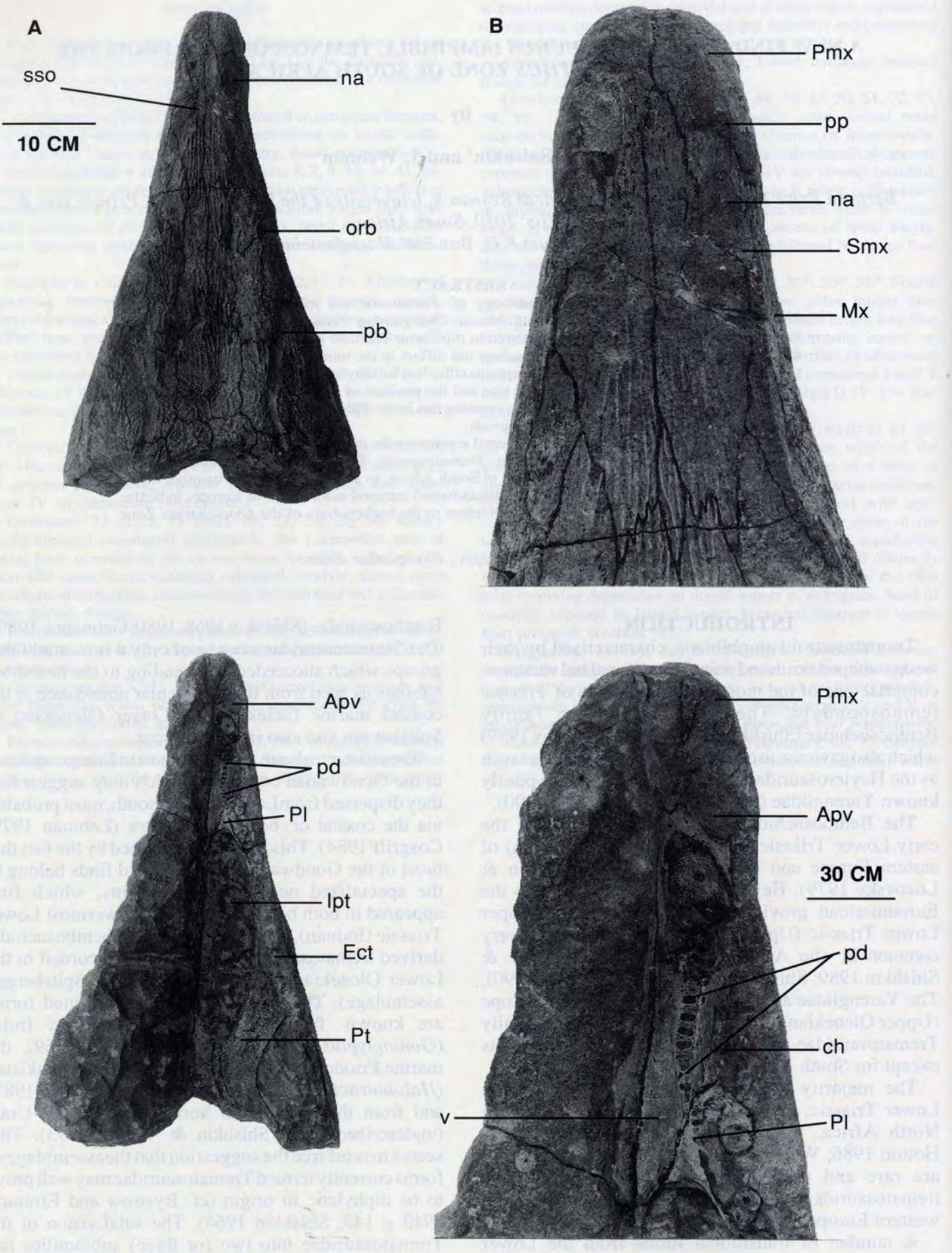


Figure 1. *Trematosuchus sobeyi* SAM 2979 (Holotype) A. Dorsal view of the skull, B. dorsal view of the snout, C. ventral view of the palate, D. ventral view of the anterior part of the palate.

Apart from the finds from Madagascar, India and Pakistan mentioned above, Gondwanan trematosaurids are known only from Australia and South Africa. All the Australian finds belong to the long-snouted forms and include the type of *Erythrobatrachus* from the Blina Shale (Cosgriff & Garbutt 1972) and unidentifiable fragments from the Arcadia Formation and the lower part of the overlying Glenidal Formation (Warren 1985), the former two stratigraphic units being most probably lower Olenekian (Smithian) in age.

In South Africa trematosaurids were first recovered in the early part of this century and are represented by two Triassic forms from the Beaufort Group, *"Trematosaurus" kannemeyeri* and *Trematosuchus sobeyi* (Broom 1909; Haughton 1915, 1925; Huene 1920). The former is a poorly known long-snouted *Aphaneramma*-like form described from a fragment of skull (Broom 1909), the provenance of which is uncertain. Kitching (1978) considers it to come from the *Cynognathus* Zone (Upper Beaufort Group) which is variously considered to be Upper Olenekian (Spathian) to Anisian in age (Ochev & Shishkin 1989).

Trematosuchus sobeyi, is of particular importance since it represents the only instance in Gondwana where a complete trematosaurid skull (Figure 1) is recorded from a purely fresh water environment (fluvial-lacustrine deposits of the Upper Beaufort Group). Furthermore, it is the only Gondwanan form which is comparable with the European *Trematosaurus*.

Both the type (Figure 1) and referred specimen of *T. sobeyi* described by Haughton (1915, 1925) were obtained from a sandstone quarry of the *Cynognathus* Zone in the Queenstown area, Cape Province. According to Kitching (pers. comm.) the fossil-bearing sandstone belongs to the lower part of the *Cynognathus* Zone. No further finds of this genus have been reported until recently when another specimen (Figures 2-5) was recovered in the *Cynognathus* Zone of the northeastern Orange Free State (Welman *et al.* 1991). The new *Trematosuchus* find (NMQR 3263) includes two fragments of the same skull collected at Verdun Farm, Paul Roux district. The narrowness of the snout fragment combined with paired elongated anterior palatal vacuities and strong reduction of the interchoanal tooth row immediately suggest the trematosaurid affinity of the specimen. Although no more fossils were discovered from this site, the faunal assemblage of this stratigraphic unit includes *Cynognathus*, trirachodontid cynodonts, an erythrosuchid thecodontian and *Parotosuchus*-like capitosauroid amphibians (Welman et al. 1991). Hancox *et al.* (in press) show that this faunal complex is distinct from the main faunal assemblage of the *Cynognathus* Zone known from the Cape Province and the southern Orange Free State, and underlies it. This makes the new find of *Trematosuchus* important for biostratigraphic subdivision of the *Cynognathus* Zone.

In addition, the new find provides data on the cranial morphology of *Trematosuchus* which cannot be discerned in the type.

SYSTEMATIC PALAEONTOLOGY

Trematosuchus sobeyi (Haughton 1915)
Trematosaurus sobeyi: Haughton 1915, p.47, pl.VIII, IX
Trematosuchus sobeyi: Watson 1919, p.41
Trematosaurus sobeyi: Huene 1920, p.443
Trematosuchus sobeyi: Haughton 1925, p.250, fig.15

Holotype

SAM 2979, a nearly complete skull; Queenstown, Cape Province, Upper Beaufort (*Cynognathus* Zone). (Figure 1).

Referred specimens under description

NMQR 3263 A & B (two fragments of the same skull) Verdun Farm, Paul Roux District, Orange Free State, *Cynognathus* Zone (Figures 2-5).

Generic and specific diagnosis

Large form (skull about 420mm in midline length); orbits extremely small and round; septomaxilla and interfrontal present; parietals not narrowed anteriorly; supraorbital sensory groove alongside the medial lachrymal margin rather than crossing the lachrymal.

PRESERVATION AND METHODS

NMQR 3263 (Figures 2-5) consists of Block A: the snout broken off obliquely behind the nasochoanal area, and Block B: a part of the right side of the palate immediately in front of the subtemporal fossa, together with the dorsal portion of the jugal.

Both blocks, obviously from a fine-grained grey sandstone lens, were found lying close together on the surface but not in situ.

They exhibit the same type of mineralization and weathering (the surface of the bones being brown and glossy) and are consistent in size. There seems to be no doubt that both fragments belong to the same individual, in spite of the lack of immediate contact between them. The fresh fracture surfaces of the specimen indicate that fragmentation of the skull almost certainly occurred only after it weathered out of the embedding rock. The good preservation of sharp edges on the specimen suggests that the skull was neither transported over any long distance prior to burial nor did it suffer post depositional sedimentary reworking.

NMQR 3263 was mechanically prepared under a stereo microscope with a pneumatic engraver. The engraver was fitted with a sharpened, round tungsten-carbide tip. Exposed bone was covered with a Glyptal cement solution, diluted with lacquer thinners.

MORPHOLOGICAL DESCRIPTION

The fragment comprising block A (Figures 2, 3, 5 A-C) is comparable in size with the corresponding part of the type skull. It includes both premaxillae, septomaxillae, the anterior parts of the nasals and maxillae, a part of the left palatine and both vomers, the right of which lacks most of its parachoanal area.

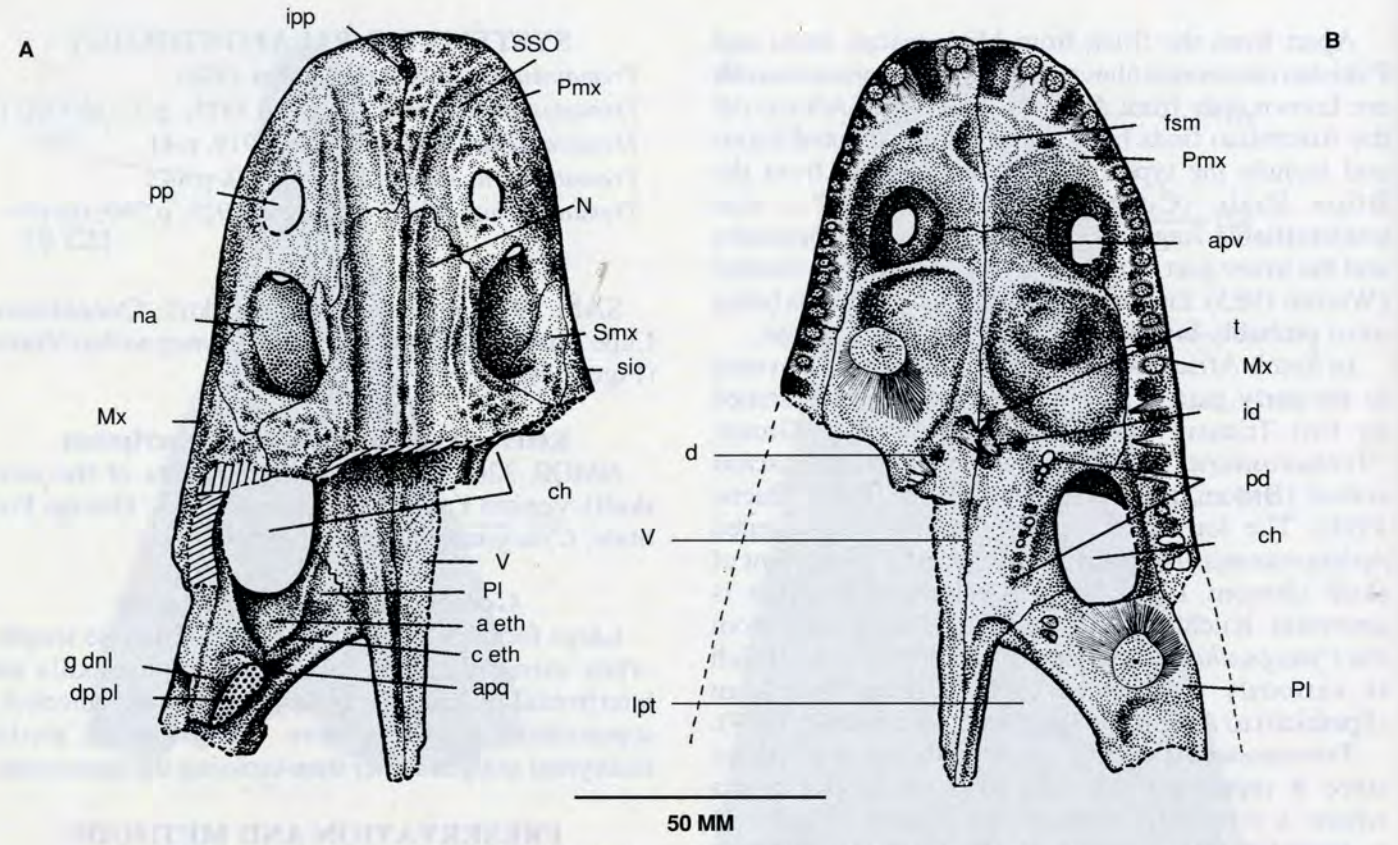


Figure 2. *Trematosuchus sobeyi* NMQR 3263A. Anterior part of the skull. A. dorsal view, B. ventral view.

Skull roof

The snout is narrow, with a blunt end. The nares are elongated and irregular in shape. They differ from those in the type skull (Figure 1A) in their more anterior position and in that they diverge anteriorly rather than being parallel. In front of them, the dermal roof is pierced by paired foramina (Figure 2A; pp) which housed the tips of the symphyseal tusks of the lower jaw. Although their margins are partially damaged it is clear that they were regularly oval. The left foramen is somewhat larger than the right.

It is difficult to decide whether these prenarial perforations are also present in the type skull. The irregular prenarial opening seen on its left side (Figure 1B) is the anterior palatal vacuity exposed dorsally due to erosion of the dorsal surface of the premaxilla. Prenarial perforations similar to those seen in our specimen, are typical for mastodonsaurids (Fraas 1889; Wepfer 1923; Ochev 1972) and may occur in the large individuals of other Triassic temnospondyls, such as cyclotosaurids (Fraas 1913). They were also figured by Zittel for *Trematosaurus* (Woodward 1932, fig. 311).

The right naris and the prenarial foramen as well as the right premaxilla in our specimen are slightly displaced forward relative to their left counterparts. The small foramen in the center of the median premaxillary suture described in the type (Haughton 1915) is not present, but there is a corresponding pit (Figure 2A; ipp) situated more anteriorly in the new material.

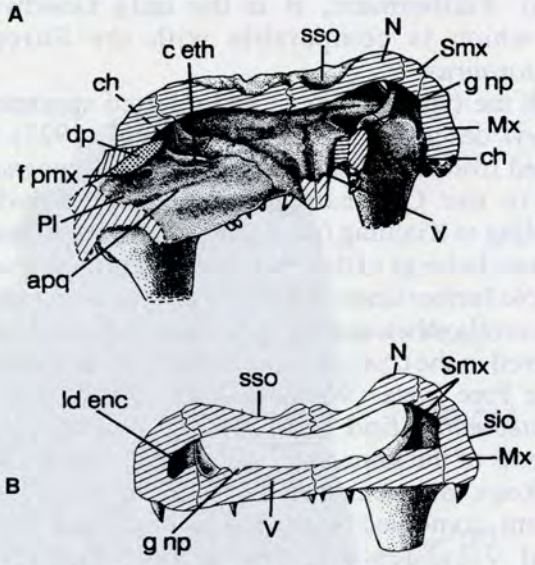


Figure 3. *Trematosuchus sobeyi* NMQR 3263A. A. Anterior part of the skull in posterior view, seen slightly from the top, B. Diagram of transverse section through the anterior end of the choanae in posterior view.

The dermal sculpture is coarsely pitted. On the anterior part of the maxillary and lateral to the prenarial perforation on the premaxilla, the pits are elongated.

The supraorbital sensory grooves (Figures 2A, 3; sso) are very broad, but shallow and run (in the snout area) along the midline of the skull roof towards the anterior end of the snout where they diverge slightly. The ends of the preserved portions of these grooves diverge posteriorly, immediately posterior to the nares.

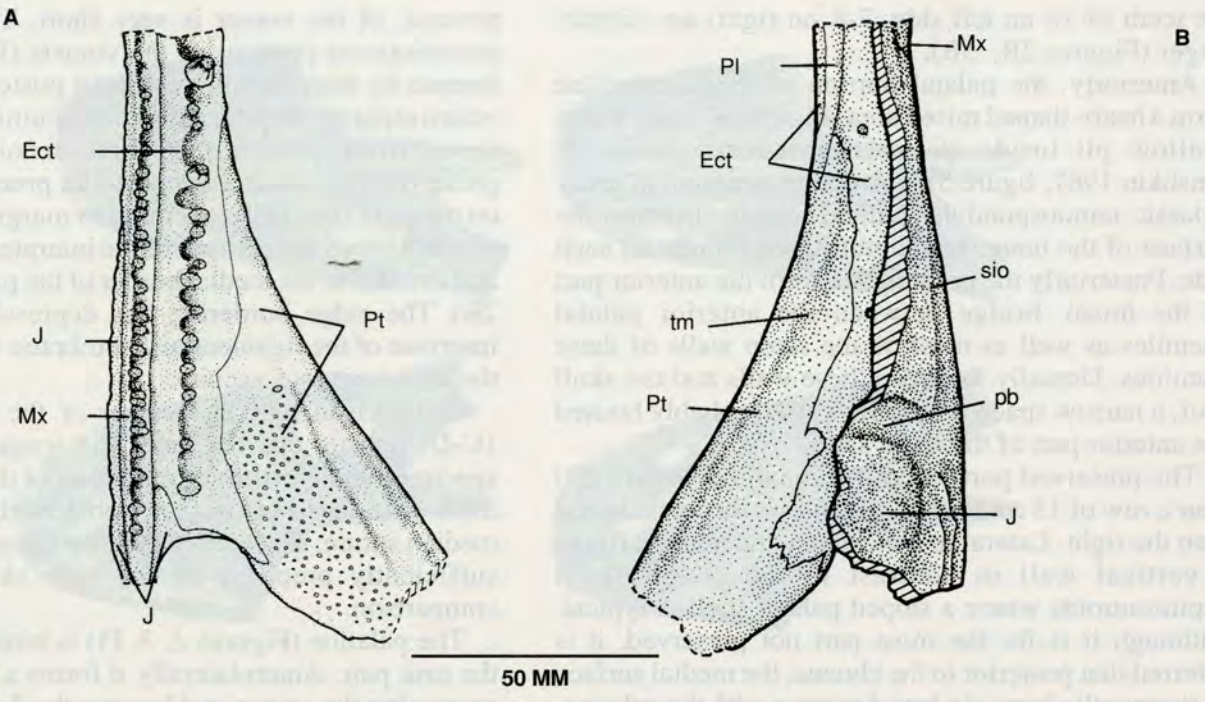


Figure 4. *Trematosuchus sobeyi* NMQR 3263B. Fragment of palate. A. ventral view, B. dorsal view

The anterior parts of the infraorbital grooves (Figures 2A, 3B, 4C; sio) are similarly broad but expressed less markedly as they run along the smooth labial surface of the maxillae. The sensory grooves of the type skull (Figures 1A-B) have the same pattern, but their anterior (snout) segments are poorly preserved except for the postnarial exposure of the supraorbital grooves.

The premaxillae have a long median suture anteriorly. Their posterior parts, separated by an anterior projection of the nasals, are much shorter than the median suture. In contrast, in the type of *Trematosuchus* (Figures 1A-B) the separated posterior parts of the premaxillae exceed the anterior contacting parts in length, and their sutures with the nasals form a sharper angle.

The septomaxilla (Figures 2A, 3B, 5A; Smx) forms the posterolateral rim of the naris and consists of two parts. The dorsal semilunar part belongs to the skull roof and is ornamented. It extends anteriorly along 3/5 of the lateral border of the naris and reaches the premaxilla-maxilla suture. It constitutes a concave smooth plate forming the posterolateral wall of the naris and extending down to the dorsal surface of the vomer (Figure 3B).

The structure and position of the septomaxilla as described is much the same as in the type skull except for the triangular rather than semilunar shape of the dorsal part of the bone in the latter. The figure by Haughton (1915, plate VIII, figure 2) showing the septomaxilla limited to the area behind the naris is inaccurate and at variance with his description (Figures 1a-b).

The maxilla broadens dorsally behind the septomaxilla to contact the nasal and is ornamented in this area (Figure 2A). The labial strip of the bone alongside the tooth margin is smooth. The maxilla-premaxilla contact begins dorsally on the lateral narial border, extends down to the marginal tooth row and crosses it at the level of the anterior vomerine tusk (Figures 2A-B).

Palatal complex

The palatal view of block A exhibits the paired anterior palatal vacuities common in trematosauroids, the left choana and the anteriormost part of the left interpterygoid vacuity (Figures 2B, 5B). The anterior palatal vacuities are very deep with steep walls, and appear to be more widely separated and situated closer to the tip of the snout than in the type skull (Figures 1C-D). Perforations of the skull roof are situated (Figure 2B) immediately dorsal to these vacuities. The choana is clearly shorter and broader than in the type, (Figures 1C-D). The anterior end of the interpterygoid vacuity in our specimen is pointed at the level of the posterior end of the vomer-palatine suture and extends anteriorly far as the posterior border of the choana (Figures 2A-B). In contrast, the anterior end of the interpterygoid vacuity in the type is broadly rounded and situated far posterior to the choana (Figure 1C).

On the ventral side the premaxilla consists of the tooth bearing marginal area and the palatal shelf (Figure 2b). In the tooth row of each premaxilla the anteriormost 3-4 teeth are large and subsequent teeth decrease slightly in size posteriorly. The next posterior set consists of uniformly small teeth, 10-11 in number including the empty tooth pits. Behind these teeth, posterior to the midpoint of the anterior palatal vacuity and extending backwards to the end of the premaxilla,

the teeth (9-10 on left side; 7-8 on right) are slightly larger (Figures 2B, 5B).

Anteriorly, the palatal portion of the premaxillae form a heart-shaped raised area (Figure 2B; fsm) with a shallow pit inside (*fossa subrostralis media* cf. Shishkin 1967, figure 5), a structure common in many Triassic temnospondyls. Lateral to this structure the surface of the bone bears a nutritive foramen on each side. Posteriorly the premaxillae form the anterior part of the broad bridge between the anterior palatal vacuities as well as most of the steep walls of these vacuities. Dorsally, between these walls and the skull roof, a narrow space is present which probably housed the anterior part of the nasal sac.

The preserved portions of the maxillae (Figure 2B) bear a row of 13 teeth and tooth pits on the left side and 5 on the right. Lateral to the choana, the maxilla forms a vertical wall in contrast to the condition in capitosauroids where a sloped palatal shelf is typical. Although it is for the most part not preserved, it is inferred that posterior to the choana, the medial surface of the maxilla formed a broad contact with the palatine. The teeth of the maxilla and premaxilla are moderately compressed at the base and have an almost circular cross-section half-way along their length.

The vomer (Figures 2, 3, 5A-C), although long, is somewhat shorter than in the type (ratio of its width to length, measured between the posterior end of the anterior palatal vacuity and anterior end of interpterygoid vacuity, is 0.36, as compared with 0.33 in the type). The ventral surface of the vomer can be subdivided antero-posteriorly into 4 parts. The anterior part is short and narrow and forms together with its counterpart, the posterior half of the bridge between the anterior palatal vacuities (Figure 2B). The surface of this bridge is transversely convex. The broadest part of the bone is occupied by a large depression which houses the tusk pair. On the left side of the palate the anterior tusk was functional, and is followed posteriorly by the pit for the replacing tusk; on the right side the condition is reversed (Figure 2B).

The interchoanal part of the vomer is narrow, ventrally flattened and wedges anteriorly between the elevated borders of the tusk depressions. Along the median suture of the vomers, the anterior wedged area of this portion bears one small tooth on each side (Figure 2; id) and an associated empty replacement pit. Anterior to these teeth, an unpaired central tuber (Figure 2B; d) is present which may have borne a single tooth. One more small tooth is present on each side lateral to the central group, close to the border of the tusk depression (Figure 2B; d). Lateral to this pair of teeth, just behind the tusk area, the choanal border of the vomer bears a parachoanal tooth row which is preserved only on the left side and consists of 7 teeth and 3 tooth pits (Figure 2B; pd). Posteriorly, the parachoanal tooth row converges slightly toward the median vomerine suture and diverges from the choanal border. It is separated from the palatine continuation of the same row by a broad gap crossed by the vomer-palatine suture. The posterolateral, palatine process, of the vomer is very short. The fourth and posteriormost portions of the vomers (Figure 2B) are formed by their narrow and deep posterior processes which separate the interpterygoid vacuities and underly the cultriform process of the parasphenoid, which is not preserved. The base of the posterior process, preserved on the right side, bears a semilunar marginal depression which follows the contour of the interpterygoid vacuity and extends to the medial border of the palatine (Figure 2B). The ridge bordering this depression marks the insertion of the ligamentous membrane which covered the interpterygoid vacuity.

Comparison with the vomer of the type (Figures 1C-D) reveals that the latter is longer than in our specimen and that the vomerine part of the parachoanal tooth row does not converge posteriorly towards the median suture. The area of the interchoanal teeth is not sufficiently prepared on the type skull to enable comparison.

The palatine (Figures 2, 3; Pl) is broken off behind the tusk pair. Anterolaterally it forms a broad process contacting the vomer and bearing the 2 posterior teeth of the parachoanal tooth row, referred to above. Anteriorly, the palatine sends off a small plate-like vertical process which forms part of the lateral wall of the choana. The palatine is markedly different from that of the type (Figure 1C-D) in having a shorter and much more transversely positioned suture with the vomer, whereas the anterolateral process is narrower. In accordance with this, the choana and the interpterygoid vacuity are closer to each other than in the type.

The lack of the postnarial part of the skull roof permits examination of the dorsal side of the palatine and the posterior portion of the vomer. In addition, some details of the exoskeletal nasal cavity are seen in posterior view of Block A.

The dorsal surface of the palatine is subdivided into two smooth areas. The medial area extends along the border of the interpterygoid vacuity while the lateral area is more differentiated and bordered laterally by the narrow elevation which contacted the maxilla. These areas are separated by a *processus dorsalis* (Figure 2A; dp pl) which obviously contacted the lachrymal bone as in many other late temnospondyls (cf. Säve-Söderberg 1936; Shishkin 1960, 1968, 1973). Anteriorly, the boundary between the two areas is formed by the narrow ethmoidal ridge (Figures 2A, 3A; c eth) which extends anteromedially from the dorsal process along a curved line toward the posteromedial border of the choana.

The area situated medial to the dorsal process and the ethmoid ridge, was occupied by the anterior sickle-shaped process of the palatoquadrate cartilage (Figure 2A, 3A; apq). It probably reached the posterior wall of the nasal capsule near the vomer-palatine suture where the impression of this cartilage is seen as a shallow groove wedging out anteromedially.

The area situated laterally to the dorsal process and the ethmoid ridge (Figure 2A) consists of two portions separated by a ridge extending from the posterior part of the ethmoid ridge to the posterolateral choanal border.

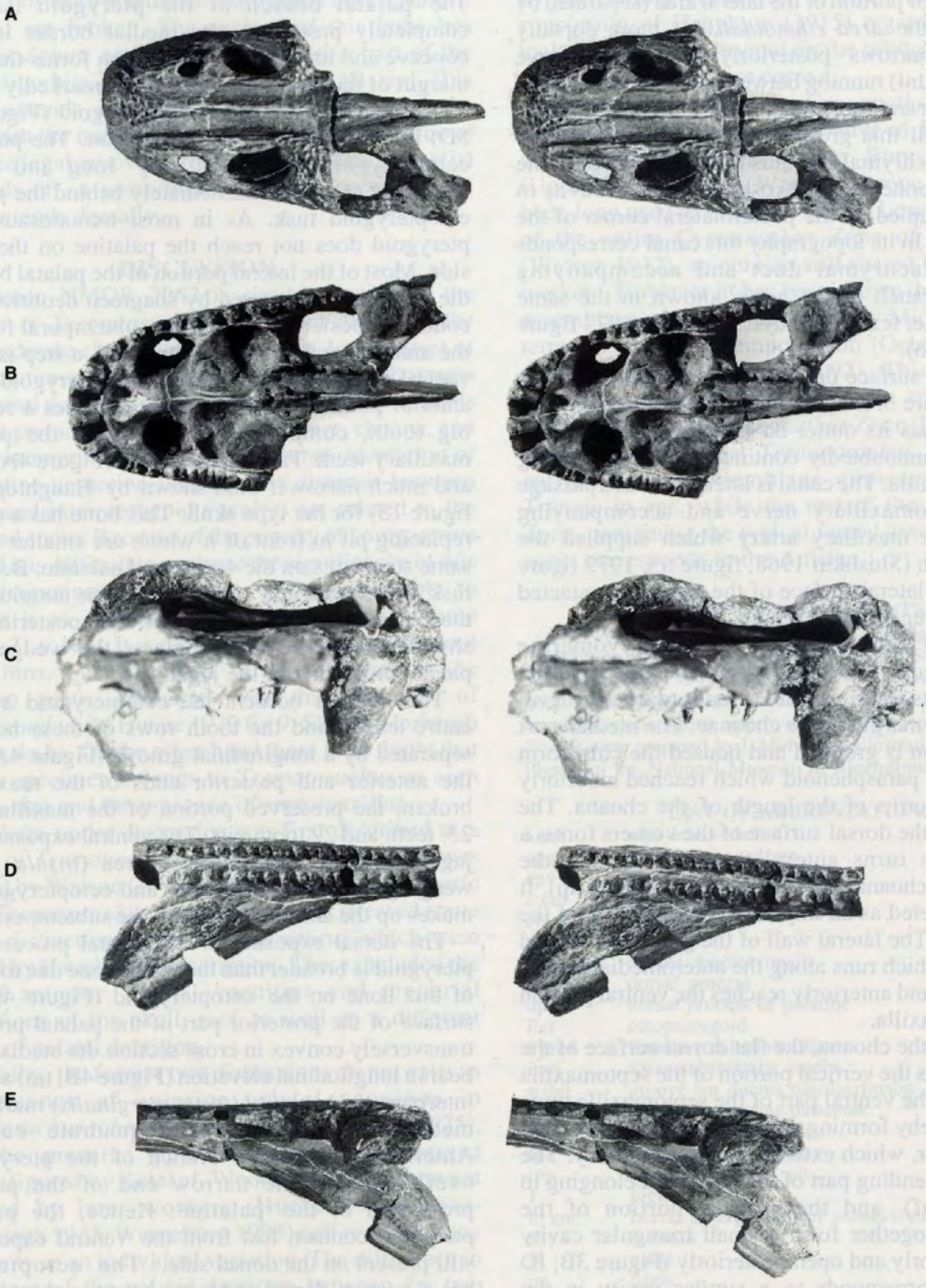


Figure 5. *Trematosuchus sobeyi* NMQR 3263A. Stereo pairs of anterior part of skull A. dorsal view, B. ventral view, C. posterior view. *Trematosuchus sobeyi* NMQR 3263B. Stereo pairs of fragment of the palate D. ventral view, E. dorsal view.

The anteromedial *area ethmoidalis* (Figure 2A; a eth) was occupied by the posterolateral continuation of the floor of the nasal capsule. This structure is comparable to the *planum triangulare* in modern anurans; the corresponding area of the dorsal palatine surface is known in a number of late Permian and Triassic temnospondyls (Shishkin 1968, figure 6B; 1973, figure 22, 60b). In *Trematosuchus* the *area ethmoidalis* differs from that of other trematosauroids in being semilunar rather than triangular, and very steeply sloped toward the choana. The lateral part of this area continues forward along the lateral border of the choana as a narrow groove between the dorsal and palatal divisions of the maxilla.

The posterior portion of the lateral area (separated by a ridge from the *area ethmoidalis*) is more dorsally situated and narrows posteriorly to form a groove (Figure 2A; g dnl) running between the lateral elevation of the palatine and the dorsal process. In a completely preserved skull this groove would be roofed by the maxilla and lachrymal and thus formed the floor of the canal which connected the exoskeletal cranial cavity to the space occupied by the posterolateral corner of the nasal capsule. In its topography this canal corresponds to the nasolachrymal duct and accompanying infraorbital branch of the nerve known in the same position in other temnospondyls (Shishkin 1973 figure 22, 48, 50, 60b).

The medial surface of the dorsal process exhibits a foramen (Figure 3A; f pmx) leading into a transverse canal which has its outlet on the lateral side of the palatine and undoubtedly continued into the missing part of the maxilla. The canal is interpreted as a passage for the palatomaxillary nerve and accompanying branch of the maxillary artery which supplied the maxillary teeth (Shishkin 1968, figure 63, 1973 figure 22, 60b). The lateral surface of the palatine contacted the maxilla over its entire length.

The dorsal surface of the posterior vomerine processes (Figures 2A, 3A) forms a median elevation which broadens anteriorly and extends toward the level of the anterior margin of the choanae. The median part of the elevation is grooved and housed the cultriform process of the parasphenoid which reached anteriorly up to three fourths of the length of the choana. The lateral part of the dorsal surface of the vomers forms a groove which turns anterolaterally following the outline of the choanal border (Figures 3A-B; g np). It can be interpreted as an impression of a branch of the palatal nerve. The lateral wall of the groove is formed by the ridge which runs along the anteromedial border of the choana and anteriorly reaches the ventral portion of the septomaxilla.

Anterior to the choana, the flat dorsal surface of the vomer supports the vertical portion of the septomaxilla (Figure 3B). The ventral part of the septomaxilla turns medially, thereby forming a zone of horizontal contact with the vomer, which extends anteroposteriorly. The vomer, the ascending part of the maxilla (belonging to the skull roof), and the vertical portion of the septomaxilla together form a small triangular cavity pointed anteriorly and open posteriorly (Figure 3B; lD enc) which corresponds to a similar cavity in the brachyopid *Batrachosuchoides* (Shishkin 1967, p. 312). This most probably housed the lateral diverticulum of the nasal sac. There is a notable variation in the structure of this cavity on the two sides of the skull. The right cavity is formed by 3 bones as described, while in the left, the floor and the lateral wall are formed only by the maxilla (Figure 3B).

Most of the ventral exposure of the fragment B (Figures 4A, 5D) belongs to the pterygoid, ectopterygoid and maxilla with a small wedge of jugal intervening from behind between the latter two bones. The palatal branch of the pterygoid is almost completely preserved. Its medial border is gently concave and its lateral border which forms the medial margin of the subtemporal fossa, is markedly convex.

The ventral surface of the pterygoid (Figures 4A, 5D) is concave in transverse section. The pterygoid-ectopterygoid contact is very long and extends anteriorly to a point immediately behind the posterior ectopterygoid tusk. As in most trematosaurids, the pterygoid does not reach the palatine on the ventral side. Most of the lateral portion of the palatal branch of the pterygoid is covered by shagreen dentition which continues posteriorly up to the subtemporal fossa. On the anterolateral margin of this field, a step is formed ventral to the smooth surface of the pterygoid. On the anterior pointed end of the shagreen, lies a relatively big tooth, comparable in size with the posterior maxillary teeth. The ectopterygoid (Figure 4A) is long and much narrower than shown by Haughton (1925, figure 15) for the type skull. This bone has a tusk and replacing pit in front of it which are smaller than the same structures on the vomer and palatine. Behind the tusk are 13 teeth and 12 tooth pits. The anterior part of the ectopterygoid is broken off. The posterior end is slightly broadened and contacts the wedge-shaped palatal projection of the jugal.

The maxilla borders the ectopterygoid along its entire length and the tooth rows of these bones are separated by a longitudinal groove (Figure 4A). Both the anterior and posterior ends of the maxilla are broken, the preserved portion of the maxilla having 23 teeth and 22 tooth pits. The ventral exposure of the jugal forms a small narrow area (*insula jugalis*) wedging between the maxilla and ectopterygoid, and makes up the anterior border of the subtemporal fossa.

The dorsal exposure of the palatal process of the pterygoid is broader than the ventral one due to overlap of this bone on the ectopterygoid (Figure 4B). The surface of the posterior part of the palatal process is transversely convex in cross section. Its medial border bears a longitudinal elevation (Figure 4B; tm) along the interpterygoid vacuity (*torus marginalis*) marking the medial border of the palatoquadrate cartilage. Anteriorly the palatal branch of the pterygoid is overlapped by the narrow end of the posterior projection of the palatine. Hence, the palatine-pterygoid contact, lost from the ventral exposure, is still present on the dorsal side. The ectopterygoid has a narrow dorsal exposure between the pterygoid and the ascending plate of the jugal and reveals a row of nutritive foramina (Figure 4B). The jugal is very thick on the anterior border of the subtemporal fossa and consists of two parts; a narrow palatal portion wedging out anteriorly (Figure 4A) and a deep ascending portion belonging to the skull roof (Figure 4B). The latter faces medially and bears a row of foramina along its base which are similar to those on the ectopterygoid.

In side view fragment B exhibits a narrow labial surface of the maxilla which is smooth and contacted dorsally throughout its length by the jugal. The

anterior, posterior and dorsal sides of the cheek plate of the jugal are broken. The surface of this bone has dermal sculpture and shows the posterior part of the broad infraorbital sensory groove (Figure 4B; sio). This groove extends along, and immediately above the suture with the maxilla. Posteriorly, where this groove meets the jugal groove, it forms a step (*flexura jugalis*) and sends off a postorbital branch (Figure 4B; pb) which extends dorsally.

DISCUSSION

Specimen NMQR 3263 is similar in size to the holotype of *Trematosuchus sobeyi* but differs in the more moderate elongation of the snout. In fact most of the distinctions of our specimen noted above (shortness of prenarial distance; more limited projection of nasals between premaxillae; shortness of vomer, choana, and palatine-vomerine suture; subtransverse orientation of the palatine-vomerine suture; short distance between choana and interpterygoid vacuity) are related to the shortened snout. Because of the paucity of comparative material it is difficult to evaluate the significance of this main distinction, but it seems most reasonable to interpret it as individual variation within the same species, *T. sobeyi*. It is of interest that as regards snout proportions, our specimen is much closer to the European genus *Trematosaurus*, than the type of *Trematosuchus* (cf Huene 1920 fig 9; Säve-Söderbergh 1937 fig 4a,b). On the other hand there is no doubt that the new specimen belongs to *Trematosuchus* as seen from its size and the presence of septomaxillae.

The form under discussion was first described as a species of *Trematosaurus* (Haughton 1915). This was opposed by Watson (1919) who proposed a new generic name, *Trematosuchus*, for this form and stressed some alleged distinctions from *Trematosaurus* which were implied by Haughton's description. These included the lack of anterior palatal vacuities and prenarial perforations of the skull roof as well as a different pattern of palatal dentition.

In reality, the former two distinctions do not exist as the presence of anterior palatal vacuities in *Trematosuchus sobeyi* was shown by Haughton (1925), while the prenarial perforations in *Trematosaurus brauni* (figured by Zittel cf. Woodward 1932) were not reported by later workers (Huene 1920; Säve-Söderbergh 1935, Werneburg 1993) and probably may occur only as an individual variation. The difference in the pattern of the palatal dentition between the two forms discussed is also questionable. Nevertheless, the validity of the genus *Trematosuchus* can be substantiated on the basis of some other characters. These include its much larger size; the extremely small and round orbits; the presence of a septomaxilla and interfrontal; the lack of an anterior narrowing of parietals; and the position of the supraorbital sensory groove alongside the lachrymal margin rather than crossing this bone. This last peculiarity found by us in the type specimen, differentiates *Trematosuchus* from all other trematosauroids and is possibly accounted for by the strong reduction of the lachrymal. The conclusion of Haughton (1915) regarding the broad inclusion of the lachrymal on the orbital margin in the type of *T. sobeyi* is not correct.

Trematosuchus from the *Cynognathus* Zone can be characterised as the closest relative of *Trematosaurus* which comes form the middle Buntsandstein zone (Upper Olenekian) of Western Europe. This fact has been long used as evidence for the Lower Triassic age of the entire *Cynognathus* Zone of South Africa (Watson 1942), an opinion still shared by most recent workers. However, it has been shown that the reptilian assemblage of this zone is typically Middle Triassic in terms of its group compositition (Ochev & Shishkin 1989; Shishkin & Ochev 1992). This contradiction appears to be resolved by a recent study on faunal changes within the *Cynognathus* Zone (Hancox *et al.* in press) suggesting that *Trematosuchus* belongs to the earliest faunal assemblage considered as Lower Triassic in age, while the rest of the *Cynognathus*-Zone, containing the typical faunal assemblage of this zone, corresponds to the Anisian.

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LIST OF ABBREVIATIONS

a eth	area ethmoidalis
apq	area palatoquadrata
apv	anterior palatal vacuity
c eth	crista ethmoidalis
ch	choana
d	tooth pit
dnl	ductus nasolacrimalis
dp	dorsal process
dp pl	dorsal process of palatine
Ect	ectopterygoid
f pmx	foramen palatomaxillare
fsm	fossa subrostralis media
g dnl	groove for ductus nasolacrimalis
g np	groove for nervus palatinus
id	interchoanal dentition
Ipt	Interpterygoid vacuity
ipp	interpremaxillary pit
J	jugal
ld enc	lateral diverticulum of exoskeletal nasal cavity
Mx	maxilla
N	nasal
na	naris
orb	orbit
pb	postorbital branch (groove)
pd	parachoanal dentition
Pl	palatine
Pmx	premaxilla
pp	prenarial perforations
pqa	palatoquadrate area
Pt	pterygoid
sio	sulcus infraorbitalis
Smx	septomaxilla
sso	sulcus supraorbitalis
t	tuberosity
tm	torus marginalis
V	vomer

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