RARE TETRAPOD REMAINS FROM THE LATE TRIASSIC FISSURE INFILLINGS OF CROMHALL QUARRY, AVON

By N. C. FRASER

ABSTRACT. Disassociated assemblages from the Mesozoic of South-west Britain display considerable variation both in the numbers of species present and in their distribution. Triassic fissure deposits at Cromhall Quarry, Avon have yielded abundant reptilian remains which for the most part are readily identified to generic level. These sediments have also revealed some very rare and quite unusual skeletal elements, including jaw bones and a procoelous vertebra. These could be prolacertiform, thalattosaurian, or pterosaurian remains, but the nature of the material makes taxonomic diagnoses difficult.

VERTEBRATE-BEARING Mesozoic fissure deposits are widespread throughout the Avon and South Glamorgan areas, and most probably range in age from the Norian to Sinemurian (Fraser 1985). Research has largely centred upon the abundant mammalian remains since they constitute some of the earliest known members of the group (D. M. Kermack *et al.* 1956, 1968; K. A. Kermack *et al.* 1973, 1981). However, the sediments are also notable for the wealth of small reptilian remains which have only recently been studied in some detail (Evans 1980, 1981; Fraser 1982; Fraser and Walkden 1983, 1984; Crush 1984; D. Kermack 1984; Whiteside 1986).

Generally, the fossils occur as highly concentrated assemblages of completely disassociated bones, which are frequently quite fragmentary, although some exquisite articulated and associated skeletons are known (e.g. D. Kermack 1984; Fraser, in press). In terms of the quantity of material and total numbers of different genera at a single locality, Cromhall Quarry (ST 704 916) is perhaps the most prolific of the English localities. Here, the occurrence of ten or more different species within a single stratum is commonplace and the individual fragments of each species must be separated. To a large extent, the most abundant species can be restored with some confidence. In the first instance, the relative abundance of individual elements forms a useful guideline for the recognition of each species; and then the nature and orientation of articulation facets can be analysed to test the suspected associations (see e.g. Fraser 1982). But with the rarest species, represented by the occasional isolated element, it may prove impossible to deduce precise relationships, but they should be properly documented to complete the record of the assemblages. The purpose of this paper is to describe some of these rare elements from the Cromhall assemblages.

THE CROMHALL ASSEMBLAGES

The series of fissures at Cromhall Quarry and their associated Mesozoic reptile faunas are well documented (Robinson 1957; Fraser and Walkden 1983; Fraser 1985). The most abundant genera are two sphenodontids *Planocephalosaurus* (Fraser 1982; Fraser and Walkden 1984) and *Clevosaurus* (Robinson 1973; Fraser, in press). Two rarer sphenodontid genera are sufficiently abundant to allow partial descriptions and the definition of some diagnostic characters (Fraser 1986). A fifth sphenodontid, *Diphydontosaurus*, described by Whiteside (1986) from abundant remains at the neighbouring locality of Tytherington Quarry, is relatively common. There are also isolated fragments of *Kuehneosaurus*, a gliding diapsid reptile described by Robinson (1962) from similar fissure localities in Somerset. Included within the material awaiting full description there are well-preserved specimens of a procolophonid and abundant archosaurian remains. The latter include
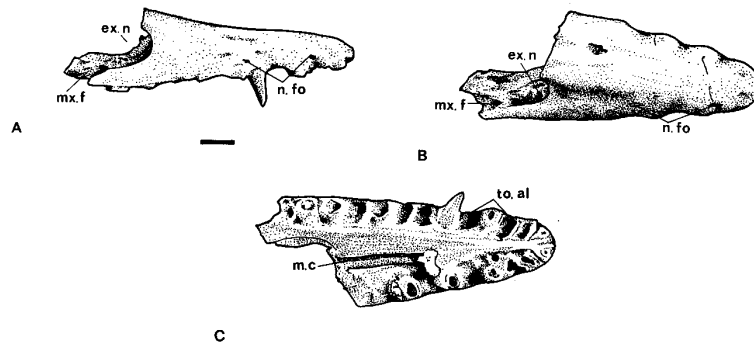
TEXT-FIG. 1. The fused premaxillae AUP 11305 in A, lateral, B, dorsal, and C,
ventral aspects. The scale bar represents 0·5 mm.

a terrestrial crocodile and two thecodontians. On the basis of various diagnostic criteria, twelve distinct reptilian taxa have been recognized, and their taxonomic relationships can be at least partially assessed. By contrast, a few quite characteristic elements have been recovered that are extremely rare indeed. From 1·5 tonnes of rock processed at Aberdeen University Geology Department, which have yielded in the region of 10 000 identifiable bone fragments, two different types of premaxillae, two maxillae, and a procoelous vertebra are exceptionally rare—only six specimens of the vertebra have been found, and there are even fewer examples of the four jaw bones. By contrast, the same quantity of sediment produced 150 *Planocephalosaurus* maxillae and 120 premaxillae. The rare forms are quite distinct from the more ubiquitous genera in the deposits, and they are consequently very difficult to treat taxonomically. It is undesirable to erect new genera or species on such isolated material, yet they merit description as additional taxa.

JAW BONES

Premaxilla I

Five specimens of a long, slender, bilaterally symmetrical bone represent fused premaxillae (text-fig. 1). Four originate from levels M, K, and L of site 4, and one from Level A of site 5 (for details of the fissure stratigraphy and nomenclature, see Fraser 1985). The largest specimen is 6·0 mm long and the smallest 4·5 mm. Two tooth rows are exposed in ventral aspect. They meet at the sharply angled anterior end, but diverge somewhat posteriorly to leave a narrow channel between the two dental rami (text-fig. 1C). In the few instances where the teeth are preserved, they are acutely conical and set in very shallow alveoli which have a slightly higher lateral than medial wall. When restored, it is estimated that there were between ten and twelve tooth positions in each row. Each tooth alveolus is produced into a slight lateral bulge so that in dorsal view the margins of the bone are faintly scalloped (text-fig. 1B). In lateral aspect, the bone exhibits a low profile, and both sides are deeply emarginated posteriorly by separate openings, presumably representing the external nares (text-fig. 1A). The posterior boundaries of the bones are incomplete in all five specimens; as a result the full extent of the bone above and below each narial opening is unknown. Nevertheless, in one specimen (AUP 11305), the posterior process passing beneath the left naris appears to be almost complete (text-fig. 1A). On the dorsolateral surface of this process there is a small notched facet which presumably formed the articulation with the maxilla, and indicates a limited contact between the two elements (text-fig. 1B). Each specimen bears a variable number of small nutrient foramina, usually three or four on each side, which lie in a line just above the level of the tooth rami.

The general outline of this element is most reminiscent of a pterosaur. However in pterosaurs, including the known Norian rhamphorhynchoid forms (Wild 1978), the ventral border of the external naris is almost entirely formed by the maxilla and there are characteristically only three
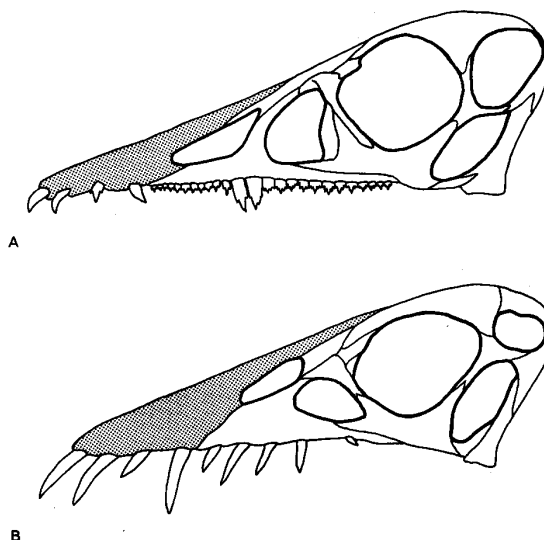
TEXT-FIG. 2. Rhamphorhynchoid pterosaur skulls in lateral
aspect. A, *Eudimorphodon* and B, *Dorygnathus* (after Wild
1978).

or four premaxillary teeth (text-fig. 2). The tooth implantation of pterosaurs is generally considered
to be thecodont or possibly subthecodont (Edmund 1969; Wild 1978). In the element under
discussion there is insufficient depth of bone to support a 'deep-rooted' thecodont dentition.
Bearing in mind that the lateral wall of the dental groove appears to be slightly higher than the
medial side, there is reason to speculate that the tooth implantation may be a modified subthecodont
type correlated with the low lateral profile and miniaturization of the jaw.

The tooth morphology and implantation is similar to *Kuehneosaurus*, but the overall shape of
the element is quite different. The elongated form is not dissimilar to a miniature crocodile or
thalattosaur (text-fig. 3). However in crocodiles, the nares are generally terminal and face dorsally.
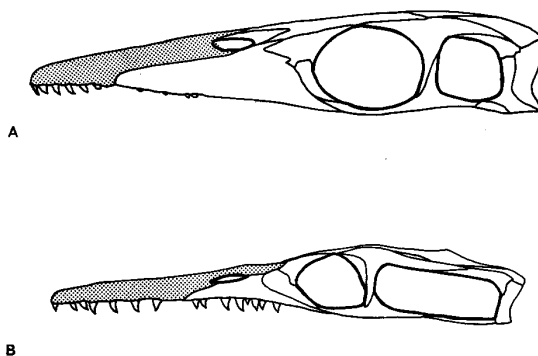
TEXT-FIG. 3. Thalattosaur skulls in lateral view. A, *Thalat-
tosaurus* and B, *Askeptosaurus*. (A, after Merriam 1905; B,
after Kuhn (-Schynder) 1952.)
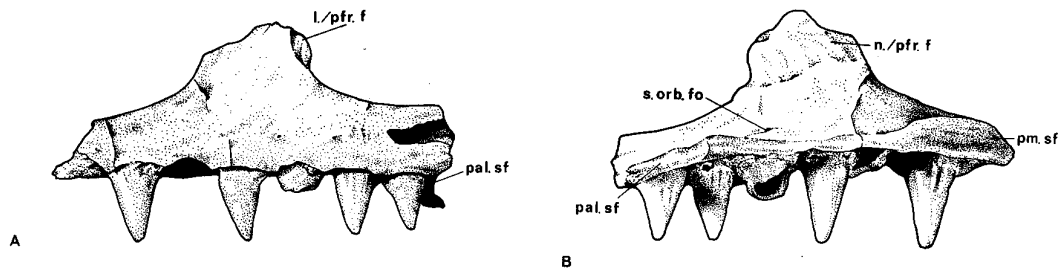
TEXT-FIG. 4. Maxilla I. AUP 11293 in A, lateral aspect and B, medial view. Scale bar represents 0·5 mm.

Tooth implantation in thalattosaurs apparently varies from thecodont in *Askeptosaurus* and *Thalattosaurus* (Kuhn (-Schnyder 1952), to acrodont in *Hescheleria* (Peyer 1936*b*), and either pleurodont or acrodont in *Clarazia* (Peyer 1936*a*; Rieppel 1987). In addition, the known thalattosaurs are much larger than the material under discussion, the premaxillae are apparently separate, and the premaxillary dentition is restricted to the anterior part of the element.
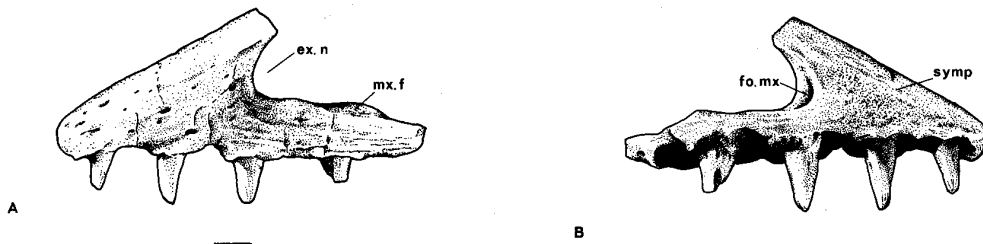
Maxilla I

A maxilla of a size and form consistent with the fused premaxillae is represented by four specimens, all from Site 4 (Levels M, K, and J). It is a relatively short but slender element (text-fig. 4) not exceeding 5 mm long, and when restored probably possessed a maximum of twelve teeth. In all specimens, the rather short ascending process is incomplete. It bears a facet on its medial aspect where it presumably overlapped the nasal or prefrontal (text-fig. 4B). There is an additional notched facet, positioned towards the posterior margin on the lateral face of the ascending process (text-fig. 4A). It is quite conceivable that this facet received the lachrymal or prefrontal, and this in turn suggests that an antorbital fenestra was unlikely. Judging by the gentle posterodorsal slope and slight concavity of the anterior margin of the bone, the external nares were elongate. In medial view there is a prominent faceted flange set obliquely to the anterior edge of the dental groove (text-fig. 4B). This presumably formed the articulation with the premaxilla (or possibly the vomer). Posteriorly, the element broadens into a medial shelf which is poorly preserved in all four specimens, although it presumably formed an articulation with the palatine. Immediately above this shelf there is a fairly prominent foramen, the suborbital foramen, which transmitted the palatine nerves and blood vessels. Where preserved, the teeth are acutely conical and only slightly recurved. They are circular in cross-section and appear hollow and thin-walled. The implantation is of the same type as the fused premaxillae described above.

In terms of overall structure, tooth morphology, and size, it is tempting to suggest that these maxillae belong to the same species as the fused premaxillae. Their relative abundance and distribution within the deposits is also consistent with this view. However, because the material is so scarce the link between the two elements remains tenuous.

Premaxilla II

The two remaining jaw bones to be described are a single premaxilla and an isolated maxilla, both from Level M of Site 4, and both having similar tooth implantation to the forms described above.

The premaxilla is from the left side, and the entire tooth ramus would appear to be present, consisting of nine alveoli (text-fig. 5B). Four teeth are preserved, three complete, and one missing the distal end; they are ankylosed at every other tooth position. Within the constraints of current inadequate definitions, the tooth implantation is best described as a shallow subthecodont type—each tooth set in a very shallow depression and with a slightly higher lateral than medial wall. The teeth themselves are subcircular in cross-section, and they are only very slightly recurved. The smooth surfaces of the teeth are relieved by fine longitudinal striations covering the distal third of each complete tooth. In lateral profile, the anterior margin of the bone is straight and extends posterodorsally at an angle of approximately 45° to the dental ramus (text-fig. 5A). The medial surface forms an elongate, almost vertical, symphysis (text-fig. 5B) that presumably articulated with its counterpart, and together they would have formed an acutely pointed snout. The bone is emarginated
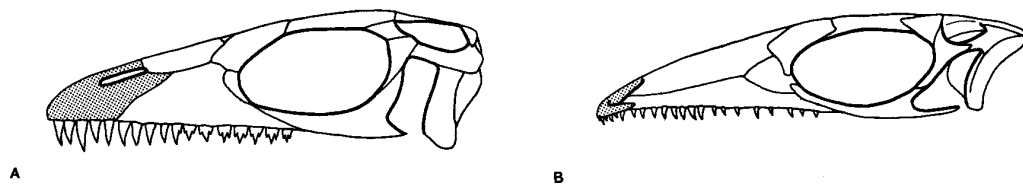
TEXT-FIG. 5. Premaxilla II. AUP 11294 in A, lateral and B, medial aspect. Scale bar represents 0·5 mm.

posteriorly by the external naris. The full extent of the process above the naris is unknown. Ventral to the naris the element is developed into a short medially directed ledge. A shallow depression on the dorsolateral surface of this ledge is satisfactorily interpreted as the maxillary facet. Situated immediately anterior to the narial opening, a posteriorly facing foramen probably transmitted branches of the maxillary artery and nerve.

In general terms, the outline of the premaxilla is perhaps most like a prolacertiform. However, in macrocnemid prolacertiforms at least, the external nares are placed further up on the dorsal surface of the snout and the premaxillae meet the maxillae in extended sutures. *Tanystropheus* is similar to the macrocnemids in this respect (text-fig. 6A). Although the arrangement in *Prolacerta* is perhaps closest to the new form (text-fig. 6B), the premaxillary tooth count of *Prolacerta*, like *Tanystropheus*, rarely exceeds five. The tooth implantation of the new form is comparable with the kuehneosaurids, a pattern which Robinson (1962) and Colbert (1970) referred to as subpleurodont. Wild (1973, 1980) also classifies the teeth of *Macrocnemus* and *Tanystropheus* as subpleurodont (or pleurothecodont), yet the tooth implantation of these two genera is rather different from the kuehneosaurids. Definitions of tooth implantation need to be much stricter if comparisons between the dentitions of such genera are to be meaningful.

Maxilla II

The last jaw element to be described here is interpreted as a left maxilla (text-fig. 7). The bone is preserved as two fragments, but only the extreme anterior and posterior limits of the bone are missing. There are eight partially preserved teeth and a total of ten tooth positions. The teeth are acutely conical, slightly recurved, and display an overall similarity to those of kuehneosaurids and the dentitions already described. The most notable characteristic of the teeth is their exceptional size relative to the depth of the bone, yet they are only ankylosed in shallow alveoli by a minimum of spongy bone of attachment. Longitudinal striae are most pronounced towards the distal extremities of the teeth, and the lateral wall of the dental groove is marginally higher than the lingual wall. An exceptionally narrow ascending process bears no obvious prefrontal or lachrymal facets, and this may indicate the presence of an antorbital fenestra. The short section of the dental ramus extending anterior to the ascending process exhibits a marked medial flexure. This hints at a snout that was somewhat shorter and blunter than those species represented by the two premaxillae described above. On the medial surface, approximately a third of the length from the anterior end of the specimen, there is a prominent foramen which presumably transmitted the palatal vessels. Immediately below

TEXT-FIG. 6. Prolacertiform skulls in lateral view. A, *Tanystropheus* and B, *Prolacerta*. (A, after Wild 1978; B, after Kuhn (-Schynder) 1952.)
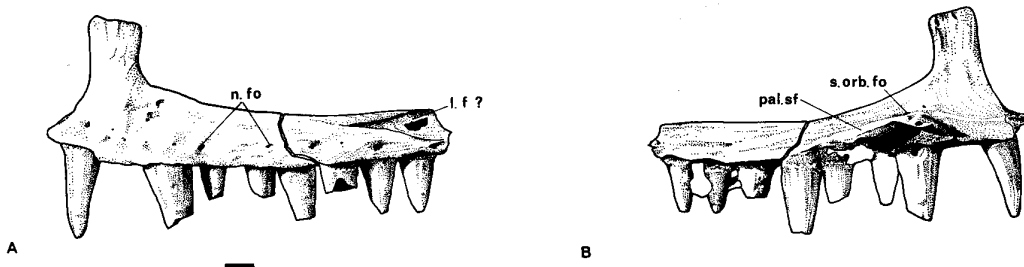
TEXT-FIG. 7. Maxilla II. AUP 11303, in A, lateral and B, medial view. Scale bar represents 0·5 mm.

the foramen, the bone is developed into a faceted medial shelf which is considered to have contributed to the palatine articulation. Further posteriorly the element bears an elongate slot facet on the external surface. The jugal might be expected to articulate with the maxilla in this region, and there is apparently no other potential jugal facet. Nevertheless some doubt exists since the articulation between these two elements in other reptiles is more usually located on the medial surface of the maxilla. If this particular species possessed an antorbital fenestra, it is possible that the facet could have received the lachrymal and that the jugal facet is not preserved in this specimen. In any event, the evidence suggests that this new maxilla represents a form with a lightly built, highly fenestrated skull such as that exhibited by the pterosaurs or the 'thecodontian' *Megalancosaurus* (Calzavara et al. 1980).

I have already mentioned that current definitions of reptilian tooth implantation are somewhat nebulous. Consequently, in the case of the new jaw material a consideration of tooth implantation as a diagnostic characteristic is not thought to be appropriate. Nevertheless, recurved teeth have been considered as one of the characters of the archosaur/prolacertiform group of diapsid reptiles (Benton 1985) (cf. the peg-like teeth of the outgroups Rhynchosauria and Lepidosauromorpha), and certainly the dentitions described herein are generally somewhat recurved and acutely conical. It may seem somewhat anomalous to imply archosauromorph relationships for the new jaw bones when they were also shown to be comparable with kuehneosaurid dentitions (a group normally supposed to have squamate affinities) (Robinson 1962, 1967; Carroll 1977; Estes 1983). However, Evans (1984) pointed out that kuehneosaurids lack the basic lepidosauromorph characters of single-headed ribs on all dorsal vertebrae, accessory facets on the neural arch, and postfrontals entering into the borders of the upper temporal fenestrae. Benton (1985) also expressed some doubts concerning the assignment of the Kuehneosauridae to the Lepidosauromorpha, and there is good reason to suppose that they may have closer affinities to the Archosauromorpha. These include reduction of the postfrontal, the laterally placed carotid foramina, and the contribution of the basisphenoid to the lateral walls of the braincase. Unfortunately, the ankle joint, which is crucial to the question, is unknown in all kuehneosaurs. The rarity and very fragmentary nature of the new material does not permit a detailed taxonomic study. Generally these jaw bones exhibit a mosaic of characteristics which cannot be readily reconciled with any one particular taxon. It is also likely that the overall features are associated with adaptations towards miniaturization and insectivory and they are therefore not necessarily indicative of taxonomic affinities.

The Procoelous vertebra

Different jaw bone types are readily identifiable within the assemblages, and variation in dental morphology is at least a good indicator of the number of genera, if perhaps not necessarily diagnostic. By contrast, it is by no means apparent with which other elements in a disassociated assemblage isolated postcranial bones should be grouped. This can be particularly true of the axial skeleton where some taxa are known to exhibit marked variation in basic structure within the length of the vertebral column (e.g. the Chelonia, where the cervicals may be a mixture of

TABLE 1. The distribution of the procoelous vertebrae and small jaw bones within the Cromhall fissure deposits. (For details of fissures and horizons see Fraser 1985.)

| | Total | Site 4 | | | | Site 5 |
		Level J	Level K	Level L	Level M	Level A
Premaxilla I	5		2	1	1	1
Maxilla I	4	1	1		2	
Premaxilla II	1				1	
Maxilla II	1				1	
Procoelous vertebra	6	1	1	2	2	

procoelous, amphicoelous, and opisthocoelous). Therefore, the occurrence of a most unusual and rare procoelous vertebra within the Cromhall assemblages poses its own special problems.

The great majority of vertebrae in the assemblages are of the amphicoelous or notochordal amphicoelous type, but the new specimens are quite distinctive and it is not clear whether they are representative of a species partially described previously on the basis of other material, or indicate the occurrence of a new form. The six specimens are of uniform size, attaining a length of 6 mm, a height of 4 mm, and a width of 4 mm. These dimensions are likely to be consistent with the species represented by the fused premaxillae, and the occurrences of the two elements follow similar distribution patterns (Table 1). Although it is tempting to suggest that they may represent the same species, there is no other evidence to support this view. All six specimens have an identical structure, and they are therefore assumed to originate from exactly the same region of the vertebral column. In addition, the lack of any further remains of procoelous vertebrae strongly suggests that the remainder of the vertebral column may have been more typical, and perhaps fragments of indeterminate amphicoelous vertebrae are representative of the major portion of the axial skeleton. Other workers have noted that there is a tendency for small braincases to exhibit a certain degree of structural convergence towards vertebrae (A. R. I. Cruickshank and O. Rieppel, pers. comm.), and the possibility that these specimens might represent a rather unusual braincase has been investigated. Whilst certain features can be reconciled with such an identification (e.g. a possible parasphenoid rostrum), there are no apparent paroccipital processes, and the specimens are unreservedly considered to be vertebrae by virtue of the definite anterior and posterior articulation facets.

The new vertebra (text-fig. 8) is rather elongate, a condition accentuated by the extension of the centrum posteriorly beyond the level of the zygapophyseal articulation. The diameter of the neural arch is some two to three times that of the centrum, the latter taking the form of a slender conical frustum. A narrow keeled hypopophysis, produced below the centrum, is incomplete in all specimens, but it appears to have extended beyond the intercentral articulation so that it passed under the anterior end of the succeeding vertebra. The procoelous intercentral articulation is unusual in that the anterior concavity, the cotyle, is approximately kidney-shaped, and it is inclined ventrally. The opposing convex posterior facet, the condyle, is saddle-like and faces posterodorsally. The overall intercentral articulation is therefore rather like the heterocoelous condition in birds, but lacking the bilateral expansions of the cotyle and condyle. The zygapophyses are quite unusual in that they are inclined towards the vertical plane. This would have tended to restrict lateral movement, but at the same time facilitated flexure of the vertebral column in the vertical plane. The level of the zygapophysial articulation is set forward from the intercentral articulation. There are no accessory intervertebral articulations comparable to those of lepidosauromorphs. There appear to be separate diapophyses and parapophyses. The diapopysis, although incomplete in all specimens, apparently formed a short pedicel with a small circular distal rib facet. A short bony ridge connects this pedicel to a V-shaped articular surface which is presumed to be the parapophysis. The apex of the putative parapophysis is directed anteriorly and is situated immediately above and lateral to the cotyle on the centrum. This particular
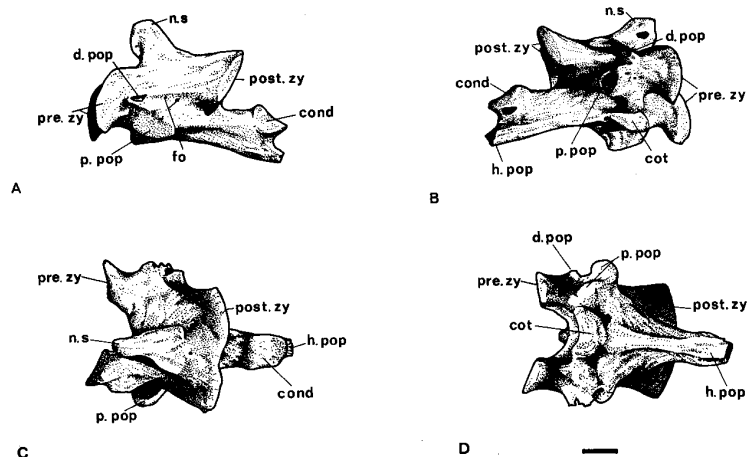
TEXT-FIG. 8. The procoelous vertebra. AUP 11362 in A, lateral, B, dorsal, and C, ventral aspects. Scale bar represents 0·5 mm.

arrangement is also consistent with the view that these V-shaped articular surfaces represent pre-exapophyses, but the apparent lack of complementary postexapophyses does not lend any further support to this identification.

The affinities of these specimens are not immediately apparent. The procoelous condition approaches the heterocoelous articulation of birds, but they are not identical since laterally the cotyle and condyle flare considerably in birds. On the one hand, separate parapophyses and diapophyses are more generally associated with archosauromorphs than lepidosauromorphs, and the lack of accessory intervertebral articulations on the mid-line of the neural arch provides further support for an assignment to the archosauromorphs. On the other hand, affinities with non-diapsid groups cannot be discounted.

It is interesting to note certain similarities between the new vertebra and the cervical vertebrae of Pterodactyloidea, as described by Howse (1986). In particular, they share a shallow centrum extending posteriorly well beyond the limits of the postzygapophyses. Howse noted that Cretaceous pterodactyloids were normally characterized by the presence of exapophyses associated with the cotyle and condyle, and a hypopophysis situated towards the anterior ventral surface of the centrum. Whilst there is a remote possibility that exapophyses are present in the new vertebra, the hypopophysis is positioned on the posterior ventral surface of the centrum, and although the new vertebra may possess certain characters indicative of pterodactyloid affinities, age considerations are not consistent with this view. The known Triassic pterosaurs belong to the Rhamphorhynchoidea, and peterodactyloids do not appear in the geological record until the Upper Jurassic. Rhamphorhynchoid cervical vertebrae are immediately distinguishable from those of pterodactyloids (Howse 1986). Apart from the procoelous nature of the pleurocentral articulation, the only character that the new vertebra might conceivably share with rhamphorhynchoids is the possible occurrence of pneumatic foramina. Immediately below the pedicel of the neural arch, each of the new specimens exhibits either one or two small foramina which may lead into larger internal excavations.

SUMMARY

Isolated elements from a disassociated vertebrate assemblage are difficult to treat taxonomically. Often the rarest components of such assemblages are only recognizable from jaw bone fragments,

yet their structure alone is generally insufficient to enable us to make substantial claims with regard to their relationships. Although jaw elements may exhibit certain diagnostic characteristics, they also reflect dietary habits, and it has been shown here that the use of reptilian tooth implantation as a fundamental taxonomic criterion is open to criticism. Accordingly, only very broad taxonomic statements have been made with respect to the rarest faunal elements, but the possible occurrence of prolacertiform, thalattosaurian, or pterosaurian remains within the Cromhall assemblages should not be overlooked.

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ABBREVIATIONS

cond	condyle	n./pfr. f	nasal and/or prefrontal facet
cot	cotyle	n.s	neural spine
d. pop	diapophysis	pal. sf	palatine shelf
ex. n	external naris	pm. sf	premaxillary shelf
fo. mx	foramen for maxillary artery and nerve	post. zy	postzygapophysis
h. pop	hypopophysis	p. pop	parapophysis
l. f	possible lachrymal facet	pre. zy	prezygapophysis
m.c	median channel	s. orb. fo	suborbital foramen
mx. f	maxillary facet	symp	symphysis
n. fo	nutrient foramen	to. al	tooth alveolus