# Critical Assessment of a Proposed Biostratigraphic Scheme for Late Triassic Fissure Sediments from South West England

by

Anne Louise Maclean Davis

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APPROVED:

R. K. Bambach, Chair

N. C. Fraser, Co-Chair

for N. L. Gilinsky

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# AN EXAMINATION OF A PROPOSED BIOSTRATIGRAPHIC SCHEME FOR LATE TRIASSIC FISSURE-FILL MATERIAL FROM SOUTH WEST ENGLAND

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Anne Louise Maclean Davis

R. K. Bambach and N. C. Fraser, Co-Chairs

Department of Geological Sciences

Questions as to the tempo and mode of changes in faunal composition at the Triassic/Jurassic boundary remain unanswered. Inquiries are hampered by a general paucity of sections containing correlatable Late Triassic/Early Jurassic strata. Vertebrate fossil material from Cromhall Quarry, recovered as part of an extended project centred on Late Triassic fissure infillings in southwestern Britain, was organized into a biostratigraphic scheme in 1993. This scheme could prove important in correlating Late Triassic continental strata.

The Cromhall data consists of taxonomic counts from individual stratigraphic levels within a series of fissures. Level counts were sorted into a series of sequential sedimentary and faunal associations that rest on the assumption that significant differences in faunal composition occur between individual fissures, but do not exist between individual sedimentary strata within any one fissure. Before the biostratigraphic framework could be utilized, the actual degree of similarity between the fissure faunas had to be quantified and tested.

The original database, and counts from newly processed material, were subjected to Principle Components and Cluster Analyses. The analyses suggest that the majority of stratigraphic levels within any one fissure contain faunas with very similar composition. Levels from fissures that are temporally seqential contain faunas that are somewhat similar in composition. Overlap, in faunas found in strata at the top and bottom of sequential fissures, can be detected. In addition, there is a trend toward increased presence of certain taxa in the younger levels. These results indicate that the biostratigraphic framework may be used to enhance Triassic-Jurassic boundary research.

Dedicated to Helen and Richard Davis.

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## INTRODUCTORY SECTION

During the Early Mesozoic, particularly in the Late Triassic and Early Jurassic, the dominant components of terrestrial ecosystems change worldwide. This global faunal change marks not only the rise to dominance and diversification of the dinosaurs, but also the appearance of almost all the major modern terrestrial vertebrate groups; including the lissamphibians (frogs, toads, salamanders), crocodiles, turtles, and mammals. Considerable debate has been generated as to the timing and possible causes for the extinction of many taxa and the radiation of others. Much of the work has focused on the success of the dinosaurs, with numerous authors citing a variety of physiological reasons for their wide-spread radiation during the end Triassic. These differences, including endothermy (Bakker, 1971 and 1980; Cox, 1967), improved locomotor skills (Bakker, 1979; Charig, 1972 and 1984), and inertial homeothermy (Spotila, 1980), have been used to discuss the faunal change in terms of gradual competitive replacement of the existing forms by better evolved taxa (Benton, 1983, 1986 and 1994). Other papers (Bakker, 1971; Benton, 1983 and 1994; Tucker and Benton, 1982; Olson, 1982; Olsen *et al.*, 1987) have cited mass extinctions of several groups of dominant terrestrial vertebrates (dicynodonts, diademodonts, rhynchosaurs, most cynodonts) near the end of the Triassic, which would allow new taxa to radiate into empty ecospace (Benton, 1986). Debate continues over the cause(s) for this faunal turnover, and as Padian (1994) indicates, there is much more work to be done

considering the patterns of tempo and mode of faunal change across the Triassic/Jurassic boundary.

Perceptions of patterns within this faunal turnover may be greatly influenced by the stratigraphic correlation of disjunct strata and faunas. This proves to be a particularly problematic issue within the Early Mesozoic as the Triassic type sections are difficult to correlate to any strata, marine or otherwise, due to complexities of lithology, structure, and definition. In fact, the Triassic system was first defined in Europe on the basis of rocks that exhibit two notably different facies. The "Germanic" northern sequence, felt to be mainly continental in origin, provides the type area for the lithologic divisions of the Triassic and the "Alpine" southern sequence, that is mainly marine, provides the type areas for the stages of the Triassic (Warrington *et al*, 1980; Olsen and Sues, 1986).

J.G. Lehman and G.C. Fuschsel defined the Buntsandstein and Muschelkalk of the Germanic Basin of Central Europe in 1780, L. von Buch defined the Keuper in 1820, and F. von Alberti united the three divisions into the Triassic system in 1834 (Colbert, 1986). The lithologic divisions consist of two continental and paralic (lagoonal and littoral) facies (the older Buntsandstein and younger Keuper, respectively) separated by a middle marine sequence (the Muschelkalk). However, the wholly marine sequences of the Alps provided the type areas for the stages of the Late Triassic. These stages were based on marine invertebrate zones, particularly those of ammonites. Thus, due to a

sparsity of macrofossils, the Triassic "Germanic" facies were been divided mainly using lithostratigraphy, while the more fossiliferous Triassic "Alpine" facies were divided using biostratigraphy (Warrington *et al*, 1980). Correlation of the "Alpine" zones with the marine sediments of the "Germanic" Muschelkalk have proved to be fairly easy. The upper and lower boundaries of the Muschelkalk appear to be diachronous (Olsen and Sues, 1986). However, correlation of the lithologic divisions of the Keuper with the "Alpine" stages is very weak (Olsen and Sues, 1986). As a result, attempts to correlate outside Europe (indeed outside individual European basins) have led to confusion.

In Britain, the "Germanic" Triassic nomenclature was largely adopted and, until the 1980s, proved to be the cause of significant stratigraphic ambiguity. In general, the marine incursion at the end of the long Permo-Triassic continental episode was termed the Rhaetic (Hallam and El Shaarawy, 1982). The Rhaetic was defined in 1861 by C.W. Gumbel on the basis of sediments in Swabia (Colbert, 1986). The base of the type Rhaetic is defined by the appearance of marine bivalve shells (*Rhaetavicula contorta*), above which are bone beds containing vertebrate remains. The rocks Gumbel deemed Rhaetic were later found to contain ammonites of Triassic affinity, leading to the creation of the topmost Triassic (Rhaetian) stage (Hallam and El Shaarawy, 1982). Debate over the placement of the Rhaetic has veered from situating it as uppermost Triassic (favoured by German workers) to placing it as basal Jurassic (the French alternative; Colbert, 1986). Revisions of the

ammonite zonations of the Alpine and Arctic Triassic sections have reduced the Rhaetian to a single ammonite zone, and it is now sometimes included in the Norian rather than as a separate stage (Olsen and Sues, 1986). Due to the limited applicability of this stage, some authors have suggested that recognizing a separate Rhaetian be abandoned (Tozer, 1979; Buffetaut and Wouter, 1986). Benton (1994) has proposed a new zonation for terrestrial tetrapod-bearing units. The time units, not yet formally named, utilize data from palynological, ammonite, and tetrapod schemes (Benton, 1994). Benton's (1994) zonation subdivides the Carnian and Norian into Early, Middle, and Late time intervals. These time intervals can be, in turn, subdivided into first and second (oldest and youngest, respectively) units. Using Benton's (1994) notation, the Carnian is divided into the CRN E (Early Carnian), CRN M (Middle Carnian), CRN L1 (Late Carnian, part 1), and CRN L2 (Late Carnian, part 2). This zonation will be used throughout the thesis **(Figure 1)**.

In 1970, Pearson, and in 1980, Warrington *et al*, proposed that European lithostratigraphic terms like "Bunter, "Keuper", and "Rhaetic" be abandoned in British literature as their lithostratigraphic usage has lead to inappropriate chronostratigraphic applications. In the case of the "Rhaetic", palynological evidence suggesting that the British "Rhaetic" sequence was only a subset of Rhaetian time made abandonment of this term necessary (Pearson, 1970; Warrington *et al*, 1980). Instead, in Britain, local lithostratigraphic names are used in place of this term. The British "Rhaetic" is now designated the Penarth

| | | Ammonoid Zones | Palynomorph Zones | Tetrapod Zones |
|---|---|---|---|---|
| NORIAN | U. | Crickmayi | (Rhaetian) | NOR L2 |
| | | Amoenum | Sevatian | NOR L1 |
| | | Cordilleranus | | |
| | M. | Columbianus | Upper Norian (Aluanian) | NOR M2 |
| | | Rutherfordi | Lower Norian (Lacian) | NOR M1 |
| | | Magnus | | |
| | L. | Dawsoni | | NOR E |
| | | Kerri | | |
| CARNIAN | U. | Macrolobatus | Tuvalian | CRN L2 |
| | | Welleri | | CRN L1 |
| | | Dilleri | | |
| | L. | Nanseni | Julian | CRN M |
| | | Obesum | Cordevolian | CRN E |
| LADINIAN | U. | Sutherlandi | Langobardian | LAD |
| | | Maclearni | | |
| | | Meginae | | |

Figure 1

Benton's (1994) zonation of the Triassic using ammonoid, palynomorph, and tetrapod data.

Group (**Figure 2**; Hallam and El Shaarway, 1982; Warrington *et al*, 1980).

Adding to this debate is the fact that there are relatively few sections, worldwide, with complete sequences of continental deposits felt to be Late Triassic/Early Jurassic in age. Sections that may fill this criterion (sequences from the southwestern United States, the Newark Supergroup of the Atlantic margin of North America, the Bristol region of England and South Wales, the Ischiguaslasto basin of Argentina, the Pranhita-Godavari Valley in India, the Stormberg Series in South Africa, and the Yunnan region of China) are now the subject of considerable study (Benton, 1994).

Cromhall Quarry (formerly known as Slickstones Quarry) has become the focus of inquiries relating to Triassic/Jurassic boundary changes. The quarry is one of a series of sites in south west Britain and South Wales at which Lower Carboniferous limestones are unconformably overlain by Triassic deposits in the form of cover and fissure fills (**Figure 3**). Limestone quarrying has exposed these fissure fills, some of which contain rare Triassic terrestrial taxa The opportunities afforded to vertebrate palaeontologists to study bone accumulations from this poorly sampled time period have made Cromhall Quarry the subject of scientific interest (e.g. Swinton, 1939; Robinson, 1957; Halstead and Nicoll, 1971; Fraser and Walkden, 1983; Fraser, 1985; Walkden and Fraser, 1993). The site has retained its popularity due to its accessibility, the fact that the quarrying activities are concentrated such that fissure-fills are exposed but not usually destroyed by heavy machinery, and because the matrix

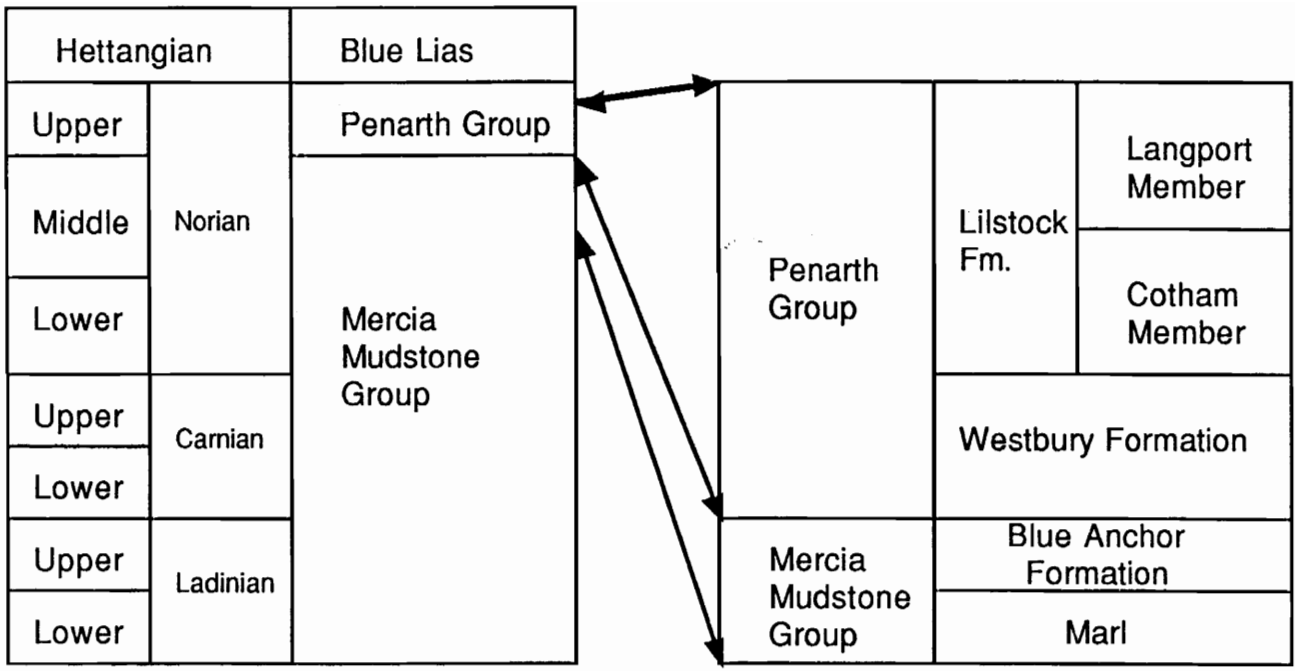



Figure 2

Upper Triassic stratigraphy of South West Britain (adapted from Fraser, 1988 and 1994).

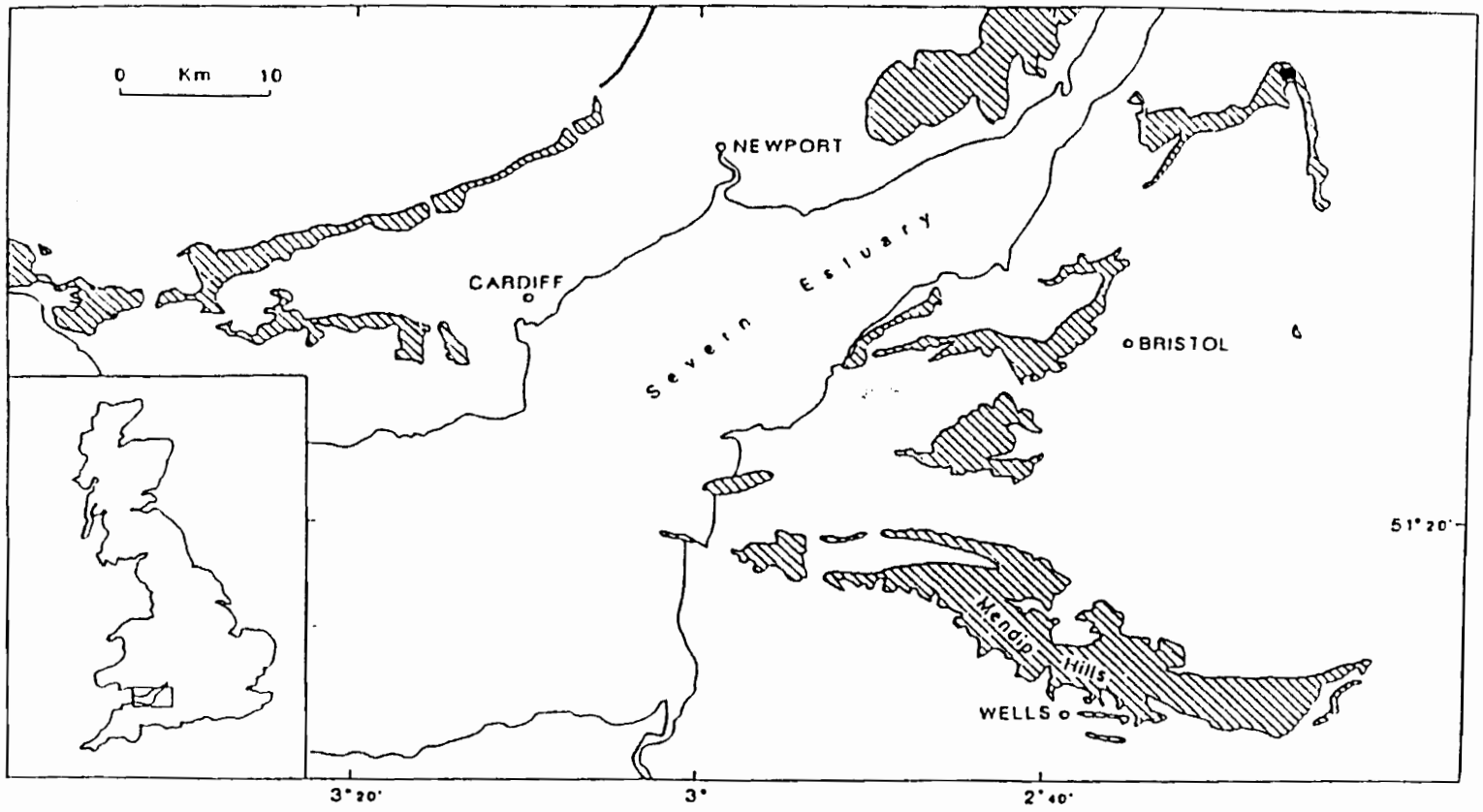



Figure 3

Map of the United Kingdom (inset) and portions of South West Britain and South Wales in the Severn Estuary region. Hatchured areas indicate Carboniferous limestone outcrop. Cromhall Quarry is marked by a filled square (from Fraser, 1985).

recovered from the site is generally fossiliferous. Consequently, repeated collecting within the quarry confines has produced fissure-specific compilations of sedimentary and faunal associations.

## REVIEW OF LITERATURE

### PART I - GENERAL GEOLOGY OF CROMHALL QUARRY

Cromhall Quarry (U.K. National Grid Reference ST 704 916), located at the northern end of the North Avon syncline, is the product of a limestone quarrying operation which cuts into well-bedded, southerly-dipping Lower Carboniferous (Tournaisian) crinoidal grainstones of the Black Rock Group (Walkden and Fraser, 1993). The Black Rock Group is represented by 250 to 300 m of Black Rock Limestone (Smith, 1975). It mainly consists of dark grey to black bioclastic limestones with large amounts of crinoidal debris in a fine-grained ground mass (Smith, 1975; **Figure 4**). These grainstones are abundantly jointed in a predominantly north-south direction, and have been partially dolomitized (Walkden and Fraser, 1993). Triassic sediments, mainly consisting of red and green muds of terrestrial origin, lie unconformably on the limestones; either as cover or as fissure fills (Walkden and Fraser, 1993).

Walkden and Fraser (1993) note that fissure systems in the south west of Britain and South Wales tend to fall into two categories: (i) deep, planar cuts; and (ii) irregularly tubular, conical, or cavernous voids. Type (i) fissures are believed to be tectonic in origin; forming along faults, joints, or fractures in the rock, while Type (ii) fissures are karstic. These two fissure types may intergrade, with tectonically mediated breaks in the rock enlarged by karstic dissolution (Walkden and Fraser, 1993). This is similar to the thesis presented by Smart *et al* (1988); void infill deposits can generally be described as neptunian dikes,

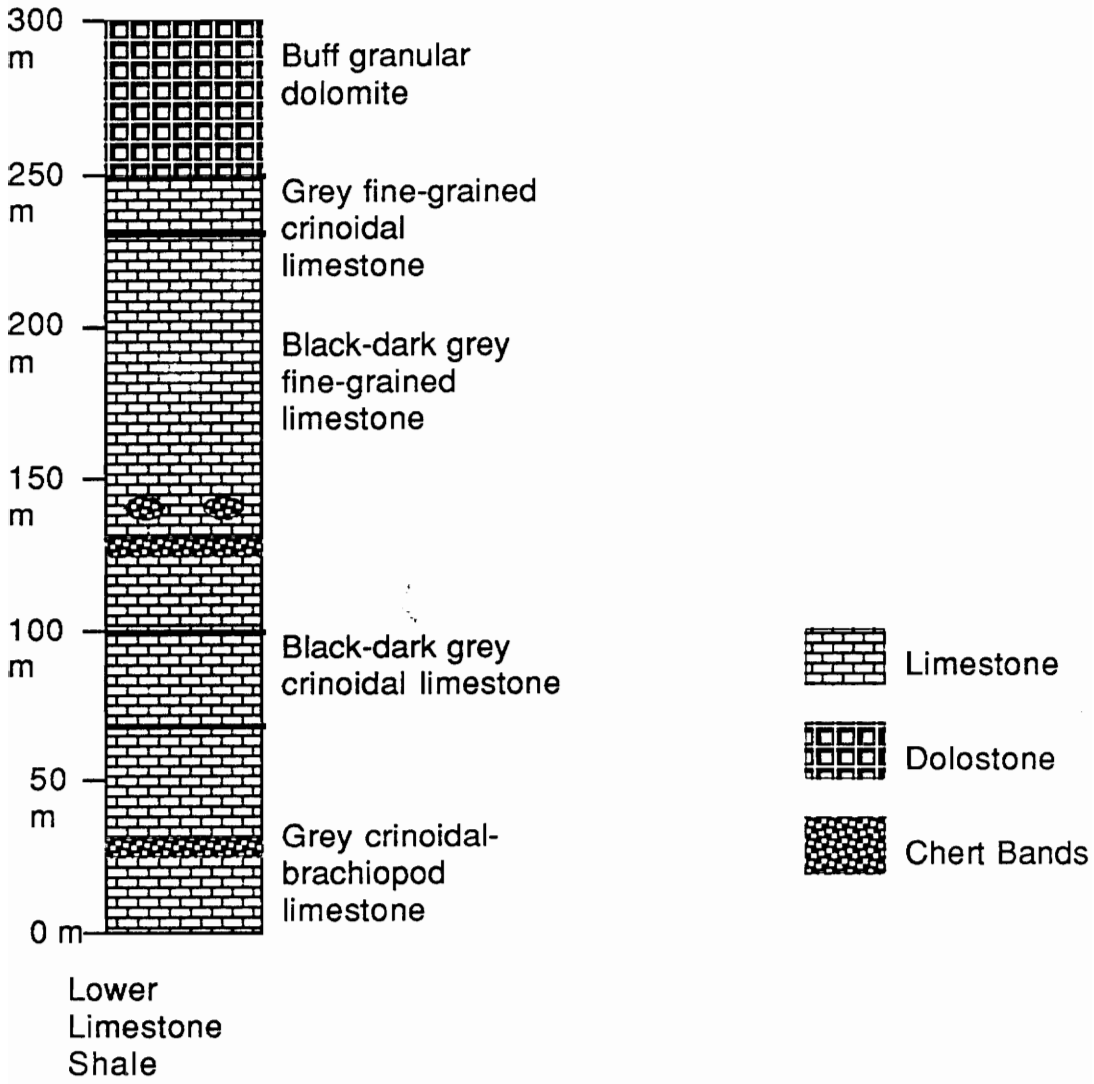



Figure 4
Columnar section of the Black Rock Group at Burrington Combe (from Smith, 1975).

terrestrial (often karstic) fissure fills, and cavern infills. Neptunian dikes consist of void infills in rocks exposed on the sea floor (Smart *et al*, 1988). They tend to be deep cuts with little evidence of void development after the initial fracture opening (Smart *et al* ,1988). Neptunian dikes are considered the marine equivalent to terrestrial fissure fills (Smart *et al*, 1988). However, terrestrial fissures may show extensive void modification (dissolution and mechanical enlargement related to subaerial processes (Smart *et al*, 1988). Cavern infills are the sediments found in subaqueous roofed voids (cavities) in brackish or freshwater phreatic environments (Smart *et al*, 1988; **Figure 5**). When dealing with neptunian dikes and terrestrial fissures, it should be noted that the type of initial void created may be genetically related (Smart *et al*, 1988). In areas of regional tectonism, fractures with strongly preferred orientations develop into neptunian dikes when opened under marine conditions (Smart *et al*, 1988). If the fracture opens subaerially, it will develop into a terrestrial fissure (Smart *et al*, 1988). In areas of repeated regional tectonism, like the Mendip Hills of southwestern Britain, fractures may be reactivated after initial sedimentation; resulting in zoning and brecciation of infill in local neptunian dikes (Robinson, 1957; Smart *et al*, 1988).

Fissures located in the west wall of Cromhall quarry are karstic, while those in the east wall are slot, or tectonic, in origin. The fact that most of the western-wall fills line up along a north-south directional axis suggests that water movement exploited existing jointing (Walkden and Fraser, 1993). Main and

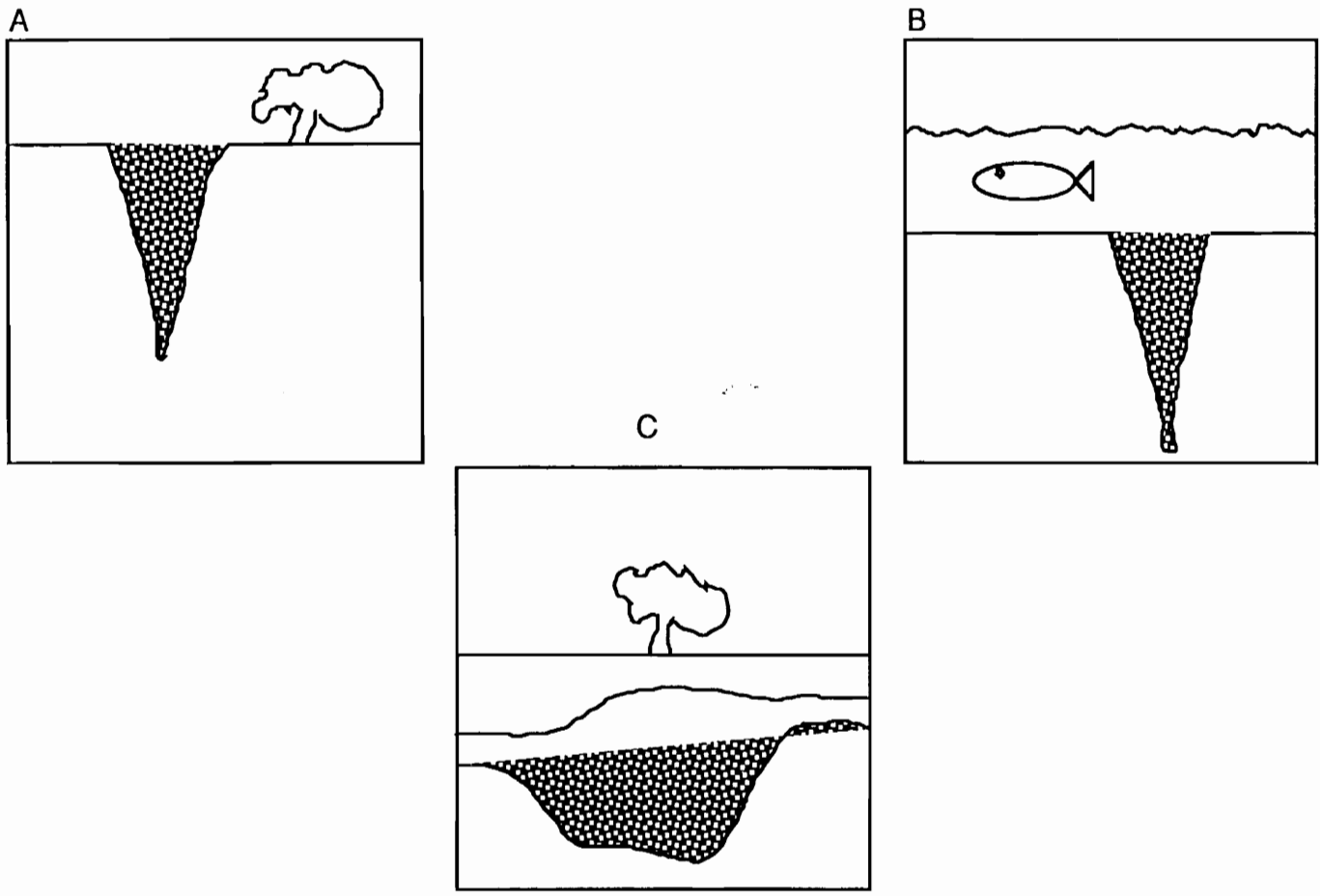



Figure 5

Diagram illustrating the relative differences between the location of terrestrial fissures (A), neptunian dikes (B), and cavern infills (C).

ancillary fossiliferous fissures distributed along the west wall of the quarry mostly consist of isolated (sites 1-3, 7, 14) or coalesced (sites 4 and 5) deep pits which widen upwards to create doline-like cones a few meters across (Walkden and Fraser, 1993; **Figure 6)**. Evidence, in the form of sediments adherent to the remnants of fissure walls, of a larger and more complex cave system is also found (site 6 and most ancillaries). The extent of the site 6 system, and the fact that portions of it extend under sites 2 and 5, suggested to Walkden and Fraser (1993) that, although the fissures on the west quarry wall exhibit mainly distinct fills and faunas, these openings likely drained through a common conduit at depth. Collecting expeditions in the past (i.e. Robinson, 1957; Robinson, Kermack, and Joysey, 1951) encountered a larger fissure (possibly a cave) at the south west corner of the quarry, but this has been removed by subsequent quarrying operations.

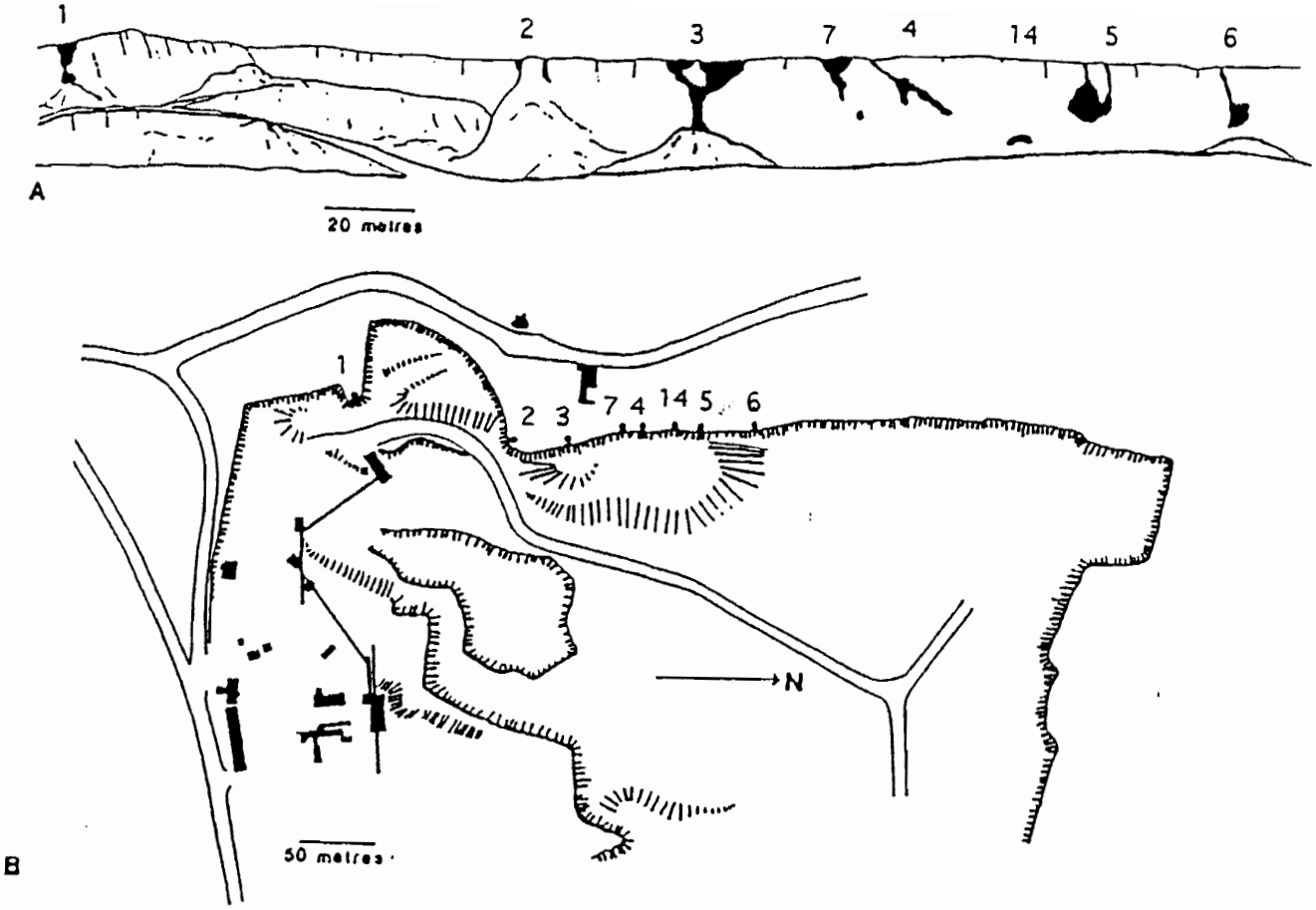



Figure 6

Sketch of the western wall of Cromhall Quarry in 1990 (A), and a plan view of the fissures exposed at that time (B; adapted from Walkden and Fraser, 1993).

## PART II - TRIASSIC SEDIMENTS AT CROMHALL QUARRY

The Triassic sediments at Cromhall Quarry can be divided into two types, fissure-fills or cover sediments, on the basis of their respective positions. Despite attempts to recover pollen and spores from Cromhall Quarry, none have been successful to date (Walkden and Fraser, 1993). This phenomenon is not unusual; Horacek and Kordos (1989) report that calcareous sediments within karst are more favourable to the fossilization of vertebrate and molluscan remains, while non-calcareous organisms (e.g. insects, plant material, pollen and spores) tend to oxidize and are not found. While advances in pollen extraction techniques have led to the discovery of some plant remains in fissure-fills, the majority of biostratigraphic data derived from palaeokarst is based on vertebrate and molluscan material (Horacek and Kordos, 1989).

The potential age of the Cromhall in-filling events was extrapolated from dates determined at other Triassic fissure-fill localities in southwestern Britain and southern Wales. Faunas not unlike those found in Cromhall Quarry have been dated as older than Nor L2 at Emborough Quarry on the basis of stratigraphic evidence (Fraser, 1986). In contrast, microfloral evidence in fissures at Tytherington Quarry suggests, to Marshall and Whiteside (1980), a Nor L2 deposition event for a fauna much like that found at Cromhall. Marshall and Whiteside (1980) report that the Tytherington fissure contains archosaur bones, including *Thecodontosaurus*, and lepidosaur bones, including *Clevosaurus*. The relative proportions of these taxa are not reported and, given

that Cromhall has not yet yielded specimens of *Thecodontosaurus*, it is difficult to determine what criteria Marshall and Whiteside (1980) utilized in deciding that the Tytherington fauna is much like that of Cromhall. Fraser (1994) suggests that this supposed similarity in faunas needs to be investigated further before it is accepted. These in-filling dates were not necessarily the only options for the filling of the Cromhall fissures, but served as guidelines. In the absence of clear time markers, it was considered feasible to first constrain the time span and then determine the relative sequence of filling of individual fissures (Walkden and Fraser, 1993).

Walkden and Fraser (1993), therefore, placed the fills in nine associations based on sediment type, superposition, and diagenetic properties. These nine associations, from oldest to youngest, are: (1) red mud and crinoidal sand, (2) calcite crystals and calcite silt, (3) dark greed/red structureless mud and laminated red mud, (4) green/red/buff muds/silts and crinoid sands, (5) nodular green mud, (6) green/buff mud with calcite scalenohedra, (7) fenestral laminated limestone, (8) dolomitized sediment, (9) green/buff bedded and graded mud/sand (Walkden and Fraser, 1993). The cover sediments, which unconformably overlie fissure-fills found in the eastern wall of the quarry, are similarly grouped in broad stratigraphic order into five associations by Walkden and Fraser (1993). These cover associations, from oldest to youngest, are: (i) channel conglomerate/breccia, (ii) buff lithoclastic muds, (iii) lithoclastic dolomite, (iv) green/red mud of Mercia Mudstone type, (v) grey clays not seen

in the quarry wall (Walkden and Fraser, 1993).

The methodology behind the relative dating of the fissure-fill sedimentary associations was straight forward. Using the Principle of Superposition (which states that, within any undeformed sequence of material, the oldest material is found at the bottom of the sequence and the youngest material is found at the top of the sequence) Walkden and Fraser (1993) were able to temporally organize the fissure-fill sediments. Fissures found in the western wall of Cromhall Quarry exhibit few of the features that can cause complexity in dating. Complications encountered when dealing with fissure-fill material include sequences of fill types in one fissure that are not the same as those seen in other fissures, types of fill that are endemic to specific fissures, and speleothems that interfere with the filling of individual fissures **(Figure 7)**. Walkden and Fraser's (1993) sedimentary associations provide an acceptable organization of the fissure-fill sediments.

The oldest sediment association determined by Walkden and Fraser (1993) is designated as (1). It is followed by the deposition of the calcite lining (2), which is shown to predate the later fissure-fill sediments via superposition. Since both of these sediment associations are found in site 6, this system is the earliest event studied in Cromhall Quarry; suggesting a long vadose phase followed by fill from surface sources. While Simms (1990) has suggested that the sediment association (2) layer of calcite crystals is indicative of the presence of thermal springs like those that created the spectacular Jewel Cave of South

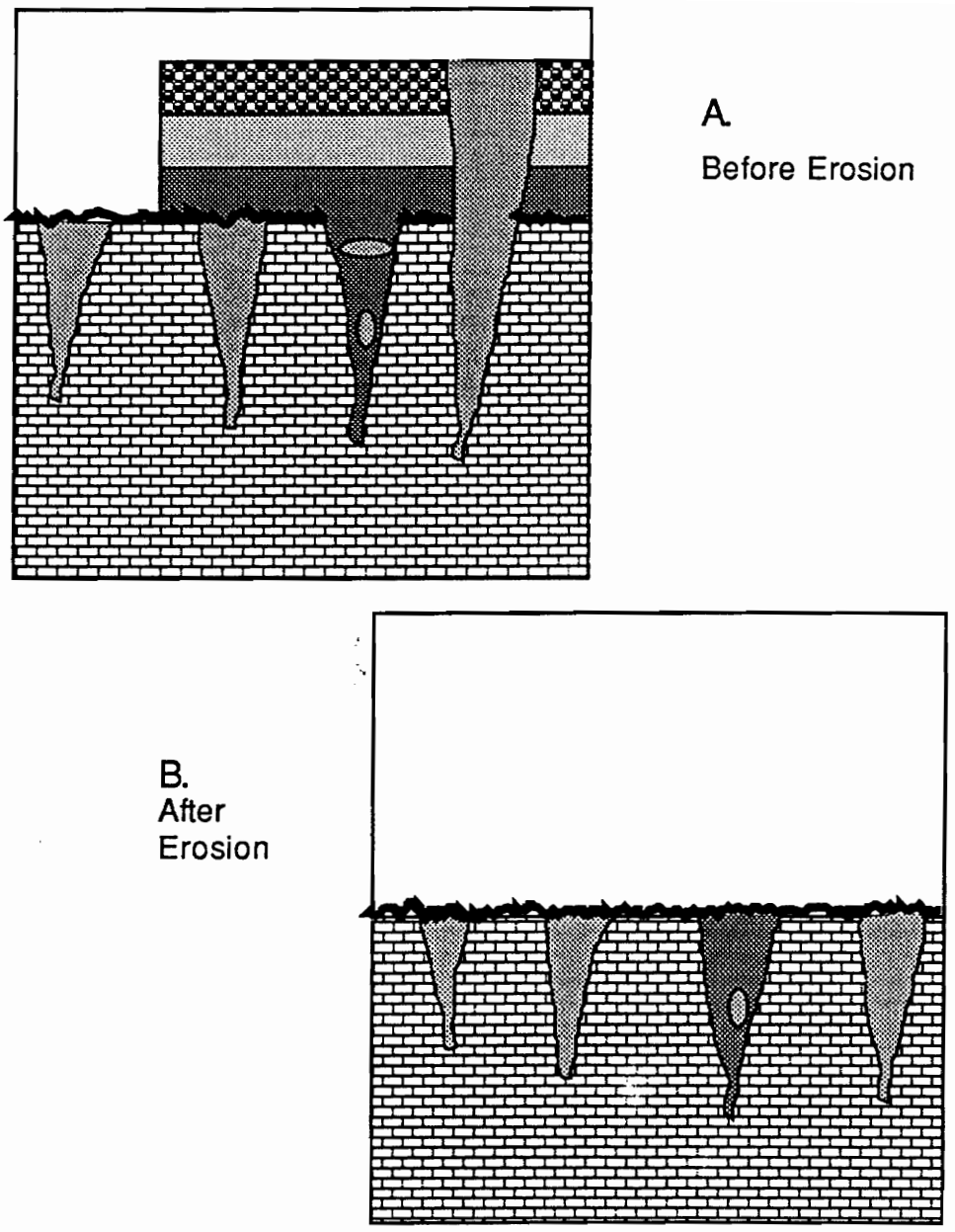



Figure 7
Problems encountered when attempting to assign dates to fissure fills.

Dakota, stable isotope palaeotemperature data from A. E. Fallick (as reported in Walkden and Fraser, 1993) does not confirm this hypothesis. Instead, it seems much more likely that the calcite lining stems from a long period of high water table and calcite-saturated water. Sedimentary association (3), found below sites 3 and 4, lies directly on the calcite lining. Sediments of associations (4) and (5) are found in pits with no calcite lining, but pieces of detrital calcite lining are found within these sediments. Concentrations of bone and surface detritus, as well as the presence of graded, slumped, channelled, or cross-bedded lenticular beds, in association (4) may be interpreted as surface lag deposits which were rapidly and periodically deposited in the fissures. Seasonally arid, then monsoonal, climate would account for this pattern, as well as the development of occasional standing-water algal stromatolites in this association. The green muds of association (5), which directly overlie association (4) sediments, may be aeolian in nature. The nodules found within (5) are carbonate, and are believed to be calcrete (Walkden and Fraser, 1993). The muds of association (5) may be linked to those of association (6), which is found in slot fissures in the east side of the quarry. Association (6) exhibits mud cracks, brecciation and root systems characteristic of exposure and the beginnings of soil formation. In addition, the laminated nature of these sediments suggests that they originated in a still pond/algal mat. The fenestral limestone of association (7) tops site 1, while similar sediment at the top of site 3 has been dolomitized; association (8). The sediment of association (9) is found

in only one slot fissure on the east side of the quarry. It is felt to resemble cover associations (ii) and (iii). Repeated grading of the sediments, and the presence of fish material, suggests that the fissure may have filled partially or completely under water. The presence of a saline water source such as a playa or a transgressing sea, as indicated by sheeted limestone found at the unconformity surface between the Carboniferous limestones and fissure-fills and the cover sediments, is further confirmed by salt pseudomorphs found in cover association (iii). The presence of abundant fish material in these sediments indicates that a marine, rather than more sterile playa, environment was more likely involved (**Table 1**).

This scenario is acceptably consistent with the general trend of palaeoenvironmental changes suggested for the Middle and Upper Triassic; arid to semiarid continents subject to flooding during monsoonal episodes of high precipitation and, rarer, marine incursions which exert increasing amounts of environmental influence during the later Triassic (Marshall and Whiteside, 1980; Olsen and Sues, 1986; Dubiel, 1987; Simms and Ruffell, 1989; Simms *et al*, 1994).

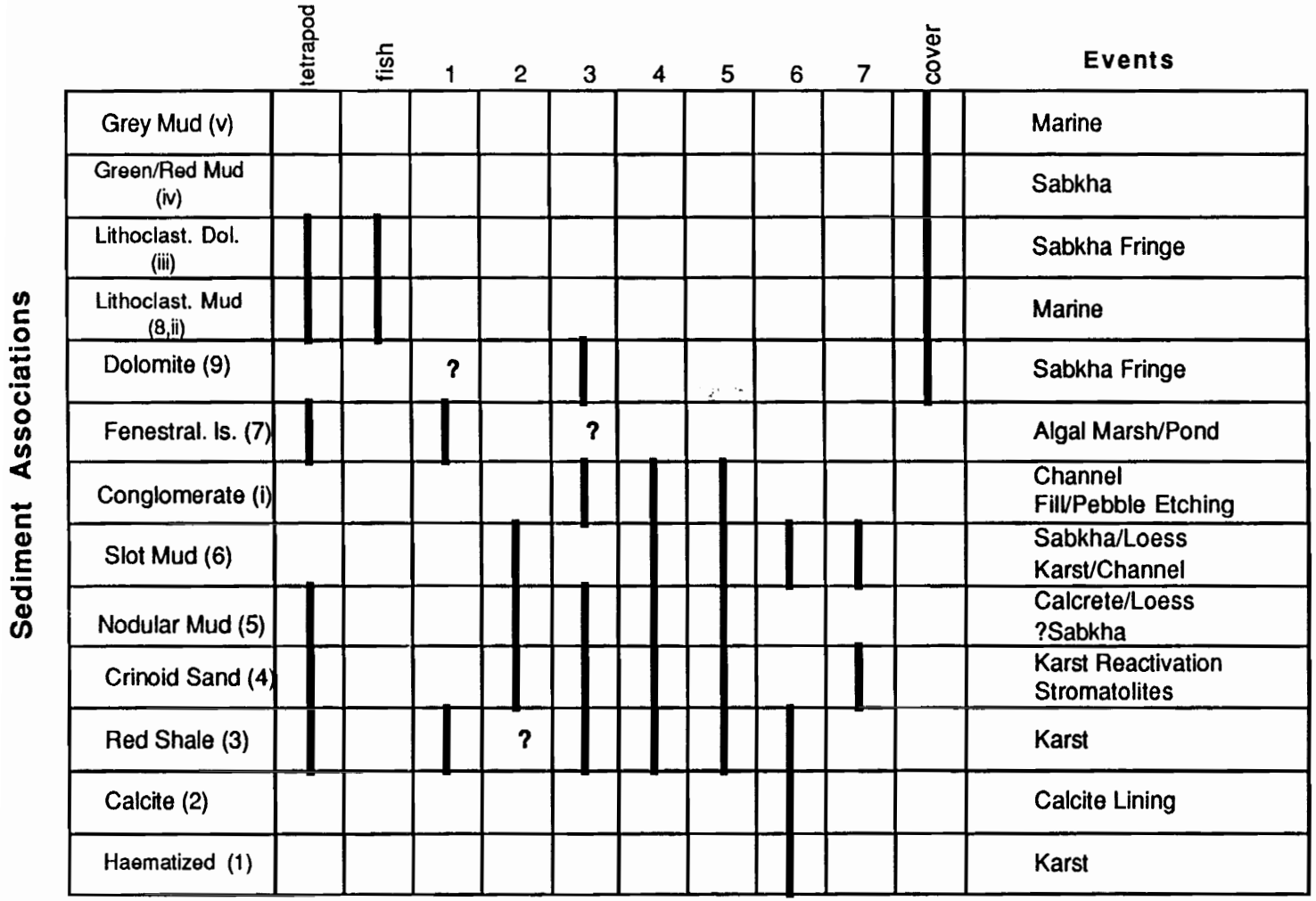



Table 1

Distribution of sediment associations within the fissures and cover, with palaeo-environmental implications (adapted from Walkden and Fraser, 1993).

## PART III - HISTORY OF BIOSTRATIGRAPHIC RESEARCH

Early work done by Robinson (1957), on vertebrate remains from Triassic and Jurassic fissure-fills from South West England and South Wales, suggested that two different assemblages were found in the fissure deposits: a sauropsid reptile assemblage containing archosaurs and lepidosaurs and a theropsid assemblage with mammal-like reptiles and mammals in addition to sauropsids. Robinson (1957 and 1971) felt these two faunal assemblages reflected Nor L1 upland and Nor L2-Liassic (as defined by Benton [1994]) lowland deposition, respectively, of the fissure-fills. Shubin and Sues (1991) later referred to these faunas as "Complex-A" and "Complex-B" assemblages. Variation in the relative abundance of archosaurs, which are found rarely in the purportedly Nor L2-Liassic deposits, were also thought to relatively date the fissure-fills (Robinson, 1957 and 1971). The Cromhall fauna was deemed sauropsid (Robinson, 1957). However, these assemblages were based on a problematic sampling scheme. As illustrated by early expeditions to Cromhall Quarry, researchers tended to concentrate on prospecting for and removing bone without recording stratigraphic data. Spoil heaps and fallen blocks constituted the majority of the collections (Swinton, 1939; Robinson, 1957). As a result, much of the material could not be referred with any certainty to specific fissures.

This assemblage theory was generally accepted until renewed sampling of these fills under more standardized regimes revealed a more diverse taxonomic list and a less decisive division between assemblages. Fraser *et al*

(1985) published on the presence of a therian mammal (*Kuehneotherium*) at Emborough in one of Robinson's (1957) presumably Norian "sauropsid" assemblages. In addition, Marshall and Whiteside (1980) identified diagnostic Nor L2 pollen in fissures at Tytherington; one of Robinson's (1957) presumed Nor L1 assemblages.

The stricter sampling regime, in force since the late 1970s, was implemented not only to provide fissure-specific data pools, but also to sample in such a way as to produce statistically useful taxonomic lists that reflected real changes in the accumulations (Fraser, 1985). In addition, if a standard regime was used in all the fissures, comparisons between them would take on greater reliability (Fraser, 1985). In the new collecting scheme, at least one rock sample per identifiable stratum (designated as a level) was removed per each fissure. Maximum vertical distance between samples generally did not exceed 50 cm, but the presence of cover sediments and the inaccessibility of some sections left gaps in the sections (Fraser, 1985). Minimum vertical distance between samples, in some cases, was 0 cm as continuous sections (2 m) were collected and processed. Each sample was analyzed sedimentologically both at a macroscopic and microscopic level. The samples were then processed using a combination of physical removal of sediment via dental tools, needles, air abrasive, and air scribe, and chemical etching in either five to fifteen percent solution of acetic or formic acid. This processing was undertaken in order to extract contained bone. Fragile bone material was stabilized for further study

using a solution of polyvinylacetate ("Vinac" brand and acetone).

The majority of bone collected in this manner was disarticulated and disassociated; although some fully (Robinson, 1962) and partially articulated (Walkden and Fraser, 1993) material was discovered at Cromhall and other British fissure localities. It was difficult to identify and reconstruct individual taxa with the disarticulated material. In addition, many of the bones were fragmentary, with the more fragile specimens disintegrating during the recovery process. This made it difficult to accurately tally the presence/absence of certain skeletal elements and of entire taxa. In order to overcome some of these problems, tally data was based on counts of jawbones (maxilla, premaxilla, dentary) as these elements tend to be robust (Kermack and Mussett, 1973). Jawbones, and the highly preservable teeth they may contain, tend to be diagnostic; making unambiguous identification of taxa possible. Post-cranial elements tend to be much less specialized, and less diagnostic.

Once the diagnostic elements were recognized and tallied, this data was used to determine the character of the vertebrate assemblages. A "landmark" system was employed by Fraser and Walkden (1983) in order to count the number of jawbones of each taxon (Fraser, personal communication). In this system, certain areas of each jaw element were established as the "landmark" required to be present in order for an element to be counted. The landmarks used included the ascending ramus of the premaxilla, the anterior articular symphyses of the dentary and maxilla in archosaurs, and the posterior tooth of

the dentary and the transitional, flanged area of the maxilla where the remnant hatchling and additional dentition meet in sphenodontians (Fraser, personal communication). No attempt was made to subdivide these counts according to side (left or right) or the minimum number of individuals (MNI) represented (Fraser, personal communication).

With Robinson's divisions having become much less certain, there was re-newed interest in whether fissure faunas could be divided into clear cut assemblages that might reflect temporal affinities. At Cromhall, the intensive collecting and processing of material led to publications on the nature of the fissure faunas. Fraser and Walkden (1983 and 1984) discovered that, of the seven fissure-fill sites available for collecting on the western wall of the quarry in the early 1980s, six yielded vertebrate remains. There appeared to be distinct variations between fissures; both in the number of taxa represented and their relative proportions (Fraser and Walkden, 1983 and 1984). However, no clear picture of vertical (level to level within any one fissure) change in the assemblages was apparent (Fraser and Walkden, 1983 and 1984).

In Walkden and Fraser (1993), the vertebrate remains tallied from Cromhall Quarry were put into 3 established associations based on the presence/absence of key species/genera. Faunal association B (sites 2-5; found in sedimentary associations (4) and (5)) had numerous sphenodontians, especially *Planocephalosaurus* and *Diphydontosaurus*. B was further broken into three sub-associations on the basis of the presence of the sphenodontian

*Clevosaurus minor* and a gracile archosaur referred to as suchian "b". In the oldest of these sub-associations, B1 (sites 2 and 5), suchian "b" was present but rare, and *Clevosaurus minor* was rare to unknown. In the middle sub-association, B2 (site 4), suchian "b" was common and *Clevosaurus minor* was present, but not abundant. In the youngest of the sub-associations, B3 (sites 3 and 7), *Clevosaurus minor* was one of the three most abundant taxa and suchian "b" was common. Faunal association C was at site 1, in sedimentary association (7). *Clevosaurus hudsoni*, along with *Diphydontosaurus*, was abundant while *Clevosaurus minor*, *Planocephalosaurus,* and suchian "b" were absent. In faunal association D ( one slot fissure and cover sediments), fish remains, in the form of the actinopterygians *Birgeria* and *Gyrolepis*, hybodont sharks *Lissodus minimus* and *Polyacrodus*, and the neoselachian *Palaeospinax*, were abundant. This association also contained *Clevosaurus minor* and *Diphydontosaurus* sp.(Walkden and Fraser, 1993).

An additional association, A, was postulated for the few bones processed from sedimentary association (4) at site 14 (basal 4/5; Walkden and Fraser, 1993). Preliminary indications suggested to Walkden and Fraser (1993) that this faunal association contained procolophonids, archosaurs, and sphenodontians. This fauna will be discussed in further detail later in the thesis.

Fraser (1985) believed that the Cromhall pattern of faunal variation implied that the fissures did not open and fill at the same time, although the actual time between the opening and filling of the first to last fissures may have

been short. Walkden and Fraser (1993) and Fraser (1994) further postulated that the changes in fissure faunas were temporally driven and that the distribution of certain taxa could be used to establish a Late Triassic vertebrate biostratigraphy. In specific, Fraser (1994) suggested that sphenodontian taxa could be of particular use as there were indications that *Planocephalosaurus* was an abundant component of the fills until the taxon's disappearance at the end of the Blue Anchor formation, while *Clevosaurus hudsoni* was present only in the young cover sediments and slot fills. Four other sphenodontian taxa (*C. latidens*, *C. minor*, *Sigmala sigmala*, *Diphydontosaurus* sp.) were also present. Further refinement of the biostratigraphy could potentially come from analysis of the rarer archosaur and procolophonid remains (Fraser, 1994; Walkden and Fraser, 1993). In fact, several workers suggested that the fissure-fill faunas of Britain could provide biostratigraphic data spanning the Triassic/Jurassic boundary (e.g. Walkden and Fraser, 1993; Benton, 1994).

Walkden and Fraser (1993) and Fraser (1994) believed that their sphenodontian-based faunal associations and proposed biostratigraphy could, in turn, be integrated into pre-existing bio- and chronostratigraphic schemes. *Birgeria*, *Gyrolepis*, and *Lissodus minimus* are all found in the British Blue Anchor and Westbury Formations; for a broad age of between Nor L1 to Nor L2 (Upper Blue Anchor) to Nor L2 (basal Westbury) for the cover sediments (Walkden and Fraser, 1993). Fraser (1994) was able to further refine this timing to the basal Penarth Group (Westbury Formation) due to similarities between

the cover faunas found at Cromhall and those found at Aust Cliff, Blue Anchor Point, and the Holwell fissures. Dating the fissure systems, and their fills, that lie below the unconformity and cover sediments was problematic. Simms (1990) suggested that the main episode of Triassic cave development in Britain occurred in the early late Triassic (Carnian). He based this date on the fact that there is no evidence of sediments or minerals of pre-Carnian age in any of the caves studied (Simms, 1990). In addition, earlier work (including Simms and Ruffell, 1989) had suggested that a wet and monsoonal climate necessary for karst formation interrupted Triassic aridity in the CRN M to CRN L2. If this was correct, then the oldest of Walkden and Fraser's (1993) sedimentary associations would be slightly younger than CRN M. Given these two possible upper and lower age limits, and that a relative fill sequence for the fissures had been determined, it was theoretically possible to determine the ages of the fills with reference to either the overlying Westbury Formation or the CRN M cave formation (Fraser, 1994). Further refining of the fill dates for Cromhall was thought to come from base level changes. As Walkden and Fraser (1993) noted, the major changes in the water table that led to karstification and then sediment accumulation were much more likely to be due to base level oscillation accompanying eustatic sea level changes than local rainfall variations. Walkden and Fraser (1993) considered it possible that they were able to recognize two base level lows in the Cromhall record (during the formation of the site 6 cave system and during the formation of sites 1-5) as well

as the base level high transgression that created the basal Westbury Formation cover sediments. Given that the basal Westbury Formation is Nor L2 in age, this suggested that the two base level lows were Norian or older in age (Walkden and Fraser, 1993). Walkden and Fraser (1993) fitted these two base level lows to Haq *et al*'s (1988) data on sea level changes; with the formation of sites 1-5 corresponding to either the CRN L2 (*circa* 224 MA) or CRN M (*circa* 228 MA) eustatic lows and the site 6 cave formation occurring in conjunction with the CRN E (*circa* 232 MA). If this was correct, then the faunas of associations B and C could be Nor L1 and Nor L2, respectively, while the fauna of association A might be Carnian (Walkden and Fraser, 1993).

The key assumptions behind this framework were: i) that bone tallies derived for each of the fissures revealed no clear differences in relative proportions and presence/absence of taxa in the material within any one specific fissure, but showed measurable differences between assemblages in different fissures, and ii) that any differences in faunal composition detected between fissures could be attributed to temporal changes rather than variations in the operation of taphonomic and/or palaeoenvironmental controls (Fraser and Walkden, 1983 and 1984; Fraser, 1985; Walkden and Fraser, 1993). However, the means of analysis by which the first assumption was reached is debatable. For example, abundance of taxa at any site or level within a site was presented as a measure of the percentage of the total number of jaw elements recovered. These percentages were visualized as bar graphs **(Figure 8)**.

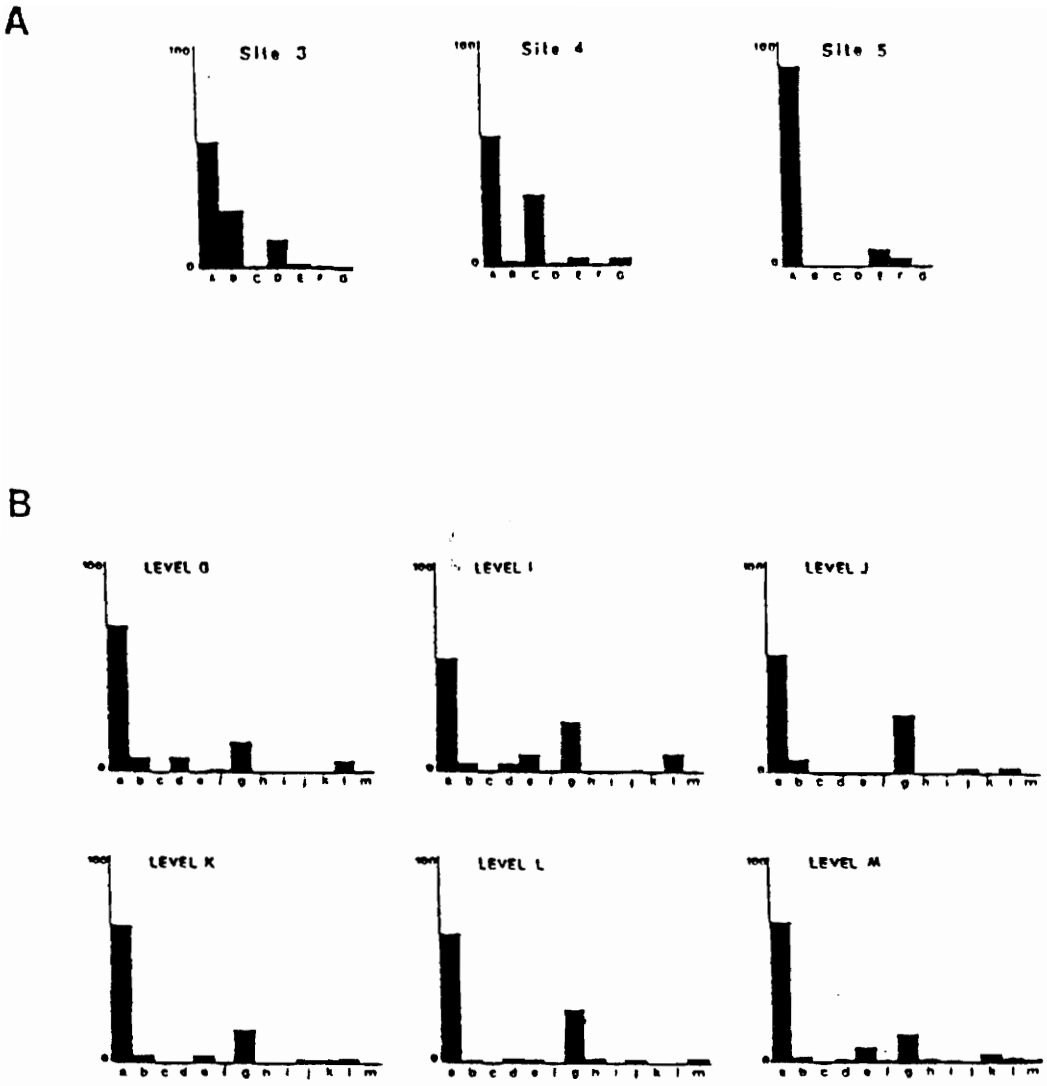



Figure 8

Bar graphs used to analyze the degree of similarity between faunas found in different fissures (A) and in different levels within fissure 4 (B). The letters below the bars represent individual taxa (from Fraser, 1985).

There were no tables of raw data (nominally understandable as journal space was constrained), nor were there counts of the total numbers of bones represented in each graph. This is problematic as 50% of 2 bones is statistically more prone to error than 50% of 200 bones. There was also no account of what, if any, statistical method(s) was utilized to analyze the degree of similarity of the faunas. It appears that degree of similarity was based on visual observation of the relative frequency graphs. In Walkden and Fraser (1993), distribution of vertebrate taxa, on which their new faunal association hypothesis was based, was again indicated as a percentage of total fauna at each site **(Table 2)**. Again, no raw data, nor total element count, was presented. No statistical method for determining the new faunal associations was detailed.

Before Walkden and Fraser's (1993) biostratigraphic framework can be used to enhance attempts to recognize patterns of tempo and mode in Late Triassic faunal change, the question of degree of similarity must be addressed. Therefore, the goals of this thesis are to: i) expand the database by processing material from a new fissure site, ii) using the expanded database, quantify the degree of similarity found in the Cromhall fissure faunas in order to critically evaluate the proposed biostratigraphy, and iii) discuss possible factors that may have been involved in creating any differences between fissure faunas.

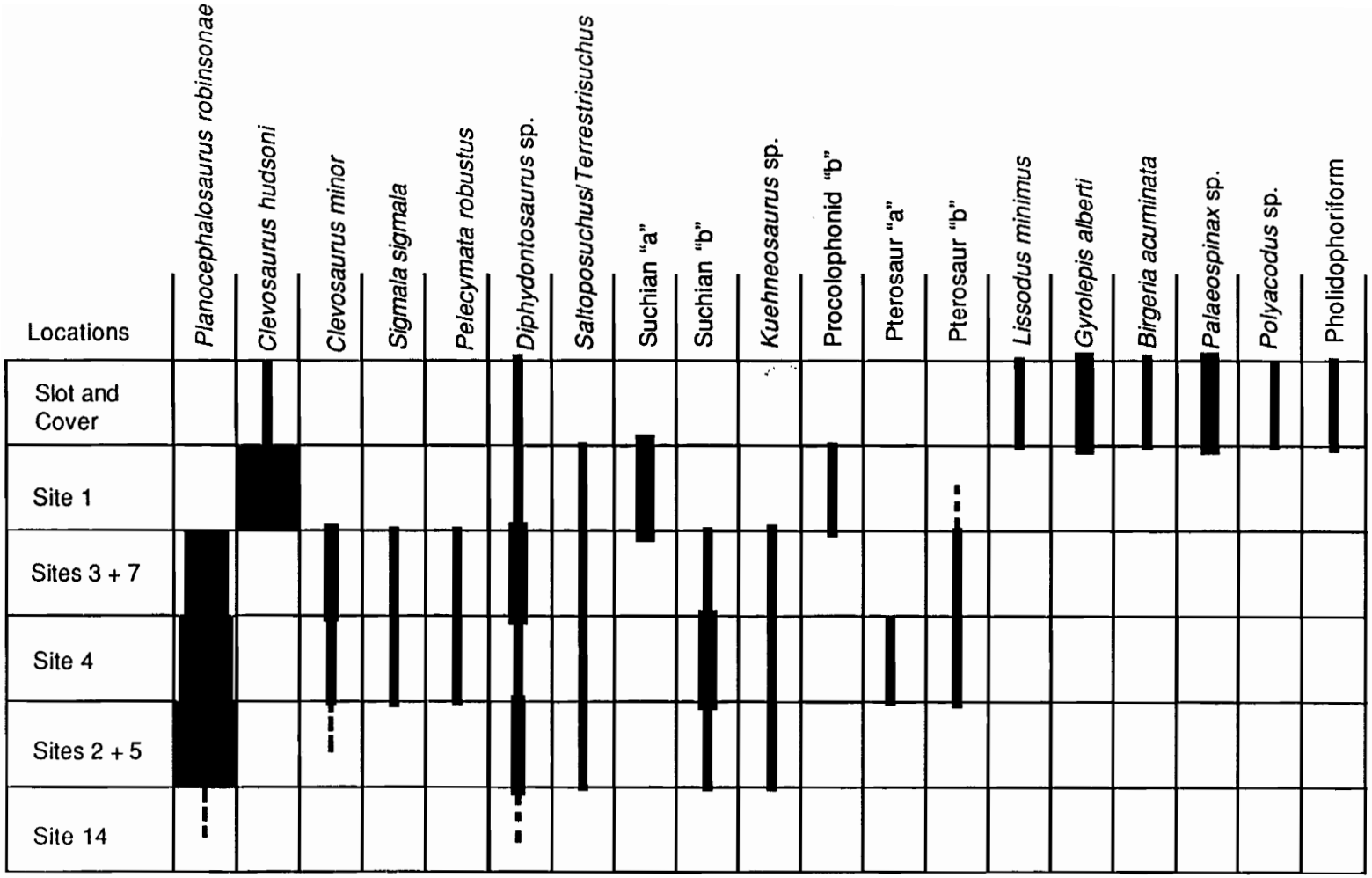



Table 2

Relative abundance table used to indicate degree of similarity between faunas found in different fissures. Width of bar gives approximate relative abundance (from Walkden and Fraser, 1993).

## MATERIALS AND METHODS

### PART I - EXPANDING THE DATA BASE

Material from a new fissure (site 14), that possibly contains the oldest fissure sediments exposed at Cromhall, was processed to extract vertebrate remains. Site 14 consists of a new fill that was exposed in 1990 by ongoing limestone quarrying. It is situated below and between sites 4 and 5 on the western wall of Cromhall Quarry. In contrast to sites 3, 4, and 5 (**Figures 9-14**), site 14 contains a high density layer of bone (level A) lying immediately upon the band of calcite crystals designated sedimentary association (2) (**Figures 15 and 16**; Fraser, personal communication). Thinner bands of calcite found further up in the fill may represent the remnants of a cave collapse (Fraser, personal communication). After processing of samples from the bone bed and the other, much less fossiliferous level (level B), new taxonomic abundance counts, of the type already collected for the previous fissures, were determined in order to facilitate comparison.

Due to problems distinguishing between the fragmentary remains of *Terrestrisuchus* sp., suchian "a", and suchian "b", as well as the presence of at least two new archosaurs in site 14, these taxa were grouped, along with *Kuehneosaurus*, into the category "Archosauromorpha". In addition, the number of individual "Archosauromorpha" taxa found in the samples was small enough that dealing with each taxon separately might have seriously skewed the statistical analyses. While this grouping of taxa into the

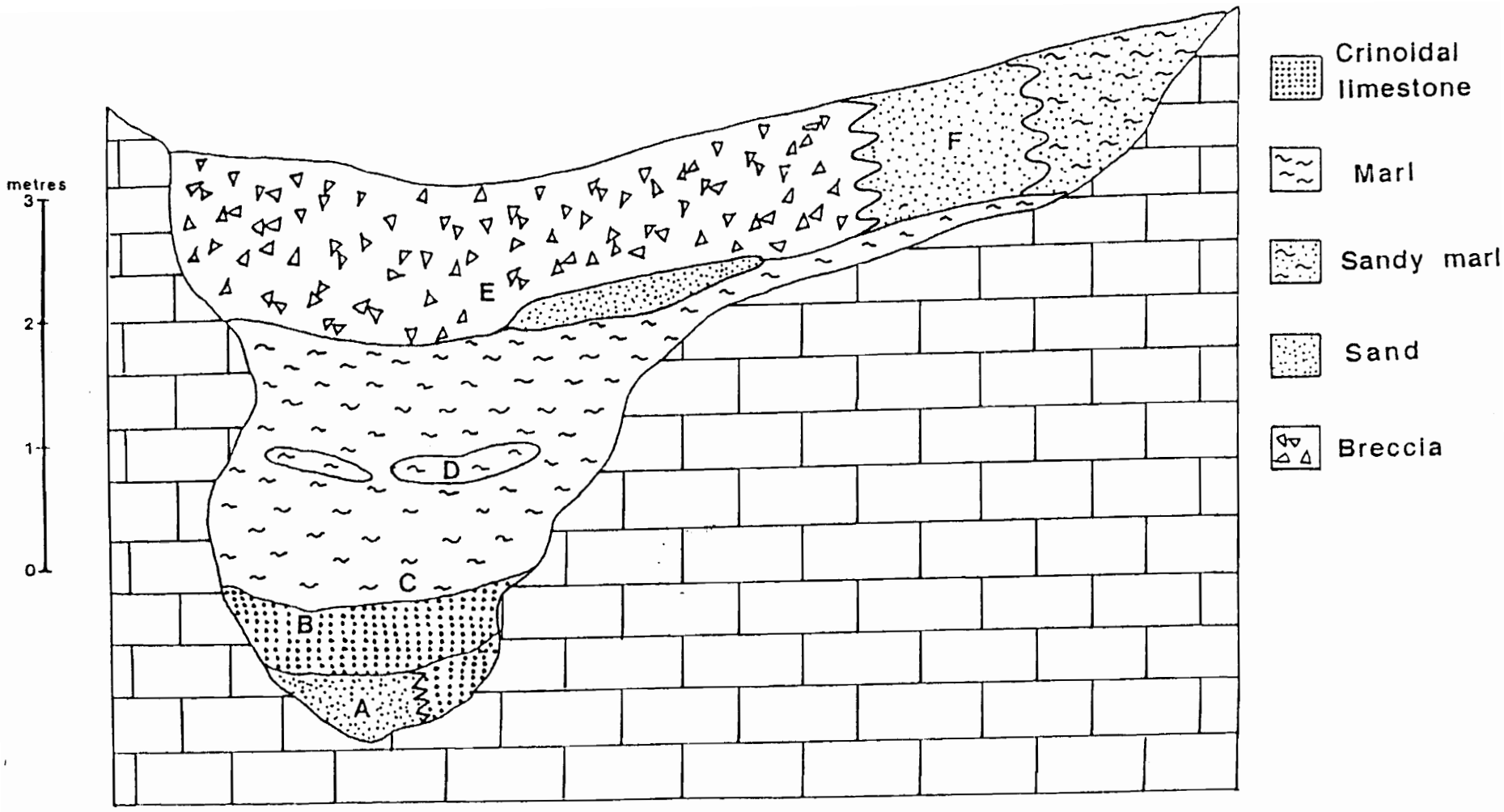



Figure 9

Diagram indicating the geology of the fissure fill at site 3. Capital letters within the diagram show levels containing vertebrate fossils.


Figure 10
The fissure-fill at site 3, Cromhall Quarry (with Nick Fraser for scale).

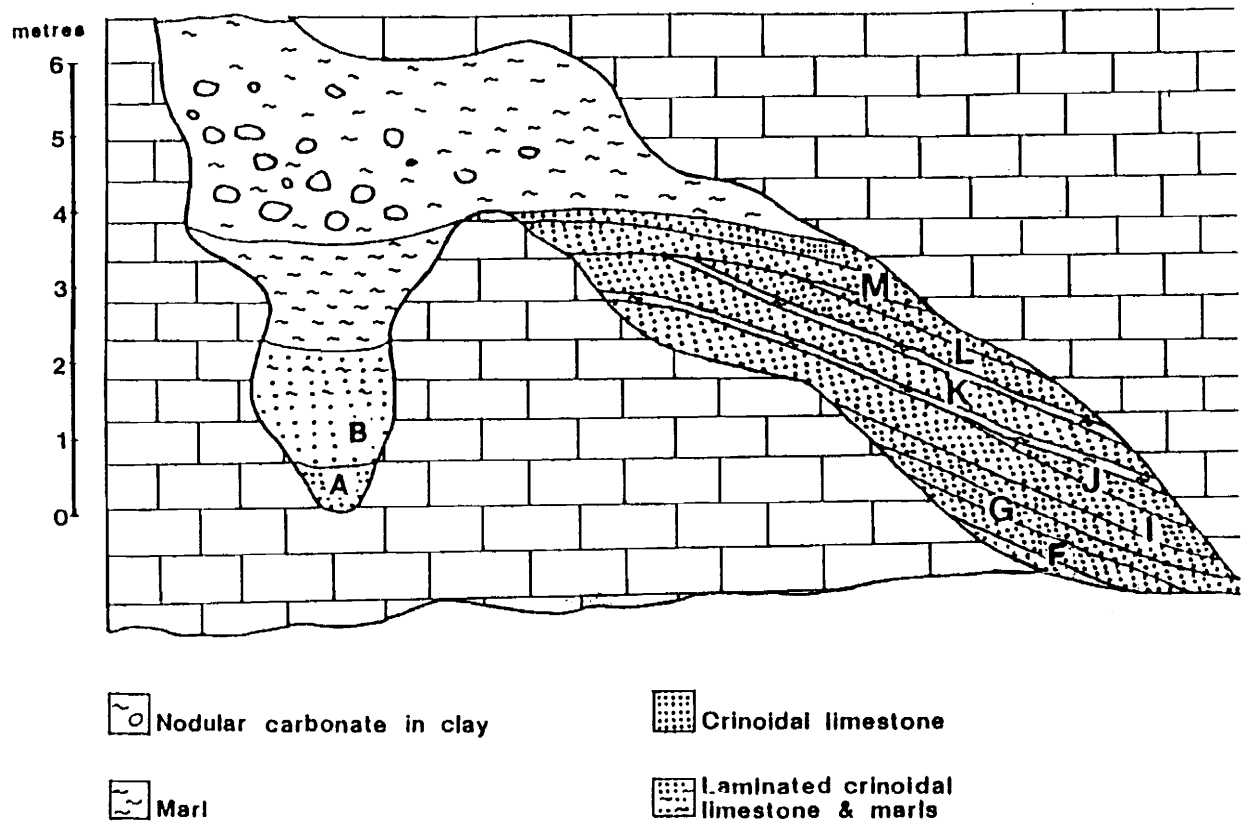



Figure 11

Diagram indicating the geology of the fissure fill at site 4. Capital letters within the diagram show levels containing vertebrate fossils.


Figure 12
The fissure-fill at site 4, Cromhall Quarry.

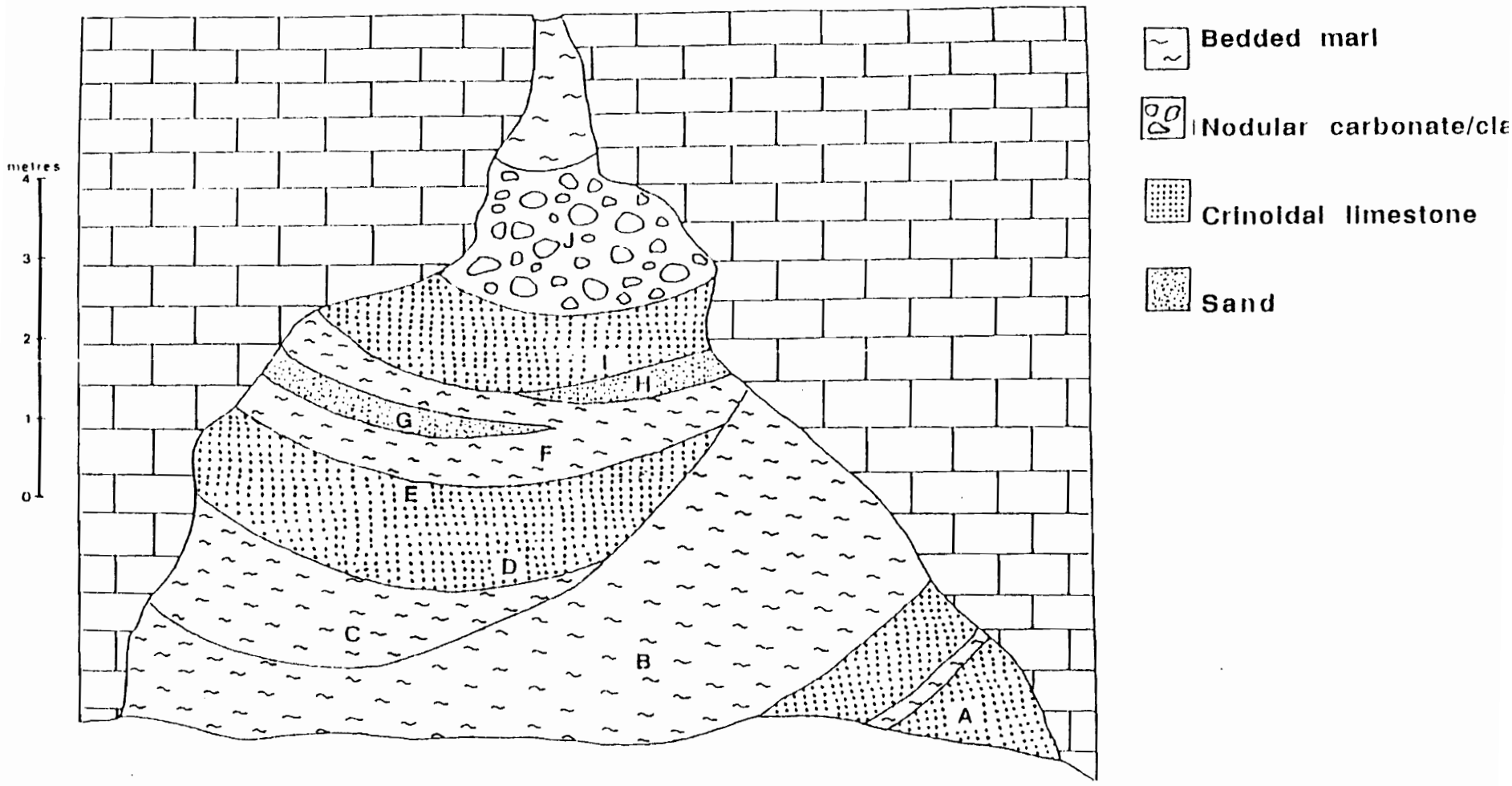



Figure 13

Diagram indicating the geology of the fissure fill at site 5. Capital letters within the diagram show levels containing vertebrate fossils.


Figure 14
The fissure-fill at site 5, Cromhall Quarry.

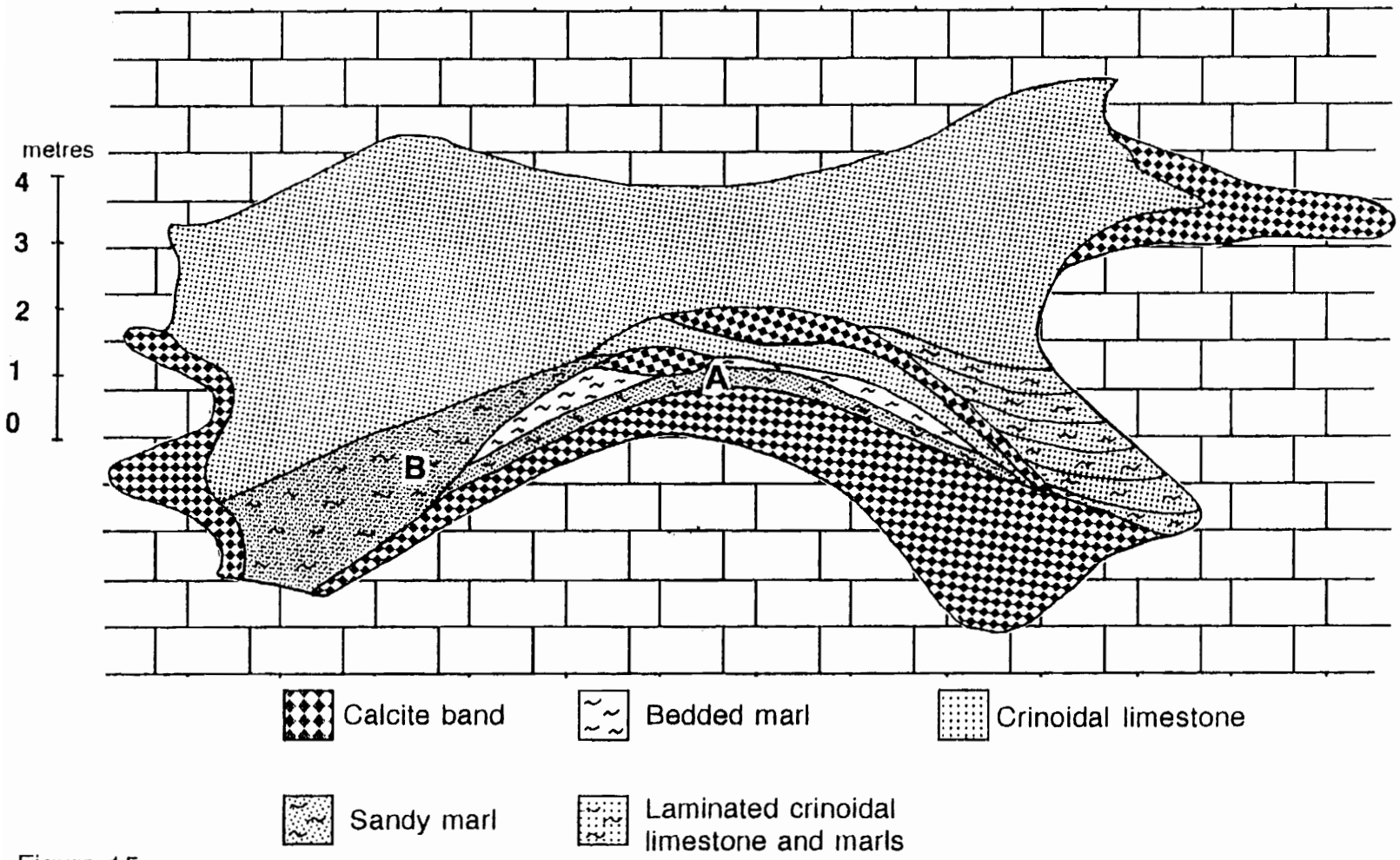



Figure 15

Diagram indicating the geology of the fissure fill at site 14. Capital letters within the diagram show levels containing vertebrate fossils.


Figure 16
The fissure-fill at site 14, Cromhall Quarry (with Gordon Walkden for scale).

"Archosauromorpha" category might lead to some loss of "fine-tuning" of the biostratigraphic framework, particularly in the recognition of faunal sub-associations B1, B2, and B3, the statistical assessment to be carried out is a "broad band" feasibility test. Thus, the effects of this grouping on the results are likely minimal. Given larger samples, with more "Archosauromorpha" taxa, and time to re-tally the previously studied samples in light of the new taxa, this lumping of taxa would not have been used. There were no specimens of *Kuehneosaurus* jawbones in the site 14 samples analyzed for this thesis. These data were then integrated into the previous data base. The expanded data base was used in all subsequent analyses **(Table 3)**.

| Species | Levels | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 3D | 3E | 3Total | 4B | 4F | 4G | 4I | 4J | 4K | 4L | 4M | 4Total |
| *Plano.* | 54 | 35 | 89 | 53 | 67 | 48 | 77 | 65 | 82 | 83 | 96 | 571 |
| *Diphy.* | 16 | 6 | 22 | 1 | 4 | 2 | 8 | 2 | 6 | 3 | 13 | 39 |
| *Clevosaurus min.* | 22 | 12 | 34 | 0 | 0 | 3 | 8 | 1 | 2 | 0 | 2 | 22 |
| *Sigmala sigmala* | 3 | 4 | 7 | 1 | 0 | 3 | 8 | 1 | 2 | 0 | 1 | 16 |
| *Pelecymala rob.* | 2 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 3 |
| Archosauromorpha | 7 | 5 | 12 | 13 | 13 | 14 | 38 | 34 | 30 | 44 | 32 | 218 |

| Species | Levels | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 5A | 5B | 5D | 5E | 5I | 5J | 5Total | 14A | 14B | 14 Total |
| *Plano.* | 31 | 65 | 7 | 18 | 5 | 5 | 134 | 25 | 29 | 54 |
| *Diphy.* | 5 | 27 | 1 | 2 | 1 | 2 | 38 | 0 | 0 | 0 |
| *Clevosaurus min.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Sigmala sigmala* | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 2 |
| *Pelecymala rob.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Archosauromorpha | 5 | 5 | 0 | 2 | 0 | 2 | 14 | 3 | 1 | 4 |

Table 3

Raw counts of taxa found at Cromhall Quarry sites 3, 4, 5, and 14. Data is shown as numbers of taxa per level and per fissure. Abbreviations: *Plano.*, *Planocephalosaurus robinsonae*; *Pelecymala rob.*, *Pelecymala robustus*; *Diphy.*, *Diphydontosaurus* sp.;*Clevosaurus min.*, *Clevosaurus minor.*

## PART II - TESTING TO DETERMINE DIFFERENCES IN FAUNAL COMPOSITION

Data collected for biostratigraphic analysis can be treated in two basic ways: as simple presence/absence (binary) or as relative frequency/abundance counts. These are both types of nominal scale data. Nominal scale data are also referred to as categorical measurements as their usage implies that the assignment of an observation to a category must be unique and there has to be a category for each observation. These two presumptions are called the mutually exclusive and collectively exhaustive prerequisites (Griffith and Amrhein, 1991). Since binary code is the basis for computer languages, binary scale data is very powerful despite the fact that the amount of information provided by an individual measurement is limited to which category a measurement fits (Griffith and Amrhein, 1991). Both relative frequency/abundance counts and simple presence/absence data can be utilized in numerous statistical techniques.

The first portion of the statistical testing, in the form of Principle Components Analysis, is applied to the data from sites 3, 4, 5, and 14 in order to determine the degree of similarity of the collections on a site to site and a level to level basis. Only sites 3, 4, and 5 from the original work were used as material from other fissures from the western wall of the quarry was collected as "float" (e.g. fallen blocks; Fraser, personal communication). Level to level comparison allows for critical evaluation of previous work (e.g. Fraser and

Walkden, 1983 and 1984; Fraser, 1985) which suggests that faunas found at different levels within any one fissure are more similar to each other than to any faunas from other fissures. If, as it seems equally logical, level data corresponds to the same sediment associations in each fissure and there is no significant difference in the operation of taphonomic forces between individual fissures, material found in the same sediment association, no matter what fissure, should be of the same relative age and composition. Should a level count resemble more closely counts from levels of the same sedimentary type in other fissures, as opposed to resembling other levels contained within the same fissure, then the existing biostratigraphic scheme has to be modified to deal with level to level faunal changes as fissure to fissure changes would represent time-averaged accumulations.

Principle Components Analysis (PCA) is used primarily as a dimension reducing technique; a method of summarizing as much of the information/variation in a data set in as few dimensions as possible (Neff and Marcus, 1980). Principle components analysis is also useful as an exploration technique in that it allows the investigator to plot the data, on easily read axes, in order to identify outliers amongst the observations (Neff and Marcus, 1980). PCA treats each individual observation as a single point within a scatter of points in n-dimensional space. The n-dimensional space is organized around a series of axes, each representing a variable used in the analysis (Neff and Marcus, 1980). For example, a biologist studying sexual dimorphism in a

species might make 100 individual observations (measurements) of variables such as weight of individual, forearm length, width of head, and so on. PCA is then used to find new orthogonal axes through the scatter of points such that each new axis runs in the direction of greatest variance among individual points (Neff and Marcus, 1980). These new axes, the principle components, are erected so that the first axis line (the first principle component; first eigenvector) contains/tracks the individual observations which have the maximum variance in all of the scatter. The sum of the squares of the distances between each point and the line is minimized (Neff and Marcus, 1980). The first axis essentially runs between the points in the scatter which are furthest apart. The second axis (second principle component; second eigenvector) runs in the direction of greatest variance perpendicular to the first axis, and so on (Neff and Marcus, 1980). Thus, each principle component accounts for less and less of the variance in the data.

The creation of each principle component is not done directly from the raw observations. As summarized by Bennington (1995), PCA works with a matrix, either of correlations or covariances, between individual observations. The matrices are constructed after the raw observations have been transformed (Bennington, 1995). The first of these transformations, row centring, acts such that the mean value for any one row is subtracted from individual counts in that same row (Bennington, 1995). Row centring acts to position the origin of the original data collection to the centre of gravity of the n dimensional scatter

(Bennington, 1995; Ludwig and Reynolds, 1988). If this first transformation is not done, then the first principle component will likely only reflect the relative sizes of the respective samples (Bennington, 1995). A second transformation may be used to standardize all the variables such that their means are all 0.0, and their variances are all 1.0 (Bennington, 1995). Without this transformation, the matrices created will be composed of covariances; with the transformation, they will contain correlations (Bennington, 1995; SAS Inc., 1988). A covariance matrix is influenced by the relative abundances of observations as large variances are strongly associated with abundant components with large eigenvalues (Bennington, 1995; SAS Inc., 1988). Correspondingly, less abundant components with smaller eigenvalues will be strongly associated with small variances.

Several assumptions, statistical and biological, lie behind the application of PCA. Valid use of PCA assumes that the data involved are multivariate normally distributed, and that the data is homogeneous and not a mixture of sources of variation (Neff and Marcus, 1980). Secondly, there is an implicit assumption that the most important phenomena will be tracked and represented by the first few principle components (Neff and Marcus, 1980). In fact, if all of the variables in the data are randomly distributed, there is no reason that the principle components should provide a clearer picture of the variance than the original variables (Bennington, 1995; Davis, 1986). As Bennington (1995) emphasizes, the more underlying structure their is to the data, the more

variance will be accounted for by the first few principle components. The amount of variance explained by the first few principle components is generally felt to be about 75% (cumulative) by the first five principle components (Bennington, 1995). Finally, the researcher is acting under the assumption that the variables have been tallied accurately; a particularly important assumption when dealing with small sample sizes in which errors in data collection may be magnified (Neff and Marcus, 1980).

Interpretation of PCA may be complex. As Neff and Marcus (1980) point out, it can be argued that there is no reason to expect principle components to track meaningful combinations of observations as biologically important combinations are not necessarily orthogonal (joint perpendicular directions through space). Instead, they feel that the value of PCA lies in the fact that it provides a two or three dimensional space that contains as much of the information about variation in the total data as possible (Neff and Marcus, 1980). In order to glean maximum information from the analysis, the relationships of interest should be assessed visually via graphs (Neff and Marcus, 1980). In addition to this caveat, Neff and Marcus (1980) point out that interpreting the results of PCA involves the assumption that variables that are highly correlated are somehow causally linked. Indeed, there is a further assumption upon which all of the analysis rests; that the relevant groups/phenomena being analyzed exist and are present in the data collected (Neff and Marcus, 1980). For example, if variation in a particular species is

being analyzed, the researcher assumes that the species in question exists and that it has been properly identified in the samples.

Two types of SAS (a form of computer software) PCA were used to analyze the Cromhall data; one using a correlation matrix and another using a covariance matrix. The results from both types of PCA are expressed here as data/number tables and as three dimensional graphs.

The results of interest from the data/number tables are contained within two separate tables: Eigenvalues of the Correlation/Covariance Matrix and Eigenvectors (see Tables 4 and 5 in the "Results" section). The Eigenvalues indicate how much of the variance in the data is explained by the first three principle components. The first principle component explains the most variance; with each successive principle component explaining less. The amount of variance explained per individual principle component is contained under the Proportion heading, while the cumulative amount of variance explained by the all the principle components considered is found under the Cumulative heading. The Eigenvectors indicate how much each variable (i.e. taxon) is contributing to each principle component axis. Eigenvectors (also called loadings) are Pearson correlations between the variables and the principle components such that their strength and direction can be used to relate how each original variable and principle component interact (Bennington, 1995). Loadings range from -1.0 to 1.0, with high positive loadings being interpreted as a strong contribution by a particular variable to a particular

principle component axis. As Bennington (1995) emphasizes, negative loadings are more complicated and are generally used in a contradictory or "versus" sense in combination with a positive loading. In other words, if loadings on any two (or more) variables on any one component axis are high and opposite in sign, it is generally taken that movement along the axis results in local enrichment of one species relative to the other.

In contrast to these tables, graphic interpretation is based on visual inspection of three dimensional plots of the data. Determination of tendency to group is visual and tends to be less rigidly quantifiable .

## PART III - TESTING TO DETERMINE INTERNAL CONSISTENCY

The aim of the second part of the statistical testing is to indicate the degree of internal consistency within the originally proposed biostratigraphic scheme and sedimentological associations. If it is revealed that the material from the "new" fissure (site 14; presumably the oldest) groups most closely with the material from the assumed second oldest fissure (site 5, faunal association B1), even if the principle components analysis suggests level to level taxonomic change will provide a more accurate biostratigraphy, then the organization of the sedimentological and faunal associations Walkden and Fraser (1993) created will be confirmed as to internal logic. Of course, this second test will only be valid if the time, and/or the faunas, averaged within the fissures exhibit a certain degree of similarity. If all the faunas are significantly unlike each other, no coherent clustering will result.

The obvious technique to extract areal locations from information contained within variables is cluster analysis. Cluster analysis is a group of algorithms/techniques in which **n** areal units, each with scores on variables, are grouped into clusters (**K**). There are two basic ways of approaching clustering: partitioning and hierarchical (Kaufmann and Rousseeuw, 1990). In partitioning methods, the **K** clusters or groups are classified such that there are, at most, as many groups as there are objects and that two different clusters cannot have any objects in common (Kaufmann and Rousseeuw, 1990). **K** is chosen by the analyzer, and may be "fitted" in order to give the most meaningful looking

partitioning (Kaufmann and Rousseeuw, 1990). In contrast, hierarchial methods do not create a single partition with **K** clusters. Instead, the output consists of a stepwise transition from a point where all the objects are included in a single cluster (**K** = 1) to the point where each object is a separate cluster (**K** = **n**; Kaufmann and Rousseeuw, 1990). All the **K** values in between are covered in a gradual transition (Kaufmann and Rousseeuw, 1990). The difference between these two methods is best illustrated in a diagram (**Figure 17**). Hierarchical and partitioning methods are not usually considered alternative methods as they describe data, to different ends, in totally different ways (Kaufmann and Rousseeuw, 1990). Hierarchical methods are most often used in biological applications (Kaufmann and Rousseeuw, 1990; Griffith and Amrhein, 1991). Hierarchical methods are considered rigid in that they cannot repair an error made in an earlier step (Kaufmann and Rousseeuw, 1990). In other words, once two objects are joined in a cluster, they cannot be separated later in the process. This rigidity has lead to the popular usage of hierarchical methods as they require short computational times (Kaufmann and Rousseeuw, 1990).

Hierarchical algorithms may be further divided into agglomerative and divisive types. Both create hierarchical clustering, but in opposite directions. Agglomerative algorithms begin with all the objects separated i.e. at step 0 in the process, there are **n** clusters (Kaufmann and Rousseeuw, 1990). At each subsequent step, two clusters are merged until there is only one cluster left

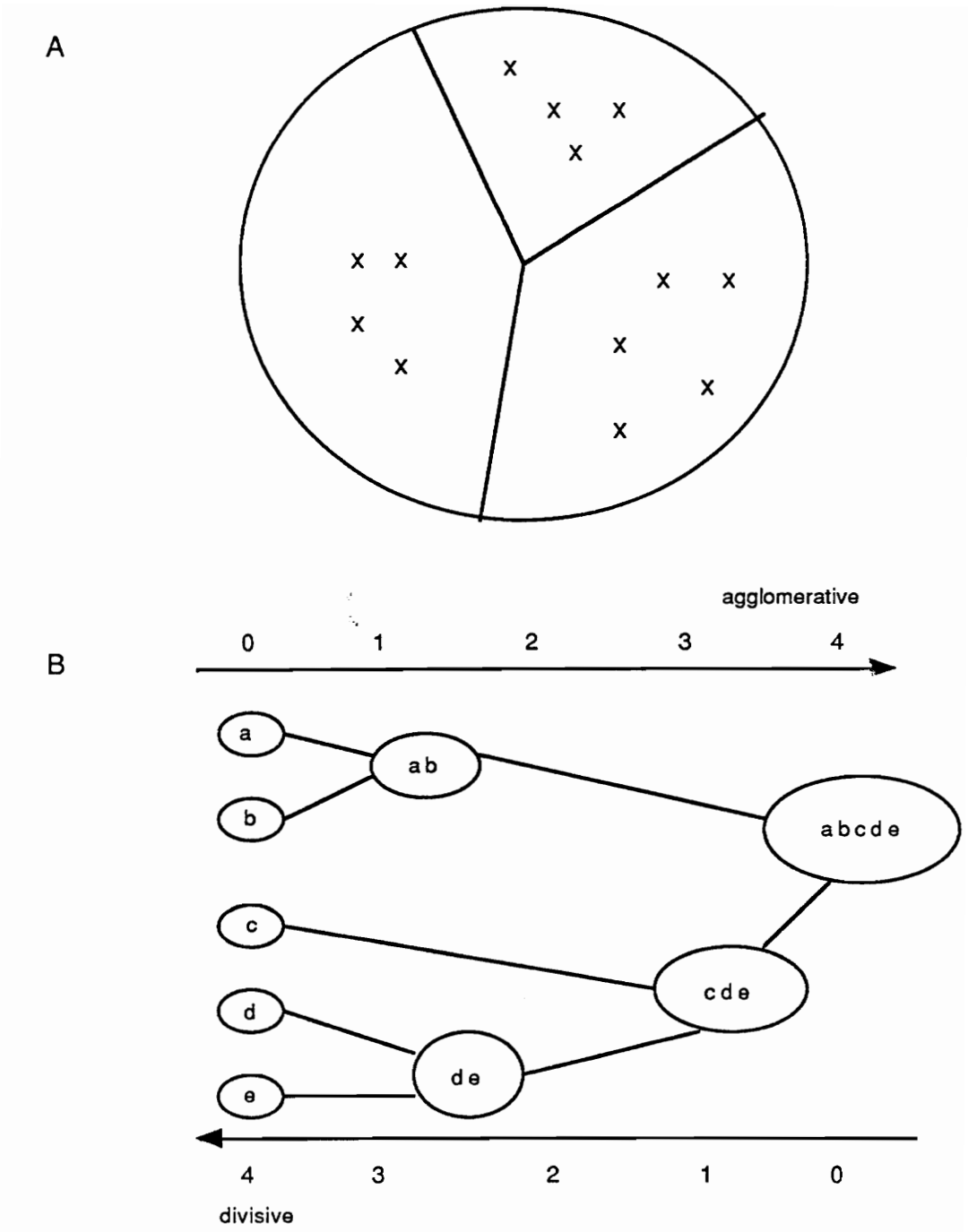



Figure 17
Partition (A) and Hierarchical (B) methods of clustering (from Kauffmann and Rousseeuw, 1990).

(**K** = 1). Divisive algorithms begin with all the objects in a single cluster, and separate the objects in subsequent steps (Kaufmann and Rousseeuw, 1990).

In order to preform cluster analysis, a definition of the similarity between clusters, based on the similarity of objects within the clusters, must be determined prior to analyzing the data with a similarity coefficient (Neff and Marcus, 1980; Kaufmann and Rousseeuw, 1990; Griffith and Amrhein, 1991). In Unweighted Pair-Group Average Method (UPGMA), the similarity between any two clusters **R** and **Q** is taken as the average of all the similarities between objects in cluster **R** to objects in cluster **Q**. This method of defining and calculating similarity between clusters is illustrated in a diagram (**Figure 18**; Kaufmann and Rousseeuw, 1990). UPGMA is commonly used in biological analyses (Neff and Marcus, 1980).

A great many cluster programs and coefficients that have been produced in the last thirty years. The reasons for this are three-fold; i) automatic (computerized) classification is a relatively young scientific discipline and is experiencing rapid growth, ii) there is no general definition of a cluster, and iii) different applications use different data types to establish groups (Kaufmann and Rousseeuw, 1990). As a result, conventional wisdom suggests that it is a good idea to apply more than one coefficient to the data and then analyze and compare results (Griffith and Amrhein, 1991; Kaufmann and Rousseeuw, 1990). Interpretation of results can then be based on insight into the original data (Kaufmann and Rousseeuw, 1990). However, work by N.L Gilinsky on the

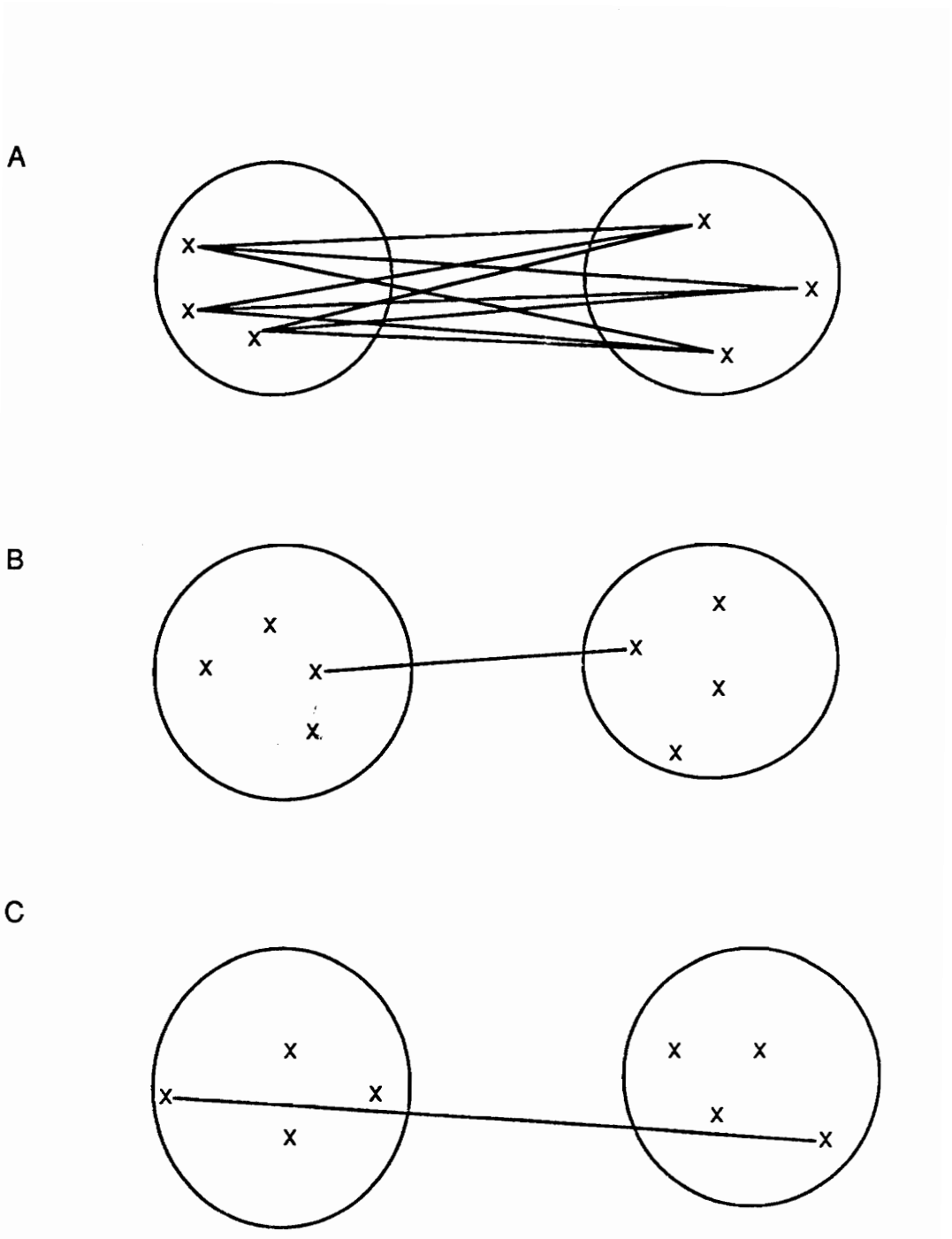



Figure 18

Graphic representation of some definitions of intercluster similarity. A; Unweighted Pair-Group Average, B; Nearest Neighbour, C; Furthest Neighbour (Kaufmann and Rousseeuw, 1990).

nature of cluster analysis has proved that this assumption is not productive (Gilinsky, personal communication). Using an unpublished program that reads data, calculates one of (or all) six similarity coefficients provided, then estimates the p-values for the similarity coefficients via boot-strapping, Gilinsky discovered that while the values for calculated similarity change with each different coefficient used, the p-values for significance maintain the same relative position to each other (personal communication, 1995). Each of the six coefficients (Jaccard, Simple Matching, Dice, Simpson, Braun-Blanquet, Raup-Crick) provides the same degree of probability. Thus, it is possible to run the data with only one coefficient and achieve significant results.

Cluster techniques exhibit two basic complications in interpretation: stability of clusters and determining distinct clusters (Bennington, 1995). As Bennington (1995) summarizes, there is some instability in connections between clusters dependent on slight differences in the data used to generate the groupings. Over the long term, clusters of groups of data with relatively high similarities tend to be stable, but clusters of groups of data with relatively low similarities are more apt to change (Bennington, 1995). As a result, clustering tends to divide a data set into coherent groups, but the relationships between these groups may be peripatetic (Bennington, 1995). Problems with cluster stability may stem from the fact that clustering programs force all the samples into clusters, whereas this may not be a "real world" result (Springer and Bambach, 1985). Limited dimensionality of clustering algorithms may create

clusters where none exist; particularly in cases of faunal/spatial overlap (Springer and Bambach, 1985). As clustering is not an inferential technique, there are no statistical tests of significant difference that can be applied to the clusters generated (Bennington, 1995). As a result, determination of significant difference must be based on personal decisions regarding the distances between clusters in a dendrogram and potential meaning of the clusters within the study (Bennington, 1995).

The data were subjected to a hierarchical, agglomerative clustering algorithm which utilizes UPGMA definition of dissimilarity between clusters. The quantified Dice (Czekanowski) coefficient (Sepkoski, 1974) was used to produce Q-mode (samples clustered on the basis of distribution of contained taxa) and R-mode (species clustered on the basis of their distribution among samples) analyses. Within the Q-mode analysis, the raw data tallies were transformed into percentages of the total number of specimens within any one sample: percent transformed (Miller, 1988). Percent transformation was utilized as variations in sample size can influence calculation of dissimilarity between samples (Miller, 1988). In the R-mode analysis, percent transformation of the raw tallies was followed by percent maximum transformation. Percent maximum transformation uses the highest individual sample abundance of a taxon as a set 100 %, then recalculates the abundances of the taxon in all the other samples as percentages of the maximum abundance sample (Miller, 1988). This allows for the results to be interpreted without worrying about

whether the taxa are clustering together on the basis of overall abundances rather than distribution (Miller, 1988).

The sequential groupings derived from the clustering process may be pictorially (2-dimensionally) represented by a dendrogram (tree diagram). Dendrograms illustrate the mergers or divisions in clusters made at successive levels; with the branches of the tree representing individual clusters. These mergers or divisions, which occur at nodes, are measured along a similarity axis which runs from 0 (totally dissimilar) to 1 (identical; Griffith and Amrhein, 1991).

# RESULTS

## PART I - NEW TAXA

In addition to taxa already recognized from Cromhall, the material processed from site 14 contains two forms new to Cromhall. These two elements may also be from previously undescribed taxa. While it is generally undesirable to erect new taxa on isolated elements, and undertaking a full scale taxonomic description would be outside the focus of this thesis, the material requires additional discussion.

Premaxilla

The specimen comes from level A (bone bed) in site 14, specifically from sample CR 93 34. It is an almost complete left premaxilla; one of a pair of bilaterally symmetrical bones that are found anterior to the reptilian maxilla within the snout (**Figures 19 and 20**). The premaxilla, measuring 3.5 cm along the long axis and 2.1 cm across the thickest portion of the short axis, consists of a robust and "boxy" tooth-bearing central portion flanked anteriorly and posteriorly by bony processes. The tooth-bearing portion of the premaxilla measures 1.5 cm anterior-posteriorly and 1.1 cm at its thickest region. It is roughly square in shape when viewed medially or laterally, with the superior edge of this square slightly concave. The posterior edge of the "box" has a wide and relatively shallow notch inferiorly. When viewed from above, the medial surface can be seen to be relatively flat while the lateral surface ascribes a shallow convex arc. Four dental alveoli open inferiorly in this central portion of

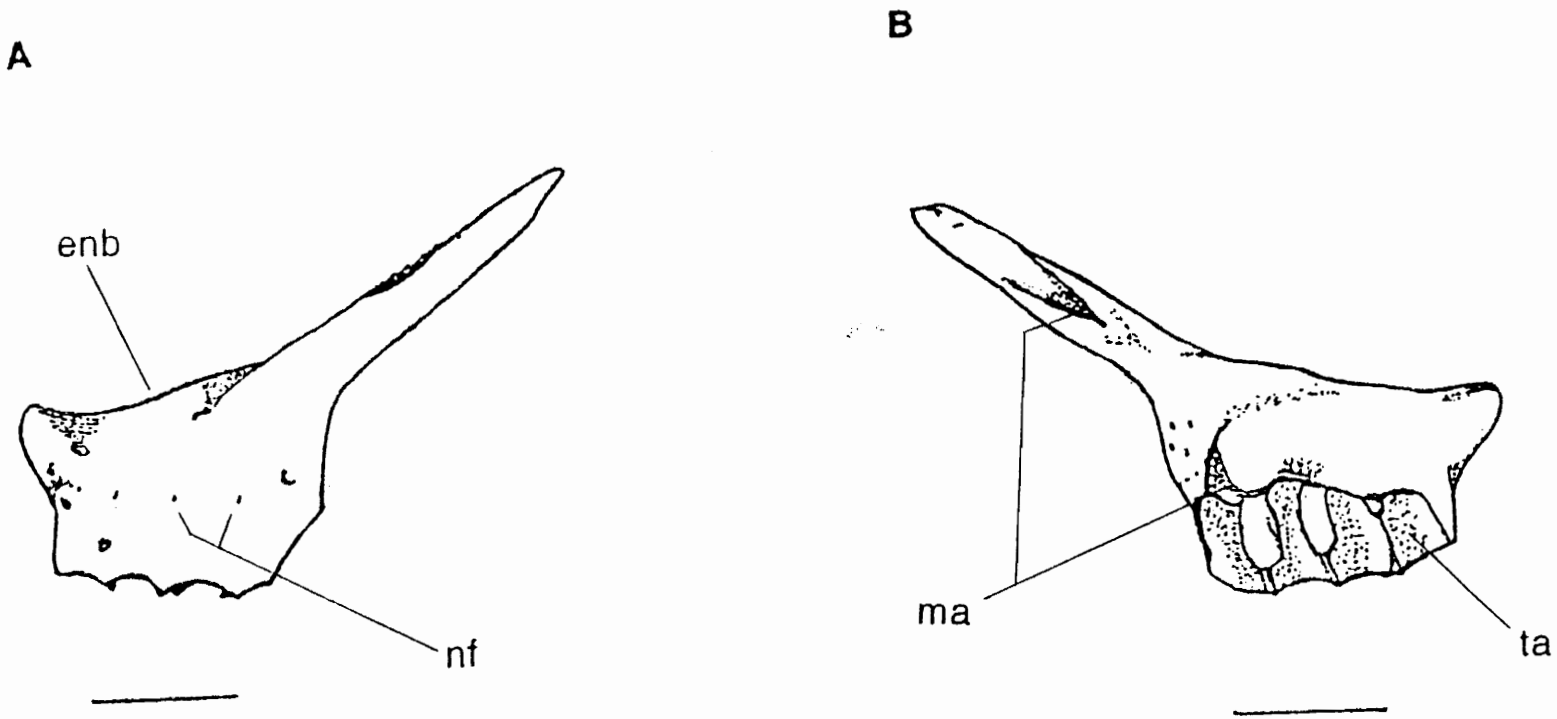
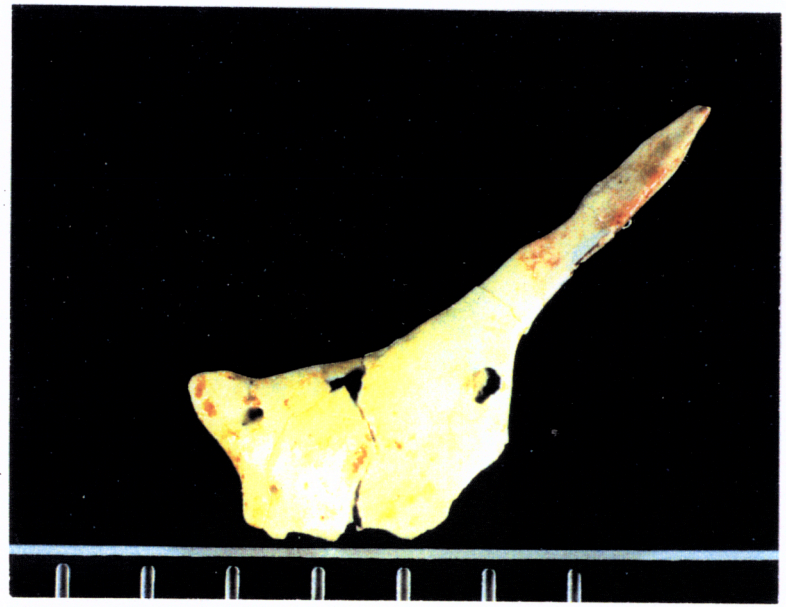



Figure 19

Line drawing of the presumed sphenosuchian premaxilla, in left lateral (A) and medial (B) views, from Cromhall Quarry, site 14. Abbreviations: enb, external narial border; ma, maxillary articulation; nf, nutrient formamina; ta, tooth alveolus. Scale bar is 1 cm.



A

B

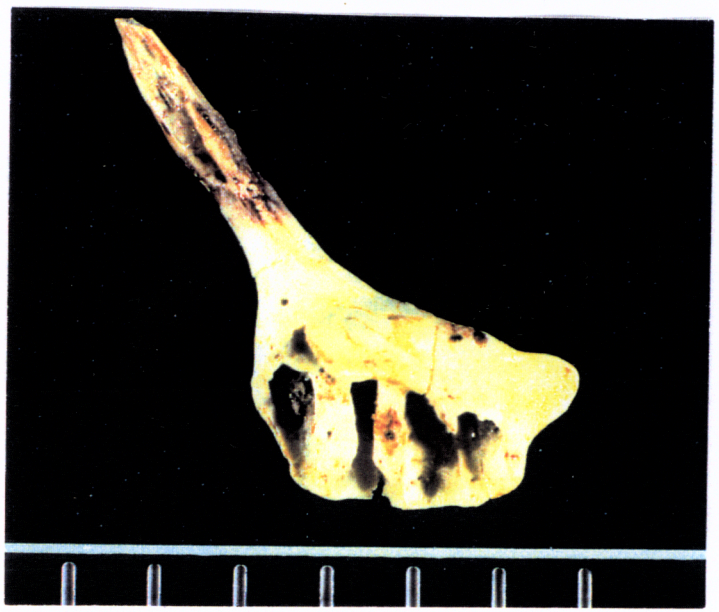


Figure 20

The presumed sphenosuchian premaxilla, in left lateral (A) and medial (B) views, from site 14, Cromhall Quarry. Scale bar is in 0.5 cm increments.

the premaxilla; with the size and depth of the alveoli increasing distally in the tooth row. No teeth are preserved in the alveoli. When viewed laterally, the inferior alveolar margins are gently scalloped. Medially, the alveoli are open and exposed. The bony walls separating the three most posterior alveoli are "capped", at right angles, by flat plates of bone that do not completely seal the long axes of the sockets. These interalveolar wall and plates do not resemble the interdental plates seen in some of the Dinosauria (Carroll, 1988). This phenomenon is not present between the two most anterior alveoli; possibly due to incomplete preservation of the premaxilla. A rounded, socket-like depression flanked by a medial extension of bone, is found just superior to the interalveolar wall between the two most posterior alveoli. This is presumed to be an articular facet for a medial extension of the maxilla that, together with the premaxilla, may have contributed to a secondary palate. Laterally, a number of nutrient foramina can be seen on this central area. Two complete and two partially damaged foramina are distributed dorsolaterally along the central "square" at the bases of the tooth sockets; with each socket having one foramen extend into it. Three smaller complete foramina are found at the anterior inferior angle of the central area of the premaxilla. Medially, a cluster of small foramina are present at the posterior superior angle of the central body "square".

Two processes, anterior and posterior, extend from the central body of the premaxilla. The wide arc ascribed by the superior surfaces of these processes, along with the central section, would have formed part of the margin

of the external nares. The anterior process is a short, robust, triangular extension projecting anterio-dorsally at approximately a 35 degree angle from the anterior and superior region of the central "square". Presumably, this process would have been matched by a similar projection on the right premaxilla to form the midline articulation or symphysis of the snout, but there is no sign of any bony symphsis or ligamentous bond found on the bone. The presence of a flattened and smooth articular facet in this area suggests that, while the premaxillae were likely in close contact in the medial area of the snout, the nares themselves were confluent (Fraser, personal communication). When viewed from above, the process exhibits a flattened medial surface and a lateral surface with a constriction or "waist", where it joins the central region of the premaxilla, that widens and projects laterally anteriorly. The posterior process is a long (2.1 cm), thin (0.5 cm at the base), and tapering extension of bone that projects posteriorly and superiorly from the central "square" at about a 20 degree angle. The cross section of this process changes anterior-posteriorly from rounded/oval, at its basal attachment to the rest of the premaxilla, to triangular/flattened. The posterior half of the process is flattened and roughened inferiorly and medially, presumably for articulation with the superior surface of the maxilla, the inferior surface of the nasal, or both. The posterior end of the process is incomplete.

When dealing with disarticulated remains, it is sometimes possible to directly link separate elements by means of matching articular facets.

Unfortunately, neither a maxilla nor a nasal with corresponding articulation facets was found in this sample. In cases where direct linkage is not possible, indirect evidence suggesting linkage of elements may be derived from assessing size, general character, and preservation of accompanying material. While no teeth were found in the premaxilla, isolated teeth were recovered from sample CR 93 34. Only one unrooted tooth, split along the midline, was of approximately appropriate size to be linked to the jawbone. A large and robust partial quadrate from the same sample may be from the same animal as the premaxilla, but without the connecting cranial elements, it cannot be attributed as such. Sample CR 93 34 also contained numerous fragments of post-cranial material, including long bones and vertebrae of archosauromorphs, that were of appropriate size and robustness to possibly stem from the same animal as the premaxilla. It should be noted the premaxilla and the other bones believed to be from the same animal are noticeably larger than the majority of the material recovered from Cromhall. Based on the size of the premaxilla, the skull of the animal from which it came would have been approximately 20 cm in length.

The premaxilla, with a short, triangular anterior process and long, thin posterior ascending process arising from a boxy tooth-bearing body, is reminiscent of those described or reconstructed for early crocodiles. Other Triassic and Jurassic taxa that the premaxilla could potentially have come from, including aetosaurs and rausuchids, either do not have teeth in the mesial portion of the mouth (ie. *Aetosaurus*, *Stagonolepis*) or have long and thin

anterior processes of the premaxilla (ie. *Saurosuchus*; Walker, 1961; Bonaparte, 1984; Carroll, 1988). Crocodiles may be traced back to the MiddleTriassic (if *Gracilisuchus* is considered a crocodile); having consistent skeletal features since the Upper Triassic (Carroll, 1988). Characteristic crocodilian features include an anteorbital fenestra (closed in modern forms), a long snout which is reinforced ventrally by variably developed medial extensions of the maxilla, premaxilla, and palatine, some type of secondary palate, and pneumatization of the skull bones; including ducts running from the eustachian tubes into the premaxilla and maxilla (Carroll, 1988). This last characteristic is difficult to determine without sectioning or scanning (with X-rays or computerized axial tomography) the specimen. Middle and Upper Triassic genera of crocodiles fall into the suborders Sphenosuchia and Protosuchia (Carroll, 1988). The majority of protosuchian genera, including *Stegomosuchus* and *Protosuchus*, are found in Lower Jurassic strata; with the exception of the Upper Triassic genus *Hemiprotosuchus* (Olsen *et al.*, 1982; Carroll, 1988). Sphenosuchian genera include *Terrestrisuchus* and *Saltoposuchus* from the Upper Triassic of Europe, and *Gracilisuchus* from the Middle Triassic of South American. *Gracilisuchus* was originally described as an ornithosuchian by Romer (1972), but Brinkman (1981) placed the genus in the Sphenosuchia on the basis of the structure of the tarsus and cheek region. However, this assignment is disputed and *Gracilisuchus* may belong to a separate, not yet recognized, lineage (Carroll, 1988; Parrish, 1993).

The external nares, in protosuchians, are terminal and dorsal to the snout (Carroll, 1988). As a result, in *Stegomosuchus* and *Protosuchus*, the premaxilla forms the anterior and inferior borders of the narial opening (Colbert and Mook, 1951). The posterior border of the premaxilla is deeply notched in all the protosuchid genera as, in occlusion, a lower caniniform tooth fits into a recess between the premaxilla and maxilla (Carroll, 1988). The posterior ascending process of the premaxilla, which articulates with the maxilla and nasal, is short and broad (Colbert and Mook, 1951; Crompton and Smith, 1980; Nash, 1975; Carroll, 1988). In ventral view, the dental arcade of the protosuchid *Nothochampsa* (*Orthosuchus*) premaxilla is arched around the anterior palatal foramen; a condition seen in other protosuchians (Nash, 1975; Carroll, 1988).

In *Gracilisuchus*, the external nares are terminal to the snout and open antero-dorsally **(Figure 21)**. The nares are confluent and the anterio-dorsal processes of the premaxillae are shortened. In outline, the premaxilla exhibits a shallow notch at the base of the posterior border of the tooth-bearing body of the element; there is no sign of a large recess between the premaxilla and maxilla. The posterior ascending process of the premaxilla extends dorsally and somewhat posteriorly at a steep angle (greater than 45 degrees). The front of the palate in *Gracilisuchus* is not known, so the degree of development of the secondary palate cannot be determined (Romer, 1972; Carroll, 1988). However, by viewing the external morphology of the snout, it can be hypothesized that the medial surfaces of the premaxillae are relatively flat and

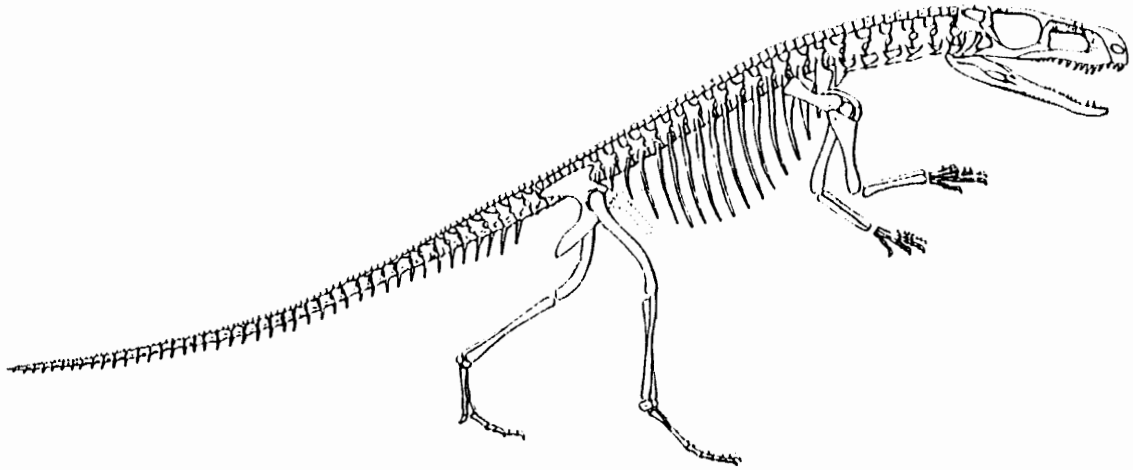


Figure 21

Line drawing of the skeleton of the possible sphenodontian, *Gracilisuchus* (Romer, 1972). The carpus and manus are restored. The entire skeleton is around 30 cm in length. Figure from Carroll (1988).

in close proximity; suggesting that there is limited development of the secondary palate and the anterior palatal foramen.

In *Terrestrisuchus* and *Saltoposuchus* there is a tendency towards elongated, low-profile snouts. The external nares are terminal, and open dorsally, with the premaxilla forming the anterior, inferior, and posterior margins of the opening. The maxilla and premaxilla articulate in such a fashion as to form a secondary palate. Tooth implantation in these forms is thecodont. In the premaxilla, tooth size tends to increase distally. Sereno and Wild (1992) illustrate *Saltoposuchus connectens* with a noticable recess between the premaxilla and maxilla, into which fits a canine-like tooth in the lower jaw, Crush (1984) does not include this recess in his reconstruction of *Terrestrisuchus gracilus*. Carroll (1988), when discussing the Sphenosuchia, indicates that this maxillary notch is present in all forms; with the possible exception of *Gracilisuchus*. Viewed ventrally, the premaxilla forms a U-shaped arch around the anterior palatal foramen (Crush, 1984). A German specimen of *Saltoposuchus connectens* has been illustrated with the posterior portion of the premaxilla present (Sereno and Wild, 1992). In this specimen, the posterior margin of premaxilla is notched and a tapering process extends posteriorly from the superior, posterior region of the tooth bearing body of the bone (**Figure 22**; Sereno and Wild, 1992). In addition, the premaxilla excludes the maxilla from the border of the external nares (Sereno and Wild, 1992). While the morphology of the posterior process is at odds with Huene's

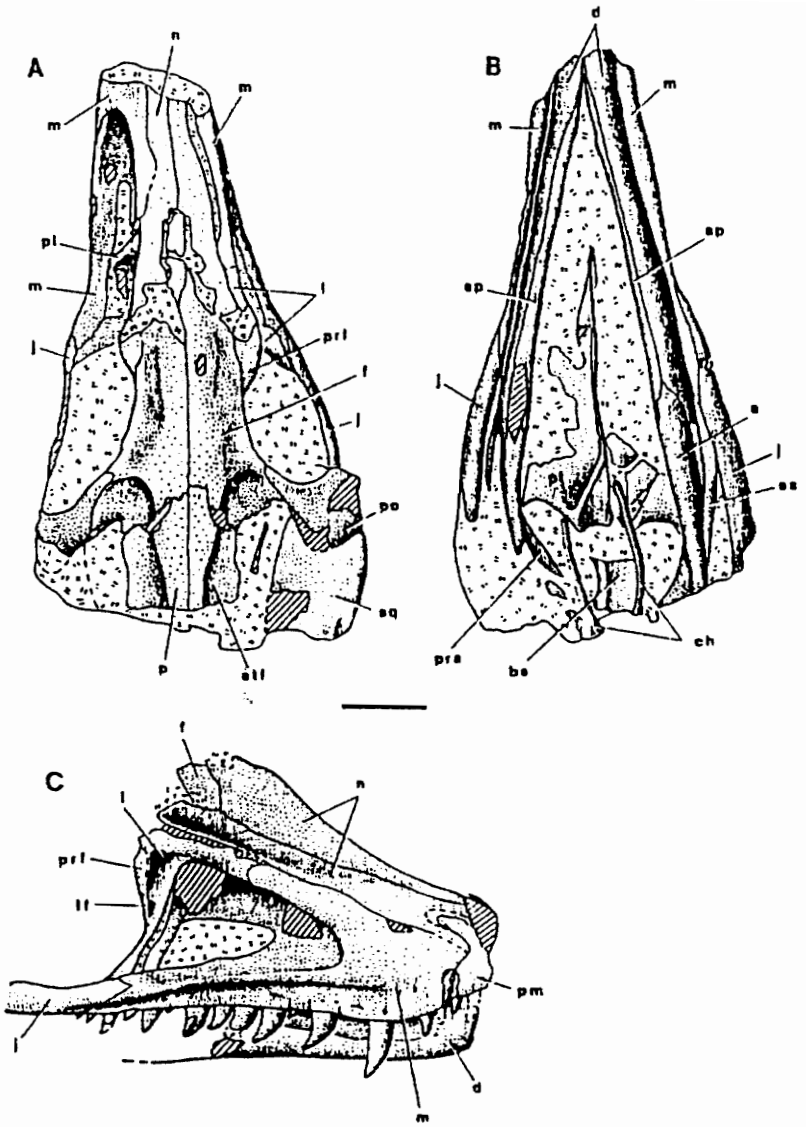



Figure 22

Line drawing of the skull of *Saltoposuchus connectens* in dorsal (A), ventral (B), and right lateral views (C; Sereno and Wild, 1992). Abbreviations: a, angular; bs, basisphenoid; ch, ceratohyal; d, dentary; f, frontal; j, jugal; l, lacrimal; lf, lacrimal foramen; m, maxilla; n, nasal; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; pra, prearticular; prf, prefrontal; pt, pterygoid; sa, surangular; sp, splenial; sq, squamosal; stf, supratemporal fossa. Hatchured area indicates broken bone. Scale bar is 1 cm.

(1921) reconstruction of the premaxilla in the original taxon description, it is much like the premaxillae attributed to *Sphenosuchus* (Walker, 1990). Unfortunately, no premaxillae have been described for *Terrestrisuchus*, so reconstructions have been modelled on articulations for the premaxilla on other skull bones (see Crush, 1984).

It should be noted that *Terrestrisuchus* and *Saltoposuchus* are similar in appearance, and numerous authors have referred to their possible close taxonomic relationship (Clark, 1986;Crush, 1984;Parrish, 1991;Sereno and Wild, 1992). Clark (1986) has suggested, as has Parrish (1991), that the name *Terrestrisuchus* is a junior synonym for *Saltoposuchus*. Sereno and Wild (1992) feel that this designation is premature, and hypothesize that *Terrestrisuchus* is more closely related to the south African *Pedeticosaurus* than it is to *Saltoposuchus*.

The Cromhall premaxilla exhibits features most like those seen in *Gracilisuchus* and *Terrestrisuchus/Saltoposuchus*. The external nares are positioned terminally and antero-dorsally, as in all three genera, but the morphology of the anterior process of the premaxilla and the potentially confluent nares are more like the situation seen in *Gracilisuchus* and in the protosuchians. There is no sign of a large notch between the premaxilla and maxilla in the Cromhall form; much like the situation in *Gracilisuchus* and in Crush's (1984) reconstruction of *Terrestrisuchus gracilis*. The medial surface of the Cromhall premaxilla, like the situation hypothesized in *Gracilisuchus*, is

uniformly flattened and relatively straight; suggesting little development of a secondary palate or anterior palatal foramen (vomeronasal foramen). However, the length and relatively low angle of extension of the posterior ascending process of the premaxilla suggests the elongated snout found in *Terrestrisuchus*/*Saltoposuchus*.

Given the current state of confusion within the Sphenosuchia (not just with *Terrestrisuchus* and *Saltoposuchus*), and with the taxonomic affiliations of *Gracilisuchus*, it is only safe to attribute the premaxilla to a broad group of taxa:

Class Reptilia
Order Crocodylia
Suborder Sphenosuchia (?)

Maxilla

This specimen is a left maxilla from level A (bone bed) of site 14. Specifically, it was processed from sample CBB 90. In outline, it consists of an elongate (3.6 cm), horizontally oriented, tooth-bearing ramus that includes some of the snout (the most anterior portion of the maxilla is missing), and a triangular plate that arises dorsally from the anterior portion of the basal long axis, and then tapers into a thinner process **(Figures 23 and 24)**. Laterally, this ramus is slightly textured anteriorly. The superior edge of the specimen creates a relatively straight and gradually sloping outline that runs from the broken tip of the maxilla to the incomplete end of the ascending ramus. While

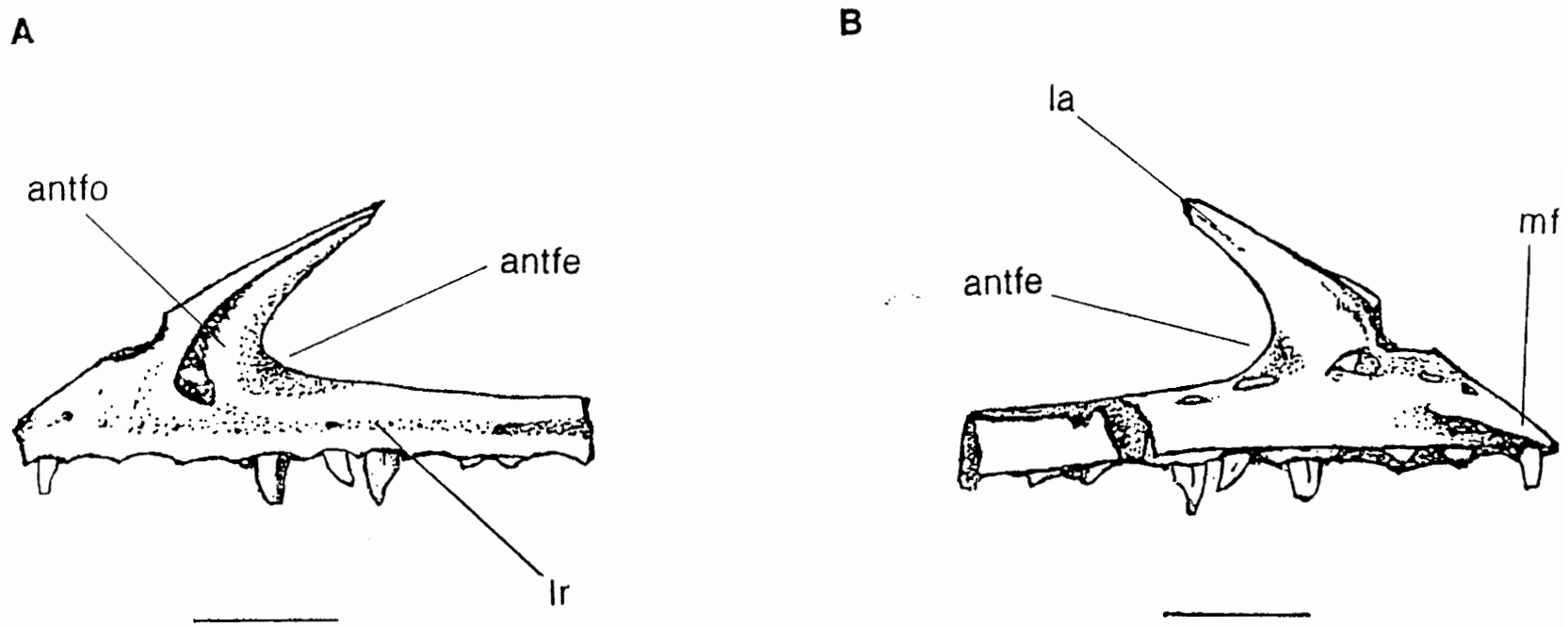



Figure 23

Line drawing of a presumed ceratosaurian maxilla, in left lateral (A) and medial (B) views, from Cromhall Quarry, site 14. Abbreviations: antfe, antorbital fenestra; antfo, antorbital fossa; la, lacrimal articulation; lr, longitudinal ridge; mf, medial flange. Scale bar is 1 cm.

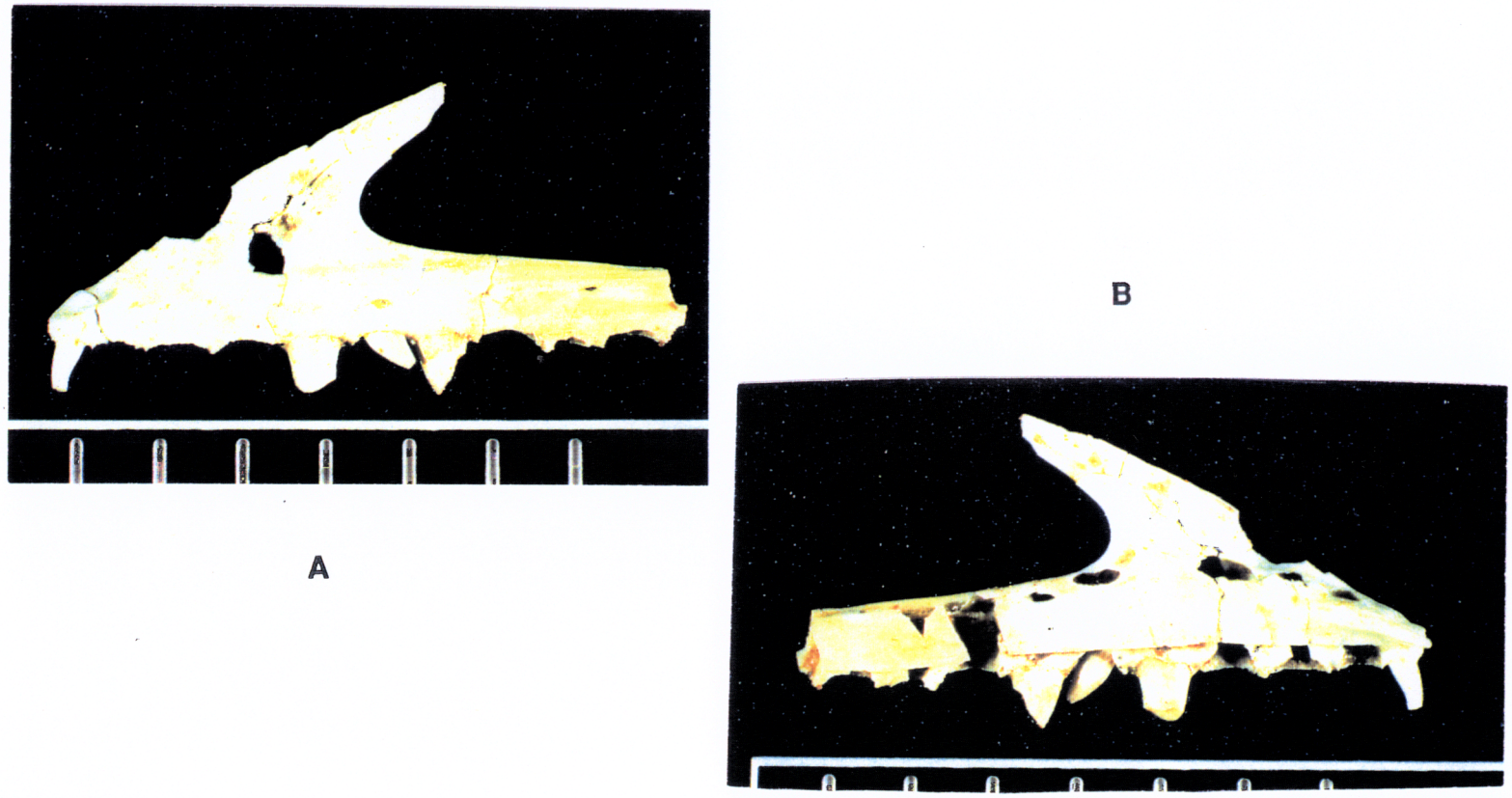



Figure 24

Colour print of the ceratosaurian maxilla, in left lateral (A) and medial (B) views, from site 14, Cromhall Quarry. Scale bar is in 0.5 cm increments.

this superior edge is chipped towards the midline of the element, three general areas can be located; an anterior flattened and grooved plain, a smooth and rounded narrow edge, and a narrow flattened and grooved blade **(Figure 25 and 26)**. Nutrient foramina, that increase in size posteriorly in the ramus, are grouped at the base of the sockets such that the mesial alveoli have two foramina while the distal ones share a single foramen between two alveoli. The most distal foramen is the largest and deepest; set into the beginning of a midline groove that stretches posteriorly to the broken edge of the maxilla. Medially, the anterior portion of the horizontal ramus is extended to form a superiorly grooved flange that presumably was involved in articulating with the premaxilla and/or the left vomer. The rest of the medial surface of the horizontal ramus is smooth and gently rounded.

The preserved portion of the tooth-bearing ramus contains sockets for ten teeth. Four of the sockets contain teeth; three mid-maxillary and one mesially. The mid-maxillary teeth are mesio-laterally flattened recurved blades. Both the mesial and distal edges of the blades exhibit serrations. The mesial edges of the tooth crowns are less labiolingually flattened, and are more rounded in profile. Serrations on the mesial edges of the teeth do not extend to the jawbone insertion. Instead, the serrations are only found on the bottom (tip of the tooth) one third of the tooth crown. In contrast, the distal edges of the tooth blades are serrated to within a millimeter of the jawbone insertion. Two of the teeth are fixed at right angles to the maxilla, and their crowns are partially

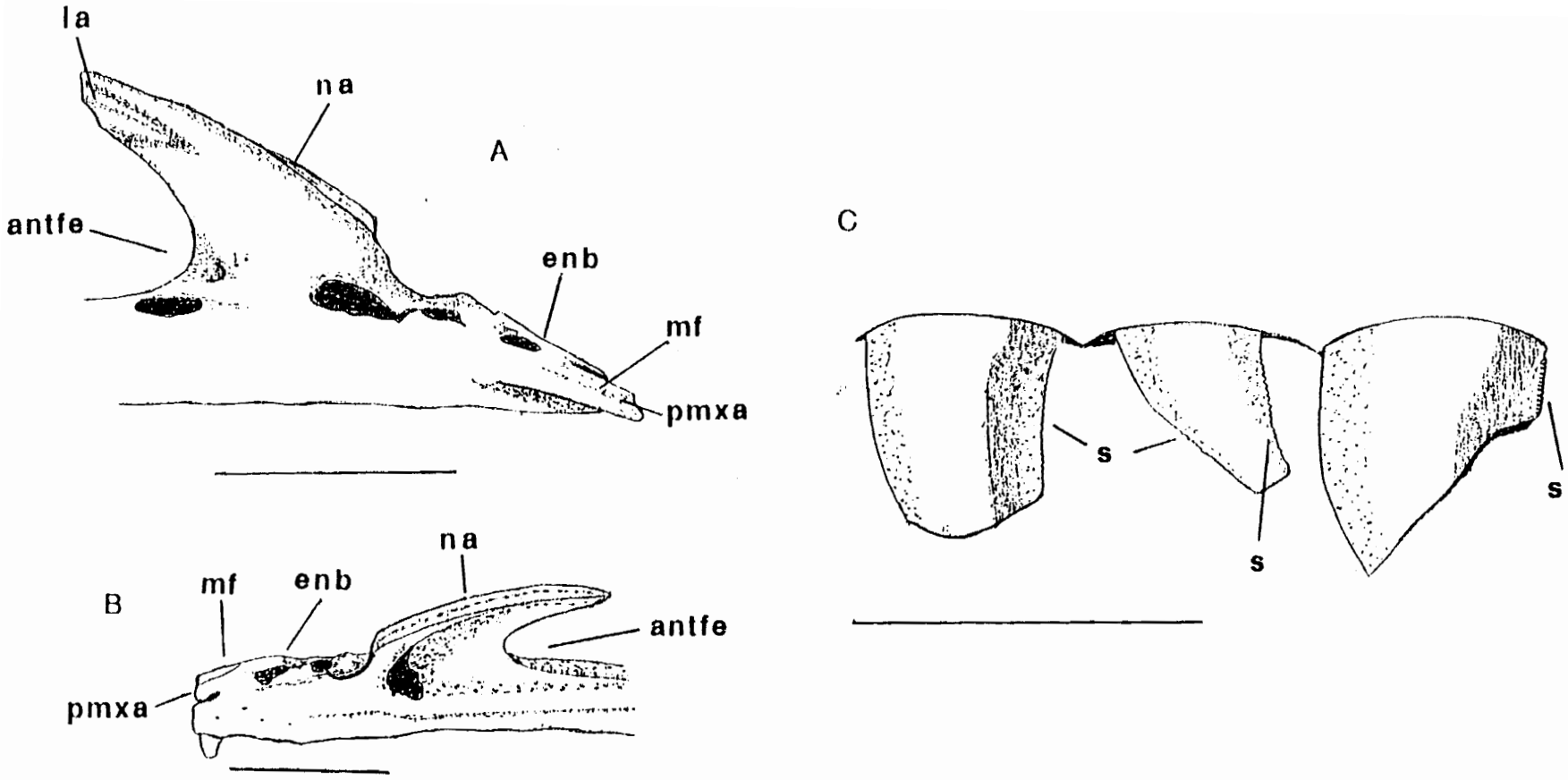



Figure 25

Line drawings of a presumed ceratosaurian left maxilla from Cromhall Quarry, site 14. The locations of some of the articular surfaces are shown, in detail, medially (A) and dorso-laterally (B). A detailed drawing of the dentition is shown, in left lateral view, in (C). Abbreviations: antfe, antorbital fenestra; enb, external narial border; la, lacrimal articulation; mf, medial flange; n, nasal articulation; pxma, premaxillary articulation; s, serrations. Scale bar is 1 cm for A and B, and .5 cm for C.

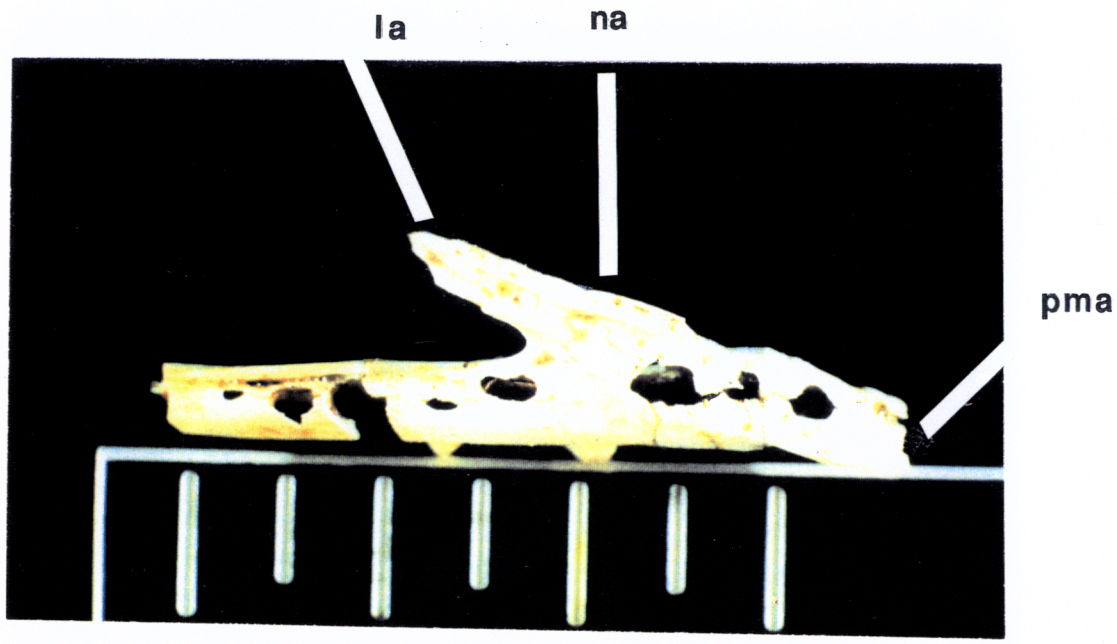



Figure 26

The ceratosaurian left maxilla from site 14, Cromhall Quarry. Locations of some of the articular surfaces are shown dorso-medially. Abbreviations: pma, premaxilla articulation; na, nasal articulation; la, lacrimal articulation. Scale bar is in 0.5 cm increments.

broken. A third tooth, situated between the two fixed teeth, is partially hidden within the socket with the exposed crown angled laterally and distally. This tooth appears to have been either just emerging from the socket, or to have been pushed back into the socket, as its position and appearance suggest an incomplete or non-existent root. It could be that the tooth is in the process of being shed and its root has been resorbed, or it is a new tooth with immature root growth. Alternately, the tooth could just have been damaged during sample processing. The fact that this tooth is between two fixed mature teeth corroborates the idea that the tooth was in the process of being shed, or newly erupted from the jaw, as Edmund (1962) has established that tooth replacement in the lower vertebrates occurs in cycles at alternate sockets. As a result, two adjacent teeth are unlikely to be shed at the same time, except in rare cases of illness and/or trauma. The mesial maxillary tooth preserved is smaller, and appears more like a slightly recurved peg with a rounded cross section. Socket size in the horizontal ramus appears largest at the third or fourth alveoli and decreases mesially and distally to this area. When viewed medially, the tooth sockets appear to be separated by thick vascularized alveolar walls which form triangular wedges pointing inferiorly.

The ascending plate (the facial plate) that arises from the tooth-bearing ramus is roughly triangular in shape, with a posteriorly extended portion of the triangle creating a process that is recurved, laterally compressed, and elongate. On the medial surface of this process, near the incomplete tip, there

is a grooved elongated triangle that is presumably an articulation for the lacrimal. The maximum distance between the superior surface of the horizontal, tooth-bearing ramus and the superior surface of the incomplete tip of the dorsal process is 1 cm. The dorsal surface of the blade-like process is flattened and slightly anteriorly flared into an articular surface, presumably for the nasals. Laterally, the basal plate exhibits a moderately deep, sharply defined, triangular fossa that extends from the posterior edge of the bone about 0.75 cm anteriorly. This fossa presumably provides the entire anterior, and partial inferior and superior, border of the antorbital fossa.

The Cromhall maxilla could be, potentially, referred to a variety of carnivorous archosauromorphs found in Middle and Late Triassic, and Early Jurassic, strata. Candidates include members of the Ceratosauria, Euparkeriidae, Erythrosuchidae, Ornithosuchidae, Parasuchia, Proterochampsidae, Proterosuchidae, Rauisuchidae, and Sphenosuchia; as well as the genera *Marasuchus*, *Lagerpeton*, *Procompsognathus*, *Gracilisuchus*, *Herrerasaurus*, *Scleromochlus*, *Erpetosuchus*, and *Staurikosaurus*.

The Euparkeriidae consists of *Euparkeria*, from a single locality in South Africa, and three genera from China (Carroll, 1988). Illustrations of the maxilla of *Euparkeria* (Ewer, 1965) indicate that the area in front of the facial plate is small, and the facial plate arises from the tooth-bearing ramus at a steep angle; unlike the situation seen in the Cromhall maxilla **(Figure 27)**.

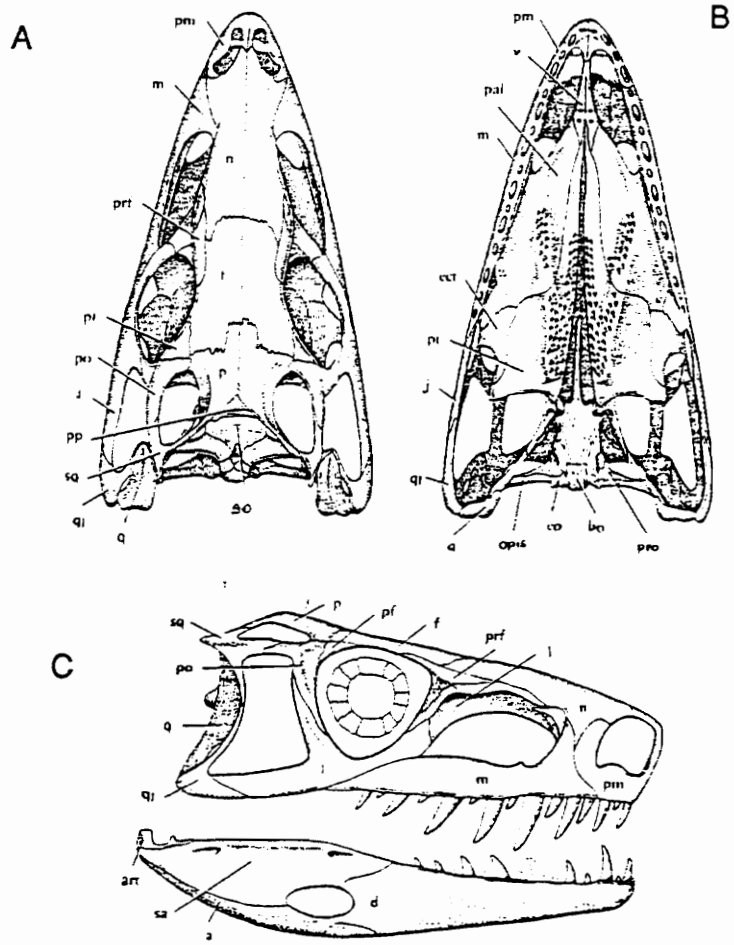



Figure 27

Line drawing of the skull of *Euparkeria* in dorsal (A), palatal (B), and right lateral (C) views (Ewer, 1965). The entire skull is around 10 cm in length. Abbreviations: a, angular; art, articular; bo, basioccipital; d, dentary; ect, ectopyerygoid; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pal, palatine; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; prf, prefrontal; pro, prootic; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; so, supraoccipital; sq, squamosal; v, vomer. Figure from Carroll (1988).

The Erythrosuchidae are generally large-headed carnivorous forms (ie. *Erythrosuchus* and *Vjushkovia*) from the Early and Middle Triassic (Parrish, 1992). The entire skull is large and massively built; with a convex ventral margin of the maxilla (Parrish, 1992). The plesiomorphic condition, in archosauriforms, for the ventral margin of the maxilla is a straight, horizontal tooth-bearing ramus like the one seen in the Cromhall maxilla (Parrish, 1992). Erythrosuchid maxillae are not involved in formation of the border of the external nares (Parrish, 1992).

*Ornithosuchus longidens* (Upper Triassic of Scotland) and *Riojasuchus tenuiceps* (Upper Triassic of South America) are both members of the Ornithosuchidae (Walker, 1964; Sereno, 1991). In both genera, unlike the Cromhall form, the maxilla is excluded from the border of the external nares. In addition, *Ornithosuchus longidens* has a much shorter and broader facial plate than that seen in the Cromhall maxilla (**Figure 28**;Walker, 1964; Sereno, 1991). *Riojasuchus tenuiceps* has an extremely deep antorbital fossa which extends to the ventral margin of the tooth-bearing maxillary ramus (Sereno, 1991).

Phytosaurs, members of the Parasuchia, are found in Upper Triassic strata from Europe, India, and North America (Carroll, 1988). Phytosaur tooth crowns tend to be long, slender, and conical (Sues *et al.*, 1994). Teeth from the mesial portion of the snout are rounded in cross-section, with smooth cutting edges (Sues *et al.*, 1994). Teeth from the distal portion of the jaw exhibit

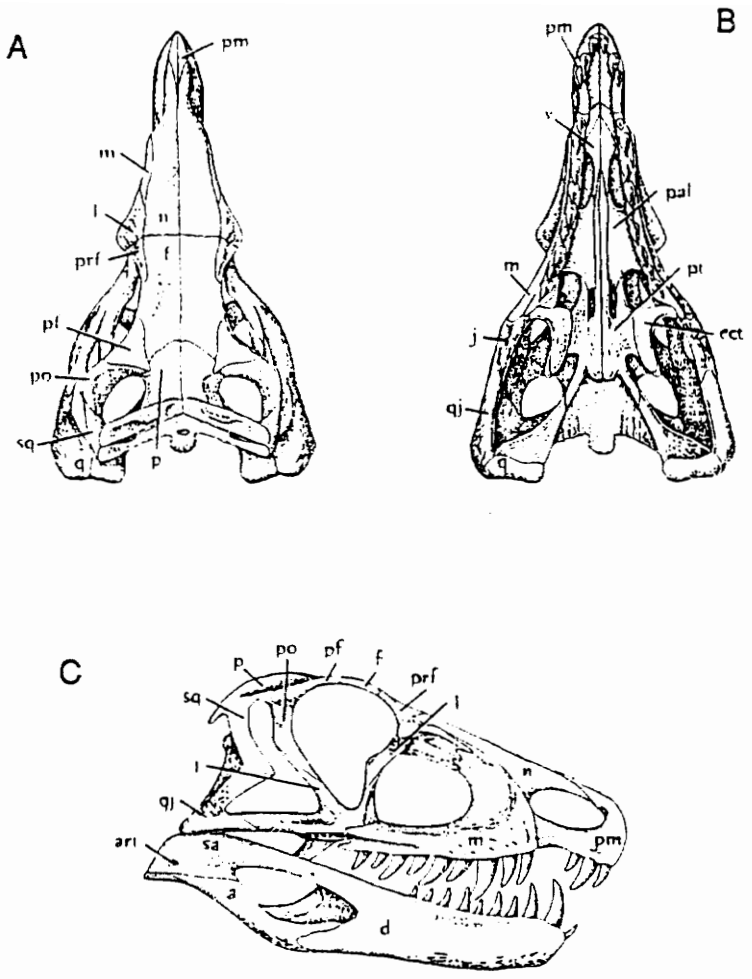



Figure 28

Line drawing of the skull of *Ornithosuchus* in dorsal (A), palatal (B), and right lateral (C) views (Walker, 1964). The entire skull is around 25 cm in length. Abbreviations: a, angular; art, articular; bo, basioccipital; d, dentary; ect, ectopyerygoid; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pal, palatine; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; prf, prefrontal; pro, prootic; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; so, supraoccipital; sq, squamosal; v, vomer. Figure from Carroll (1988).

crowns that are more labiolingually compressed, and which have finely serrated cutting edges (Sues *et al.*, 1994). This tooth crown morphology does not match that of the Cromhall maxilla.

Members of the Proterochampsidae include the Early and Middle Triassic genera *Chanaresuchus* and *Proterochampsa* (Carroll, 1988). Proterochampsids have broad, shallow skulls with elongate snouts (Bonaparte, 1984). The maxilla is not involved in the border of the external nares (Carroll, 1988; Bonaparte, 1984).

The Cromhall specimen is likely not a member of the Proterosuchidae as taxa within this family exhibit ankylo-thecodont dentition; teeth are marginal and set in very shallow sockets (Carroll, 1988). In addition, the maxilla is excluded from the border of the external nares **(Figure 29)**.

Rauisuchids, and the closely related poposuchids (represented by a single genus, *Poposaurus*, with not terribly diagnostic post cranial material) also exhibit no maxillary contribution to the external narial border (Galton, 1977; Chatterjee, 1985). These large (up to 6 m in length) carnivores of the Middle and Upper Triassic of Europe, East Africa, and North and South America, tend to be short-snouted, with serrated and recurved teeth (Sill, 1974; Chatterjee, 1985). The tooth-bearing ramus does not extend much past the facial plate, and the superior border to the facial plate is steep, unlike the situation seen in the Cromhall material (Sill, 1974).

The Sphenosuchia can be eliminated as the sphenosuchian maxilla

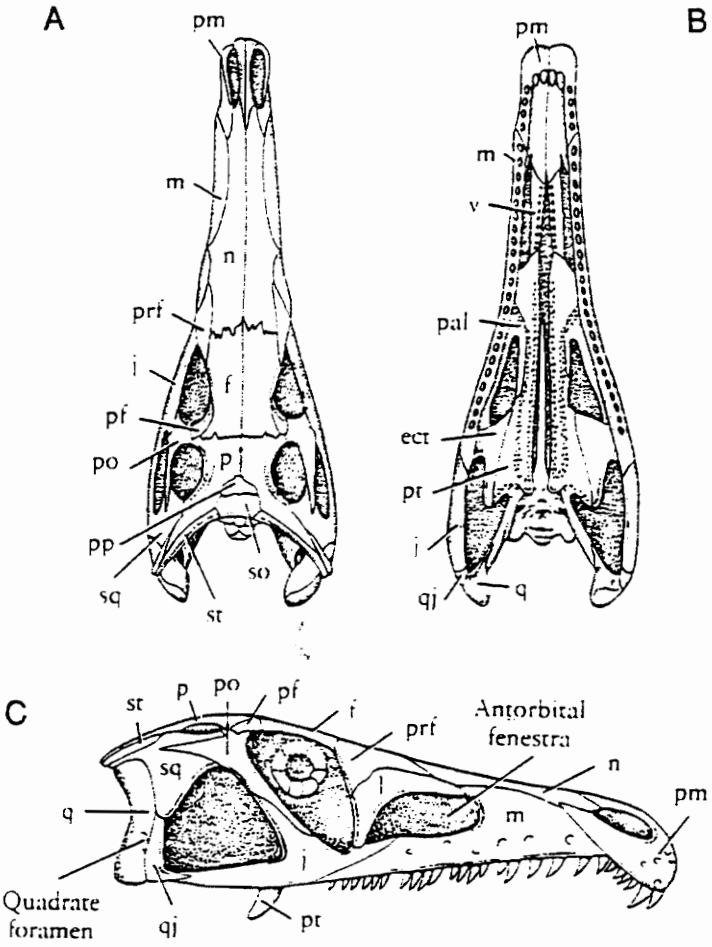



Figure 29

Line drawing of the skull of *Chasmatosaurus* (Proterosuchus) in dorsal (A), palatal (B), and right lateral (C) views (Ewer, 1965). The entire skull is around 15 cm in length. Abbreviations: ect, ectopyerygoid; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pal, palatine; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; prf, prefrontal; pro, prootic; pt, pterygoid; q, quadrate; qj, quadratojugal; so, supraoccipital; st, supratemporal; sq, squamosal; v, vomer. Figure from Carroll (1988).

does not exhibit a longitudinal ridge running along the long axis of the tooth-bearing ramus (Crush, 1984). In addition, the maxilla is not involved in the formation of the border of the external nares in the Sphenosuchia (Crush, 1984).

Only a partial maxilla is known from *Marasuchus* ("Lagosuchus") *lilloensis* (Sereno and Arcucci, 1994). While the anterior margin of the antorbital fenestra is not preserved, Sereno and Arcucci (1994) hypothesize that it might be sub-triangular in shape. However, there is no indication of any other ways it might be like the Cromhall specimen.

In *Gracilisuchus* the facial plate of the maxilla is much narrower, antero-posteriorly, than that seen in the Cromhall form. The area anterior to the facial plate is small and the facial plate arises at a steep angle; unlike the Cromhall specimen. In addition, the maxilla is not involved in forming the border of the external nares in *Gracilisuchus* (see figure 21).

*Herrerasaurus ischigualastensis* exihibits an oval fenestra; an oval opening, posterior to the external nares, which opens into the premaxilla and palate (Reig, 1965; Sereno and Novas, 1993). The maxilla forms the posterior border to the oval fenestra (Reig, 1965; Sereno and Novas, 1993). However, unlike the situation in the Cromhall maxilla, the maxilla in *Herrerasaurus* has little bone anterior to the facial plate, and the anterior border of the facial plate extends superiorly from the tooth-bearing ramus at a steep angle (Reig, 1965; Sereno and Novas, 1993).

*Scleromochlus taylori* (Late Triassic of Scotland) is known from natural molds in the Lossiemouth sandstones (Olsen and Sues, 1986; Sereno, 1991). The skull is low and broad, with a narial region that is short and tapered (Sereno, 1991). *Scleromochlus* maxillae exhibit cranial ornamentation that has not been recognized in any other basal archosaurs; the anterior margin of the antorbital fossa is raised and thickened into a low, robust ridge that diminishes posteriorly (Sereno, 1991). This form of cranial ornamentation is not present on the Cromhall maxilla.

*Erpetosuchus*, another carnivorous reptile from Elgin, may be eliminated on the basis of its dentition. The erpetosuchian maxilla has long sharp recurved teeth mesially, but distally these segue into toothless longitudinal ridges that may have been using for crushing (Benton and Walker, 1985).

Unfortunately, cranial materials from *Procompsognathus* (Sereno and Wilde, 1992), *Lagerpeton* (Sereno and Arcucci (1993), and *Staurikosaurus* (Sereno and Novas, 1993) are not known.

Several features present in the new maxilla are of particular interest as they are associated with basal dinosaur taxa. These characters, including the articular facets for the premaxilla and nasal, position of the external nares, tooth socket morphology, border of the antorbital fossa, and outline of the superior edge of the element, are somewhat problematic as there has been a tendency to rediagnose and redefine the Dinosauria in order to accommodate presumably key specimens (Padian and May, 1993; Fraser and Padian, 1995).

The resulting systematic confusion makes establishing the relative taxonomic position of new material uncertain (Fraser and Padian, 1995). On the other hand, other British fissures have yielded specimens of dinosaurs such as *Thecodontosaurus* and *Syntarsus*, so the presence of dinosaur material at Cromhall would not be surprising (Fraser and Padian, 1995).

The maxilla in question most closely resembles those seen in the Ceratosauria, which includes small- to medium-size Late Triassic to Late Jurassic taxa like *Ceratosaurus*, *Coelophysis*, *Dilophosaurus*, and *Syntarsus* (Benton, 1990). The Ceratosauria are theropods that are characterized, in part, by an anatomically distinct loose attachment of the premaxilla to the maxilla (Benton, 1990). This form of attachment, with the premaxilla being held in place by the nasal and palatine processes, results from the fact there is no bony symphysis between the premaxilla and maxilla (Rowe and Gauthier, 1990). Instead, ceratosaurs (apart from *Ceratosaurus nasicornis*), have a premaxilla and maxilla separated by a deep slot; Welles' (1984) "subnarial gap" (Rowe and Gauthier, 1990). This gap, into which an enlarged dentary tooth fits, interrupts the margin of the upper tooth row (Welles, 1984). The "subnarial gap", once believed to be the site of considerable cranial kinesis, is bridged by the palatal process of the premaxilla in such a way that it interlocks with an anterior maxillary process (Welles, 1984; Colbert, 1989; Rowe and Gauthier, 1990). In effecting this lock, the premaxillary articulation tends to extend onto the maxilla anteriorly **(Figure 30)**. The premaxilla and maxilla, with the nasal

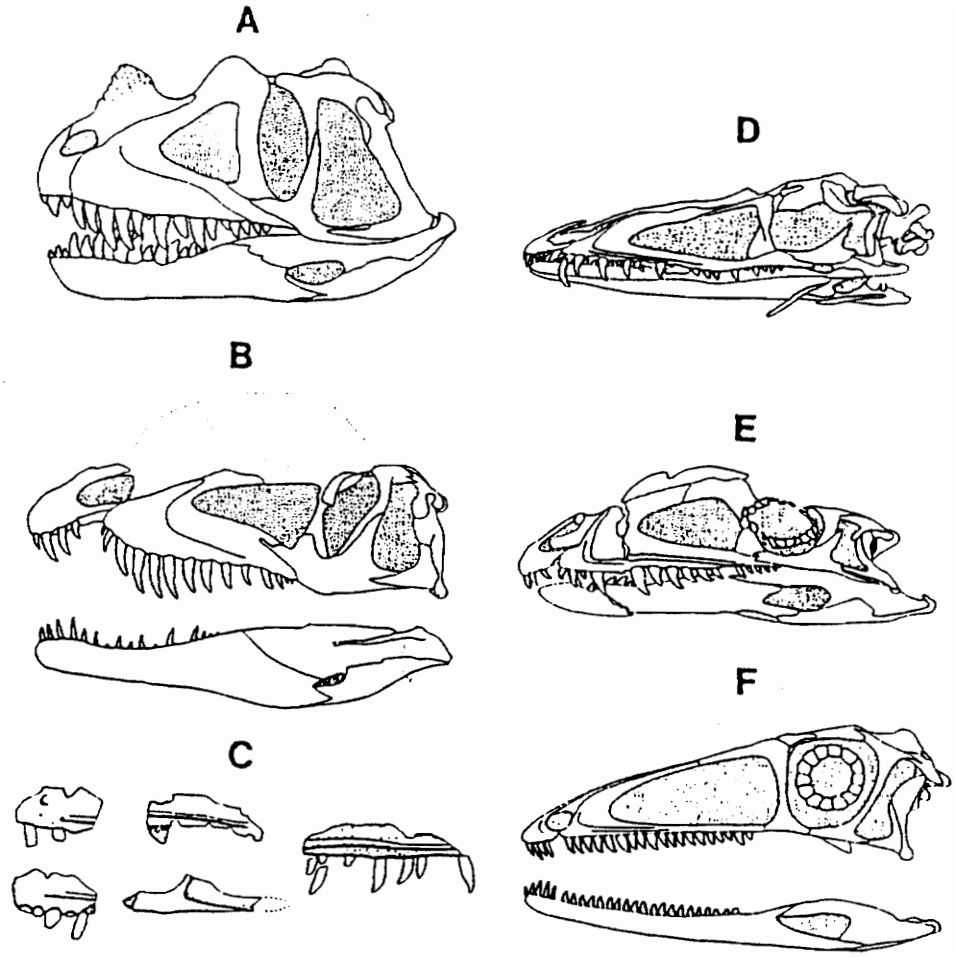



Figure 30

Line drawing of the skulls of six members of the Ceratosauria: A, *Ceratosaurus nascornis* (Gilmore, 1920); B, *Dilophosaurus wetherilli* (Welles, 1984); C, *Liliensternus liliensterni* (partial right and left maxillae; Huene, 1934); D, *Coelophysis bauri* (Colbert, 1989); E, *Syntarsus kayentakatae* (Rowe, 1989); F, *Syntarsus rhodesiensis* (Raath, 1977 and 1985). Figure is taken from Rowe and Gauthier (1990). Note the onlap of the premaxilla onto the maxilla in *Dilophosaurus*, and both species of *Syntarsus*. Also note the presence of the "subnarial gap" in the previous three taxa and *Coelophysis*.

superiorly, also form the anterior inferior and superior borders for the external nares. The external narial opening is posteriorly displaced from the tip of the snout. As a result of the positioning of the skull elements of the snout the maxillary articular facets for the premaxilla and the nasal are distinctly separate, with a portion of the border for the external nares often situated between them (Fraser, personal communication).

This appears to be the situation in the new maxilla. Although there is some breakage, it is possible to determine that the medial anterior portion of the maxillary ramus is expanded, flattened, and grooved in such a way as to provide an articulation with the premaxilla. The prominent articular facet for the nasal is situated on the superior surface of the ascending process of the maxilla. Between the two facets there is a stretch of partially preserved superior border of the maxilla. While most of this border is chipped away, a small portion (4 mm) maintains a smooth and rounded edge consistent with the border of a bony fossa: the external nares. This inclusion of the maxilla in forming the border of the external nares is unlike the condition seen in another Upper Triassic basal dinosaur, *Eoraptor*, which is also regarded as a theropod by Sereno *et al* (1993). Figures of the skull of *Eoraptor*, based on the somewhat crushed material, indicate that the premaxilla and nasal form the border of the external narial opening; excluding the maxilla from the border of the nares (**Figure 31**; Sereno *et al*, 1993). Incomplete preservation of the tip of the maxilla from Cromhall makes it difficult to determine the presence of any

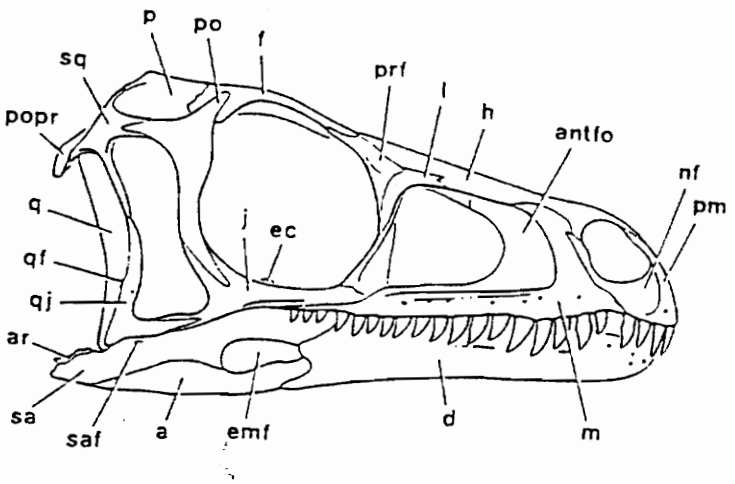



Figure 31

Line drawing of the skull of the type specimen of *Eoraptor lunensis* in right lateral view (from Sereno et al., 1993). Note that the border of the external nares is formed by the nasal and premaxilla. Abbreviations: a, angular; antfo, antorbital fossa; ar, articular; d, dentary; emf, external mandibular fenestra; ec, ectopterygoid; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; nf, narial fossa; p, parietal; pm, premaxilla; po, postorbital; popr, paroccipital process; prf, prefrontal; q, quadrate; qf, quadrate foramen; qj, quadratojugal; sa, surangular; saf, surangular foramen; sf, subnarial foramen; sq, squamosal. Scale bar is 5 cm.

"subnarial gap". Observation of the remaining teeth and the relative size of the tooth sockets in the new maxilla reveals that, like other ceratosaurs, the two most anterior maxillary teeth are subrounded in cross-section and unserrated while the more posterior dentition is laterally compressed and distinctly serrated (Welles, 1984; Colbert, 1989; Rowe, 1989; Rowe and Gauthier, 1990). Ceratosaurian maxillary teeth peak in size at or around the fourth alveolus and decrease in size mesially and distally in the tooth row, which parallels the situation seen in the site 14 maxilla (Welles, 1984; Colbert, 1989; Rowe, 1989; Rowe and Gauthier, 1990).

In overall outline, the Cromhall maxilla most closely resembles material assigned to *Syntarsus* and *Coelophysis*. In particular, the long low slope that the superior border traces from tip of the maxilla to tip of the ascending process is reminiscent of *Coelophysis* and *Syntarsus rhodesiensis* (as figured by Raath, 1969). *Syntarsus kayentakatae* appears to have a disjoint border; a low anterior slope that breaks just anterior to the antorbital fossa and becomes much steeper (Rowe, 1989; **Figure 32**). However, Colbert (1989) states that all the known *Coelophysis* material is broken and/or distorted due to its fragility. Much of the *Syntarsus* material studied is also broken/distorted (Rowe, 1989).

In both genera, the maxilla exhibits a longitudinal ridge, situated just above the tooth row, that extends from the anterior border of the antorbital fossa posteriorly along the ramus of the maxilla (Colbert, 1989; Rowe, 1989). *Liliensternus liliensterni* also exhibits this ridge, but since the skull material is

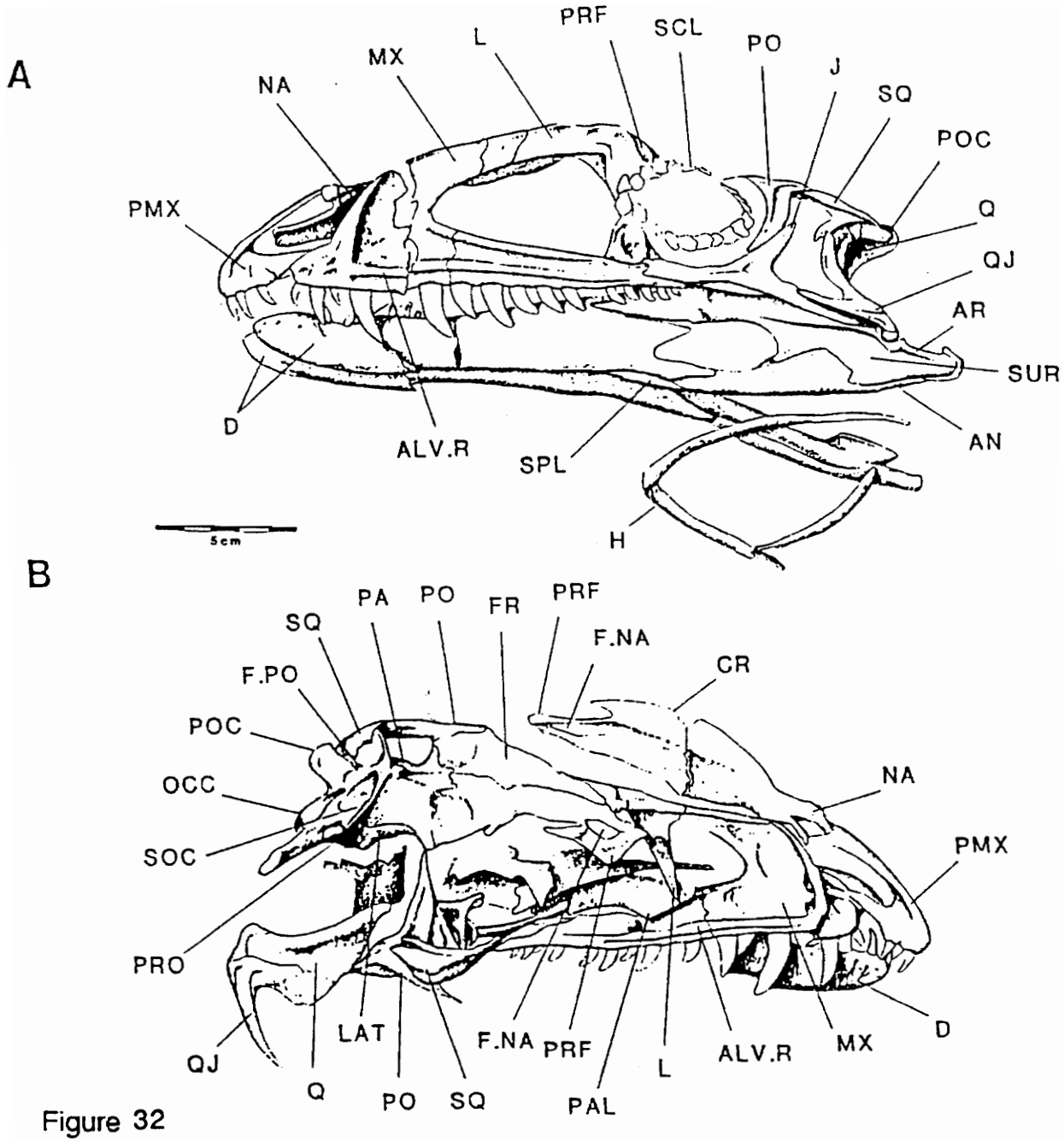



Figure 32

Line drawing of the skull of the type specimen of *Syntarsus kayentakatae* in left lateral (A) and medial view (B; from Rowe, 1989). Abbreviations: ALV.R, alveolar ridge; AN, angular; AR, articular; CR, crest; D, dentary; R.NA, nasal fenestra; F.PO, post-temporal fenestra; FR, frontal; H, hyoid; J, jugal; L, lacrimal; LAT, laterosphenoid; MX, maxilla; NA, nasal; OCC, occipital condyle; PA, parietal; PAL, palatine; PMX, premaxilla; PO, postorbital; POC, paroccipital process; PRF, prefrontal; PRO, prootic; Q, quadrate; QJ, quadratojugal; SCL, sclerotic ring; SOC, supraoccipital; SPL, splenial; SQ, squamosal; SUR, surangular.

very fragmentary, it is hard to determine whether there is any other resemblance to the Cromhall material (Huene, 1934; Rowe and Gauthier, 1990). As Rowe (1989) notes, *Coelophysis* and *Syntarsus* are very alike. Raath (1969) rejected synonymizing them on the basis of two characters, only one of which appears in the skull: presence of a nasal fenestra. In *Syntarsus*, there is a diamond-shaped opening at the junction between the nasal, prefrontal and frontal; the nasal fenestra (Raath, 1969; Rowe, 1989). This opening is not apparent in *Coelophysis* (Colbert, 1989). Colbert (1989) also states that, while Raath (1969) found interdental plates in the maxilla of *Syntarsus rhodesiensis*, there appear to be no interdental plates in *Coelophysis*. The Cromhall maxilla does not have distinct interdental plates, but does exhibit more highly vascularized wedges of bone found between, and at the base of, the teeth.

Given that the cranial osteology of *Coelophysis* is in the process of revision (Sues, personal communication), it is only prudent to go so far as to assign the new maxilla to the following taxonomy:

Class Dinosauria
Order Saurischia
Suborder Theropoda
Clade Ceratosauria (?)

## PART II - STATISTICAL ANALYSES

The results of the statistical analyses will be discussed individually, then integrated in order to provide a more complete picture.

PCA using Correlation Matrix

The Eigenvalues table **(Table 4)** indicates that the first three principle components account for 84.3% of the variation in the data, with the first principle component explaining 41.7% of the total variation. Within the first principle component, as shown in the Eigenvectors table, there is a strong contrast in loading between Y1 (*Planocephalosaurus*) and Y3 (*Clevosaurus*). This suggests that the majority of variation in the data can be explained by the relative amounts of each of these taxa in a sample. *Planocephalosaurus* is abundant in all of the samples. However, *Clevosaurus* is only abundant in two of the samples: level 3B, level 3E. In fact, looking at a graphical representation of the PCA analysis, it is obvious that both of the levels from site 3 are considerably offset from the rest of the samples **(Figure 33)**. The second principle component shows strong "versus" loading of Y2 (*Diphydontosaurus*) and Y6 (Archosauromorpha); suggesting an inverse ratio of relative abundance for the taxa. This is consistent with the tallies from site 4, with an abundance of archosauromorphs but a paucity of *Diphydontosaurus*, in particular. This can be seen in another graphic interpretation of the PCA data **(Figure 34)**. None of the other sites, in total, show such contrasting relative abundances.

Eigenvalues of the Correlation Matrix

| | Eigenvalue | Difference | Proportion | Cumulative |
|---|---|---|---|---|
| PRIN 1 | 2.50175 | 1.00495 | 0.416959 | 0.416959 |
| PRIN 2 | 1.49681 | 0.43907 | 0.249468 | 0.666427 |
| PRIN 3 | 1.05774 | x | 0.176290 | 0.842717 |

Eigenvectors

| | PRIN 1 | PRIN 2 | PRIN 3 | |
|---|---|---|---|---|
| Y1 | -.558290 | 0.197073 | 0.286116 | *Planocephalosaurus* |
| Y2 | 0.142766 | 0.555846 | -.533641 | *Diphydontosaurus* |
| Y3 | 0.526391 | 0.232958 | 0.331837 | *Clevosaurus* |
| Y4 | 0.361262 | -.108219 | -.503123 | *Sigmala* |
| Y5 | 0.490296 | 0.110402 | 0.515245 | *Pelecymala* |
| Y6 | 0.141218 | -.757646 | -.068108 | Archosauromorpha |

Table 4
Eigenvalues and Eigenvectors derived from a SAS Principle Components Analysis, using a correlation matrix, of the Cromhall data.

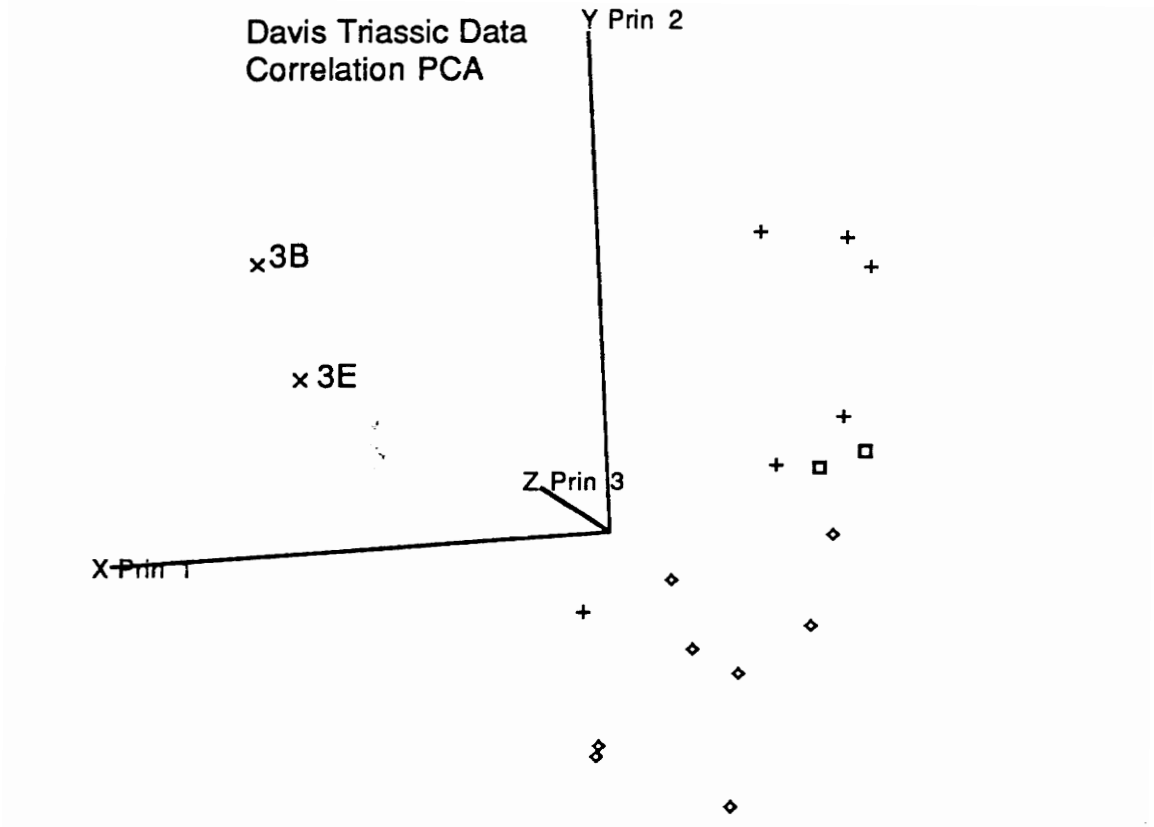



Figure 33

MacSpin graphic indicating the separation of levels 3B and 3E, when analyzed by PCA with a correlation matrix, from the rest of the Cromhall data. x = site 3 levels, diamond = site 4, + = site 5, square = site 14.

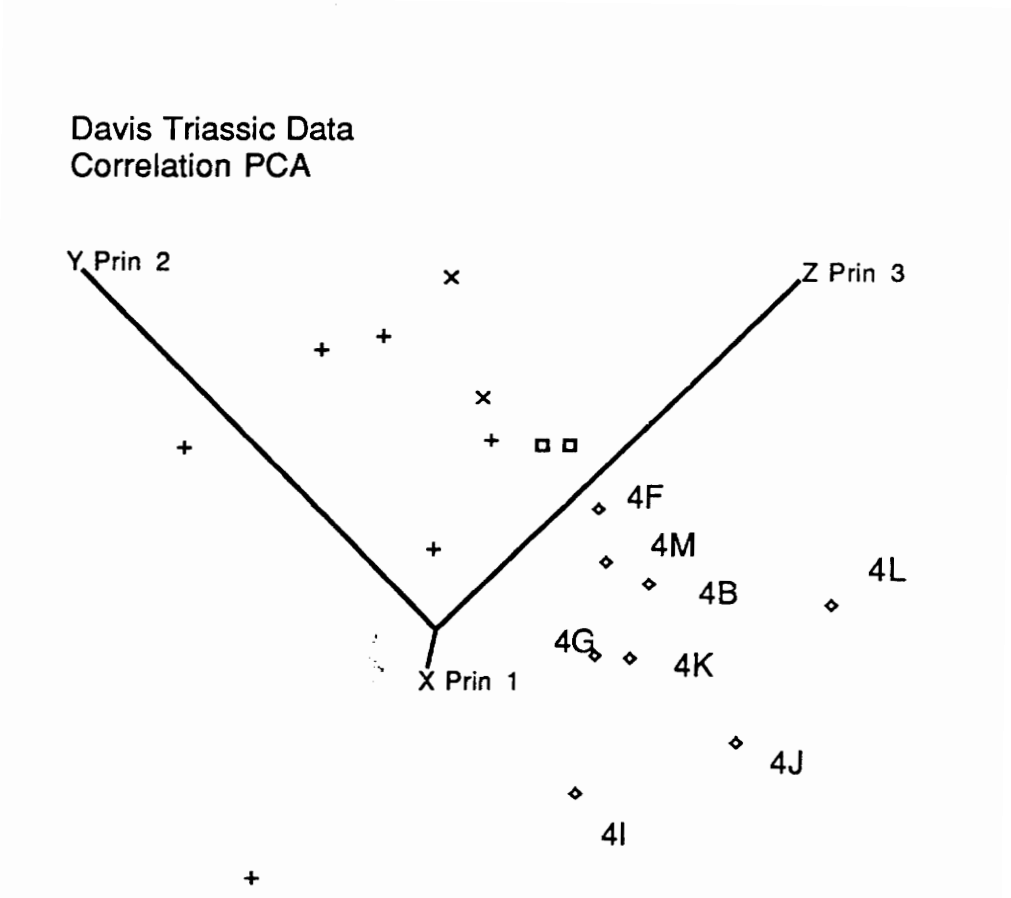



Figure 34

MacSpin graphic indicating the separation of site 4 levels from the rest of the Cromhall data. All the data shown in this graph have been subjected to PCA with a correlation matrix. x = site 3 levels, diamond = site 4, + = site 5, square = site 14.

However, level 5B has a high number of *Diphydontosaurus* versus a low number of archosauromorphs. A second, much weaker, "versus" loading between Y4 (*Sigmala*) and Y5 (*Pelecymala*) indicates an either/or relationship between abundance of the taxa. This relationship is clearly illustrated in all of the samples. The third principle component examined, which accounts for the least determined amount of variation in the data set, contains strong negative loadings for Y2 (*Diphydontosaurus*) and Y4 (*Sigmala*) contrasted with a strong positive loading for Y5 (*Pelecymala*). This suggests that samples enriched with *Diphydontosaurus* and *Sigmala* should contain few *Pelecymala*. This can be seen in all of the samples. An additional very weak "versus" loading can be seen for Y1 (*Planocephalosaurus*), Y2 (*Diphydontosaurus*), and Y6 (Archosauromorpha), which suggests that the relative presence of these taxa may be used to further refine the initial sample groupings determined by the presence of the other three taxa.

PCA using Covariance Matrix

The Eigenvalues table **(Table 5)** indicates that the first three principle components account for 98.3% of the variation in the data, with the first principle component explaining 58% of the total variation. The first principle component, as indicated in the Eigenvectors table, is based on strong "versus" loading of Y1 (*Planocephalosaurus*) and Y6 (Archosauromorpha). Relative abundances of these taxa show an overwhelming number of *Planocephalosaurus* in all the samples. However, looking at the actual mathematical ratios of

Eigenvalues of the Covariance Matrix

| | Eigenvalue | Difference | Proportion | Cumulative |
|---|---|---|---|---|
| PRIN 1 | 0.022715 | 0.011114 | 0.580290 | 0.580290 |
| PRIN 2 | 0.011601 | 0.007449 | 0.296363 | 0.876653 |
| PRIN 3 | 0.004152 | x | 0.106063 | 0.982716 |

Eigenvectors

| | PRIN 1 | PRIN 2 | PRIN 3 | |
|---|---|---|---|---|
| Y1 | -.839251 | 0.298618 | 0.009293 | *Planocephalosaurus* |
| Y2 | 0.056565 | -.584405 | 0.651365 | *Diphydontosaurus* |
| Y3 | 0.173814 | -.317212 | -.721127 | *Clevosaurus* |
| Y4 | 0.084595 | -.058274 | -.097037 | *Sigmala* |
| Y5 | 0.019680 | -.019162 | -.050066 | *Pelecymala* |
| Y6 | 0.504682 | 0.681844 | 0.209023 | Archosauromorpha |

Table 5
Eigenvalues and Eigenvectors derived from a SAS Principle Components Analysis, using a covariance matrix, of the Cromhall data.

*Planocephalosaurus* to archosauromorphs in each sample reveals that there is a considerable difference between site 14 and the rest of the sites. Site 14 has approximately 18 times the number of *Planocephalosaurus* to archosauromorphs. In contrast, the second highest ratio found in the other samples/sites is the 9.6:1 count seen in site 5. At the other end of the ratio spectrum is site 4, with 2.6 times the number of *Planocephalosaurus* to Archosauromorpha. This contrast between sites 4 and 14 can be seen graphically **(Figure 35)**. The second principle component is based around a strong negative loading for Y2 (*Diphydontosaurus*) and a strong positive loading for Y6 (Archosauromorpha). When related to the data, this highlights the relative abundance differences in sites 4 and 14 versus those in sites 3 and 5. Sites 4 and 14 contain abundant archosauromorphs and few, or no, *Diphydontosaurus*. In contrast, sites 3 and 5 contain numerous *Diphydontosaurus*, but fewer archosauromorphs. This dichotomy can also be recognized graphically (see previous figure). A secondary, weaker "versus" loading can be seen between Y1 (*Planocephalosaurus* ) and Y3 (*Clevosaurus*). As noted in the correlation analysis, this loading serves to separate levels 3B and 3E from the rest of the data **(Figure 36)**. The final (third) principle component determined shows strong "versus" loadings on Y2 (*Diphydontosaurus*) and Y3 (*Clevosaurus*). Examination of the data suggests that sites 3 and 14 have similar ratios of *Diphydontosaurus* to *Clevosaurus* ; between 1.0 to 1.5 times more of the latter than the former. Sites 4 and 5 tend to

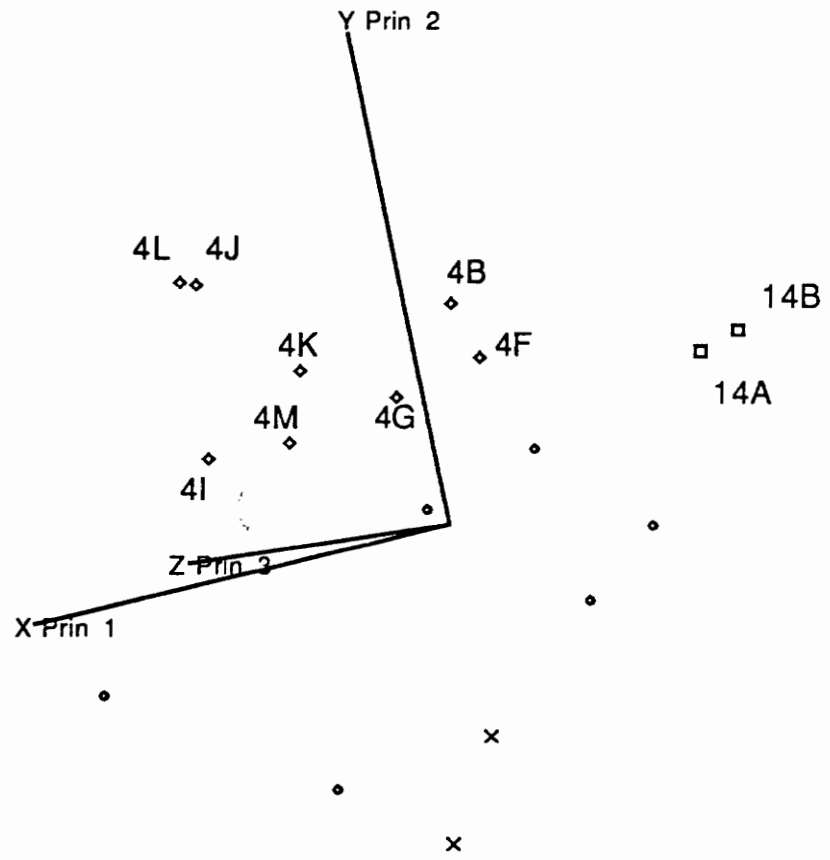



Figure 35

MacSpin graphic indicating the relative separation of sites 4 and 14 from the rest of the Cromhall data. Note also the spatial separation of site 4 levels from those from site 14. All data has been subjected to PCA with a covariance matrix. x = site 3 levels, diamond = site 4, circle = site 5, square = site 14.

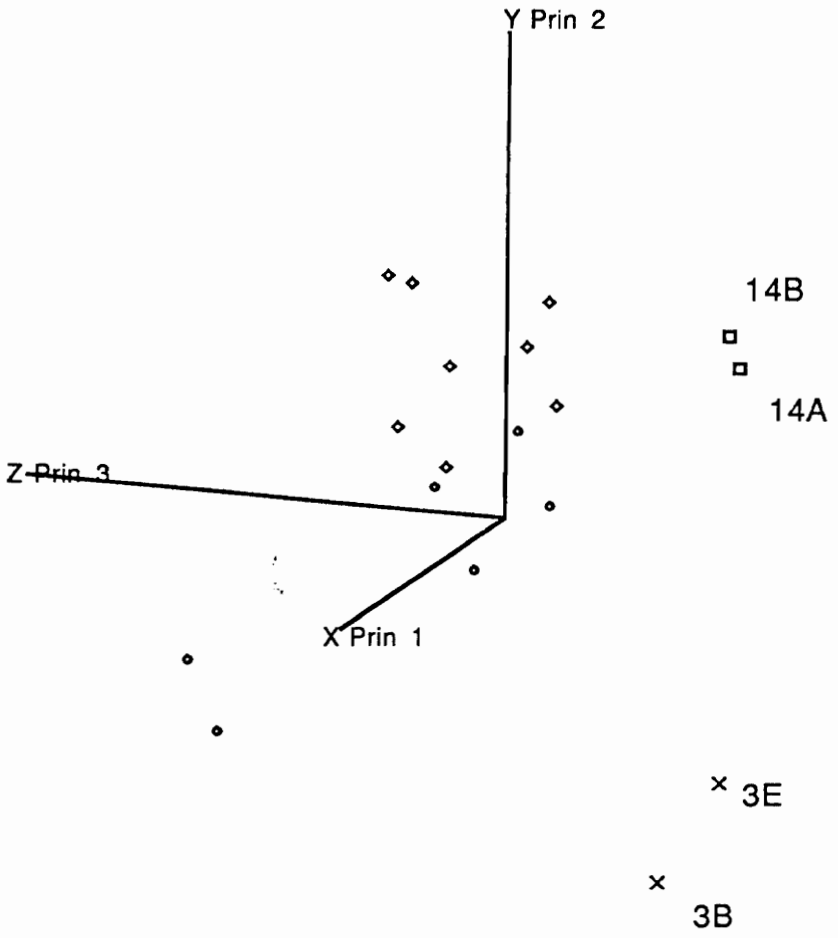



Figure 36

MacSpin graphic indicating the relative separation of site 3 and site 14 levels from the rest of the PCA- (with covariance matrix) plotted Cromhall data. x = site 3 levels, diamond = site 4, circle = site 5, square = 14.

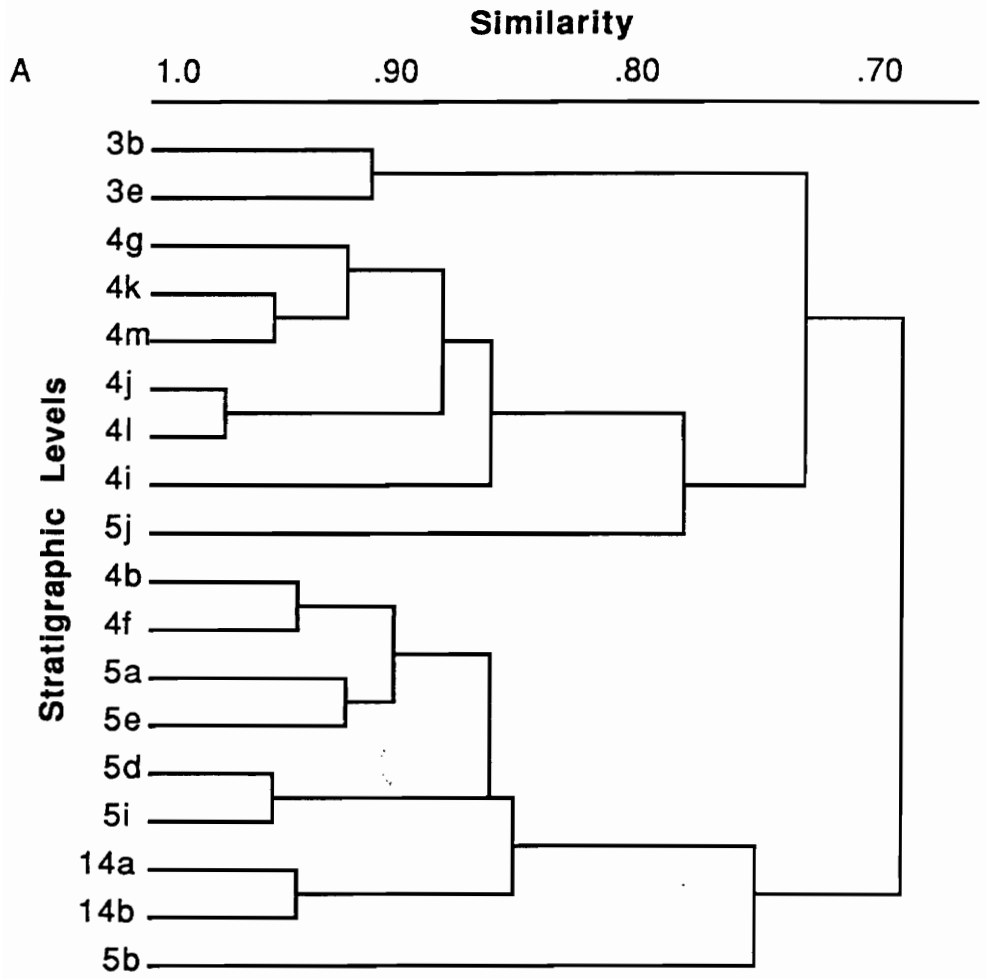
have more of the former than the latter; with level 5B having the highest ratio. This separation between sites 3 and 14 versus sites 4 and 5 is noticeable graphically (see previous figure).

It is interesting to note that, given that the covariance matrices produce principle components that are weighted by the relative abundance of the taxa, that the first three principle components are based on relationships between the four most abundant taxonomic groups: *Planocephalosaurus* , Archosauromorpha, *Diphydontosaurus, Clevosaurus.* This suggests that there may be a certain amount of generality to the first, and possibly the second, principle component as they may be registering a sample size difference. This hypothesis is also suggested by the fact that the covariance PCA second principle component is partially based on the same "versus" loadings between Y2 *(Planocephalosaurus* ) and Y3 (*Clevosaurus* ) as the correlation PCA first component. In the covariance results, only a small amount of the total variation (less than half of the 29.6% of the variation accounted for by the entire second principle component) in the data is felt to be explained by this "versus" relationship. Contrastingly, this same relationship is felt to explain 41.6%, as the first principle component, of the total variance when the correlation method is applied. Despite these differences, both methods suggest that variations in the data can be generally best described in site groupings. With few exceptions, graphic representations of the data show that the level samples tend to be found in close proximity to one another. By using the principle

components determined by both PCA methods, individual sites can be shown to be isolated from other sites.

Q-Mode Cluster Analysis Using the Czekanowski Coefficient

This method of analysis results in a broad grouping into two main clusters consisting of levels 3b, 3e, 4g, 4i, 4j, 4k, 4l, 4m, 5j, and 4b, 4f, 5a, 5b, 5d, 5e, 5i, 14a, 14b **(Figure 37)**. These two clusters join at .69 similarity, a number which is significant as it indicates that all the clusters created in previous steps occur at .69 or greater degrees of similarity. Higher degrees of similarity indicate greater confidence in the clustering results (Griffith and Amrhein, 1991). A closer look at the contents of the second main cluster reveals that both of the levels from site 14 group closely together, at .94 similarity. These two levels group, in turn, with all of the site 5 levels, with the exception of the youngest level; 5j. This result is of particular significance as site 5 (faunal association B1) is considered, by Walkden and Fraser (1993) to be the next oldest in the Cromhall sequence. Therefore, it appears that the biostratigraphic scheme erected for the Cromhall fissures is internally consistent. Sites 4 (faunal association B2) and 3 (faunal association B3), respectively, are the third and second oldest (Walkden and Fraser, 1993). Also included in this large cluster are the two oldest levels from site 4: 4b, 4f. In the second major cluster, all of the site 4 levels (with the exception of the two previously mentioned) group together at .86 similarity. This nested site 4 clustering then groups, at .78, with level 5j. Both of the site 3 levels, 3b and 3e,




B

| | | | | | |
|---|---|---|---|---|---|
| 4j | 4l | .97 | 4b | 5a | .90 |
| 5d | 5i | .95 | 4g | 4j | .88 |
| 4k | 4m | .95 | 4g | 4i | .86 |
| 4b | 4f | .94 | 5d | 14a | .85 |
| 14a | 14b | .94 | 4b | 5d | .84 |
| 4g | 4k | .92 | 4g | 5j | .78 |
| 5a | 5e | .92 | 4b | 5b | .75 |
| 3b | 3e | .91 | 3b | 4g | .73 |
| | | | 3b | 4b | .69 |

Figure 37

Dendrogram of Q-mode analysis of Cromhall data using percent transformed data and Czekanowski coeffiecient (A) and a table of numerical similarity quotients (B). The table reads; levels 4j and 4l cluster at .97 similarity, levels 5d and 5i cluster at . 95, etc..

cluster closely together (.91), and then are distantly connected with the rest of the large group at .73.

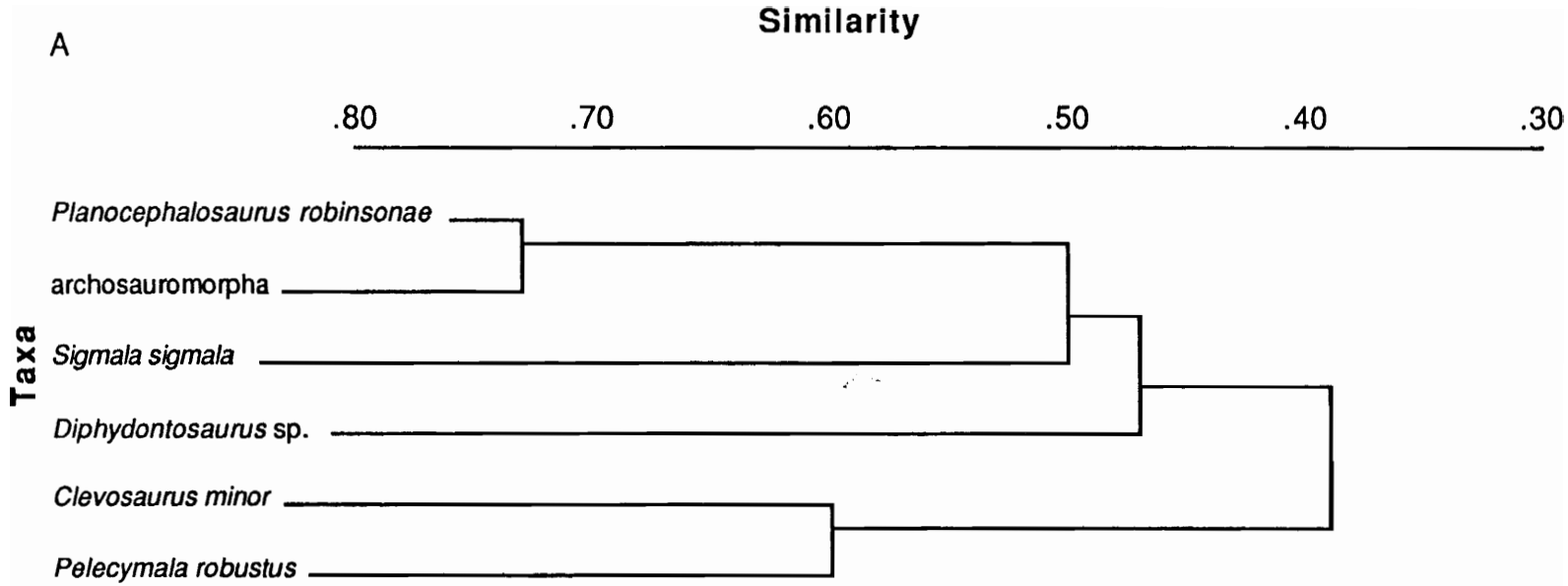
R-Mode Cluster Analysis Using the Czekanowski Coefficient

Clustering done in R-mode, with the data matrix rearranged such that rows become columns and vice versa, is generally not useful in determining natural species groupings as all the clusters produced have mutually exclusive species compositions (Bennington, 1995). Therefore, it is impossible to assess groupings in which a single species is abundant in more than one sample (Bennington, 1995). However, it is possible to utilize R-mode results in terms of probable pairing and probable exclusions. For example, while the majority of the similarity measures in the percent maximum R-mode analysis indicate low probable clustering, it is possible to say that *Planocephalosaurus robinsonae* is often (.73) found in conjunction with archosauromorphs **(Figure 38)**. It is also possible to say that *Clevosaurus minor* and *Pelecymala robustus* are found together slightly more than 50 % of the time. In addition, the analysis suggests that samples containing *Planocephalosaurus*/Archosauromorpha tend not to contain *Clevosaurus*/*Pelecymala*, as they cluster at .39 similarity.

Integrated Statistical Results

It is important to distinguish between exploratory procedures, like PCA, which make observing/defining clusters easier, and clustering methods (Neff and Marcus, 1980). PCA is not a clustering technique as it does not find groups in initially unstructured data; it simply reduces the number of dimensions that

A




B

| | | |
|---|---|---|
| *Planocephalosaurus robinsonae* | archosauromorpha | .73 |
| *Clevosaurus minor* | *Pelecymala robustus* | .59 |
| *Planocephalosaurus robinsonae* | *Sigmala sigmala* | .50 |
| *Planocephalosaurus robinsonae* | *Diphydontosaurus* | .47 |
| *Planocephalosaurus robinsonae* | *Clevosaurus minor* | .39 |

Figure 38

Dendrogram of R-mode analysis of Cromhall data after the tallies have been percent transformed and percent maximum equilibrated (A) and a data table of numerical similarity quotients (B). Table is to be read as; *Planocephalosaurus robinsonae* and archosaur cluster together at similarity .73, etc..

the data inhabits (Neff and Marcus, 1980). While it is possible to see what look like groups in PCA output, particularly in graphic output, defining these as clusters is applying an *ad hoc* procedure on top of the PCA results (Neff and Marcus, 1980). It is important to remember that PCA is an ordination technique which determines which variables explain the majority of the variation in a data set. Clustering techniques determine which observations have the maximum similarity to each other. In other words, PCA plots may be said to indicate the separation, on the principle component axes, of groups of data from other groups of data, but they cannot be used to simultaneously say that all the observations in one group are more similar to each other than they are to any other observations.

It is possible, by using integrated results from both types of analysis, to determine trends in the data. For example, both PCA and clustering suggest that, with few exceptions, levels within a fissure tend to act similarly when subjected to analysis. In other words, it seems likely that the majority of levels within any one fissure are more like each other than levels from any other fissure. In addition, levels from any one fissure tend to act most like levels from the fissure to which they are hypothesized to be most closely linked in time. Fissure 14 levels (oldest) are linked with fissure 5 levels (next oldest), which are in turn linked with fissure 4 levels (third oldest). Fissure 4 levels are then distantly linked with fissure 3 levels (youngest) **(Figure 39)**. Walkden and Fraser's (1993) biostratigraphic framework is essentially confirmed, with some

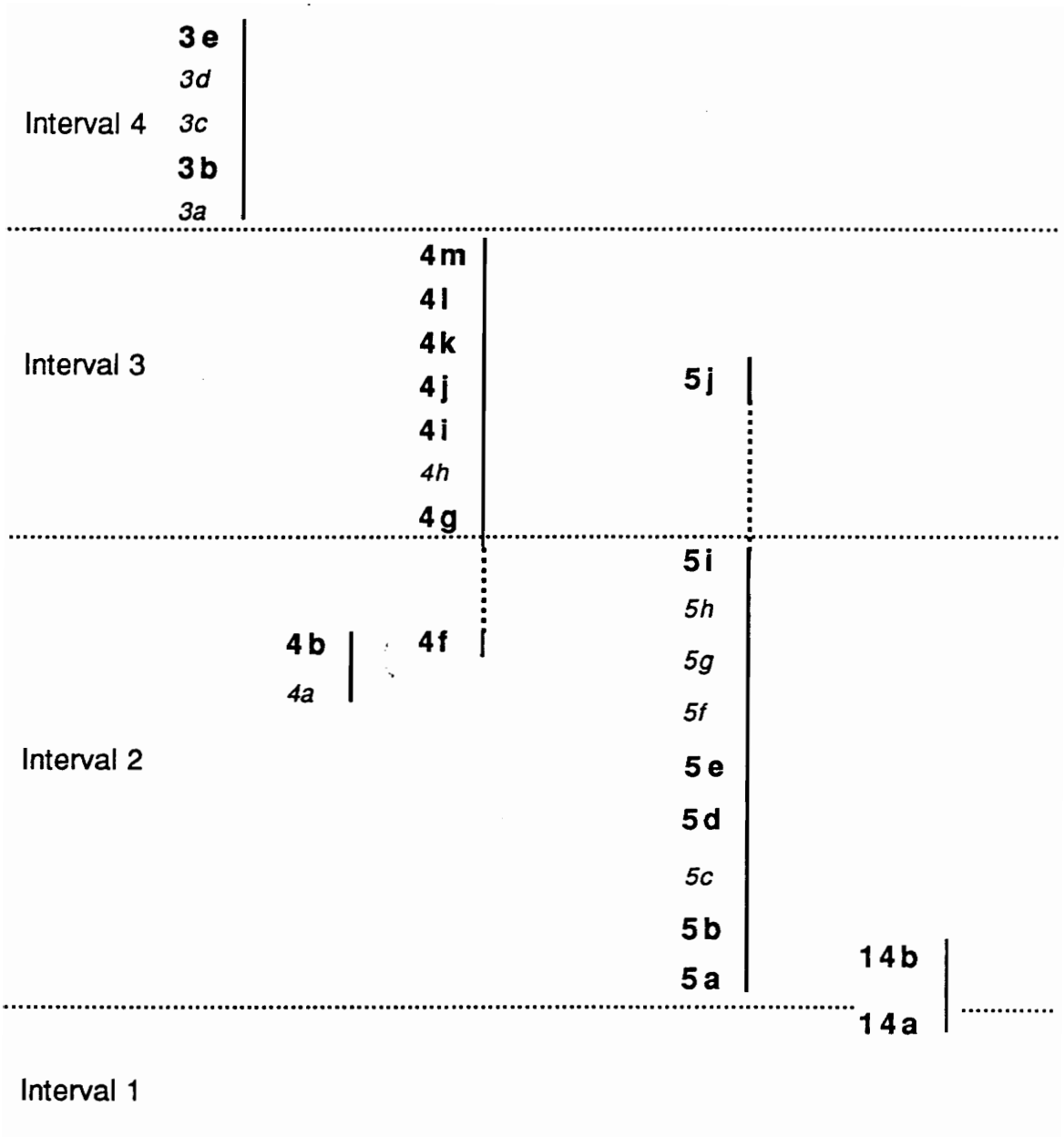



Figure 39

Graphic indicating the degree of overlap of fissure fauna similarity indicated by statistical analyses. Levels indicated by smaller print italics were not included in the analysis; either due to a lack of vertebrate material in the samples collected or because the samples have not been processed. This graphic assumes that the fissures represent a temporal continuum.

minor exceptions, by these results. Finally, there appears to be a temporally significant inverse relationship between the presence of *Planocephalosaurus robinsonae* and *Clevosaurus minor*. Both PCA and R-mode clustering show that the abundance of one of the taxa suggests that there will be few of the other. *Planocephalosaurus* is present in all of the fissures, but *Clevosaurus* becomes more abundant in fissure 3; suggesting that *Clevosaurus* may become a major part of the younger fauna.

# DISCUSSION

## PART I - PROCESSES AFFECTING BONE MODIFICATION

As Andrews (1990) has noted, the composition of a fossil fauna may differ from that of a living community as there are numerous processes involved in fossilization that can modify the faunal components. The two major complicating factors cited in palaeoecological studies are processes which modify bone and processes which account for bone accumulation.

Andrews (1990), in a comprehensive study of small mammal faunas, cites seven major stages which can potentially modify the composition of a fossil fauna: means of death, processes immediately following death, before/during burial, after burial, exposure, collection, sorting/conservation/storage **(Figure 40)**. All of these stages are marked by conditions that may act to modify and/or destroy the skeletal elements of individual animals. In extreme cases, no identifiable bones will remain and the resulting faunal composition will be biased. The second last of these stages, collection, can presumably be overcome by the type of systematic and unbiased collecting seen at Cromhall Quarry. The last stage, sorting/conservation/storage, is more difficult to assess. In the case of the Cromhall material, the taxonomic occurrence is based on the recognition of the most robust and diagnostic skeletal elements: jawbones. While this may serve to negate some of the problem of modification of the faunal composition during this last stage, it is impossible to entirely rule out, or even quantify, bone losses

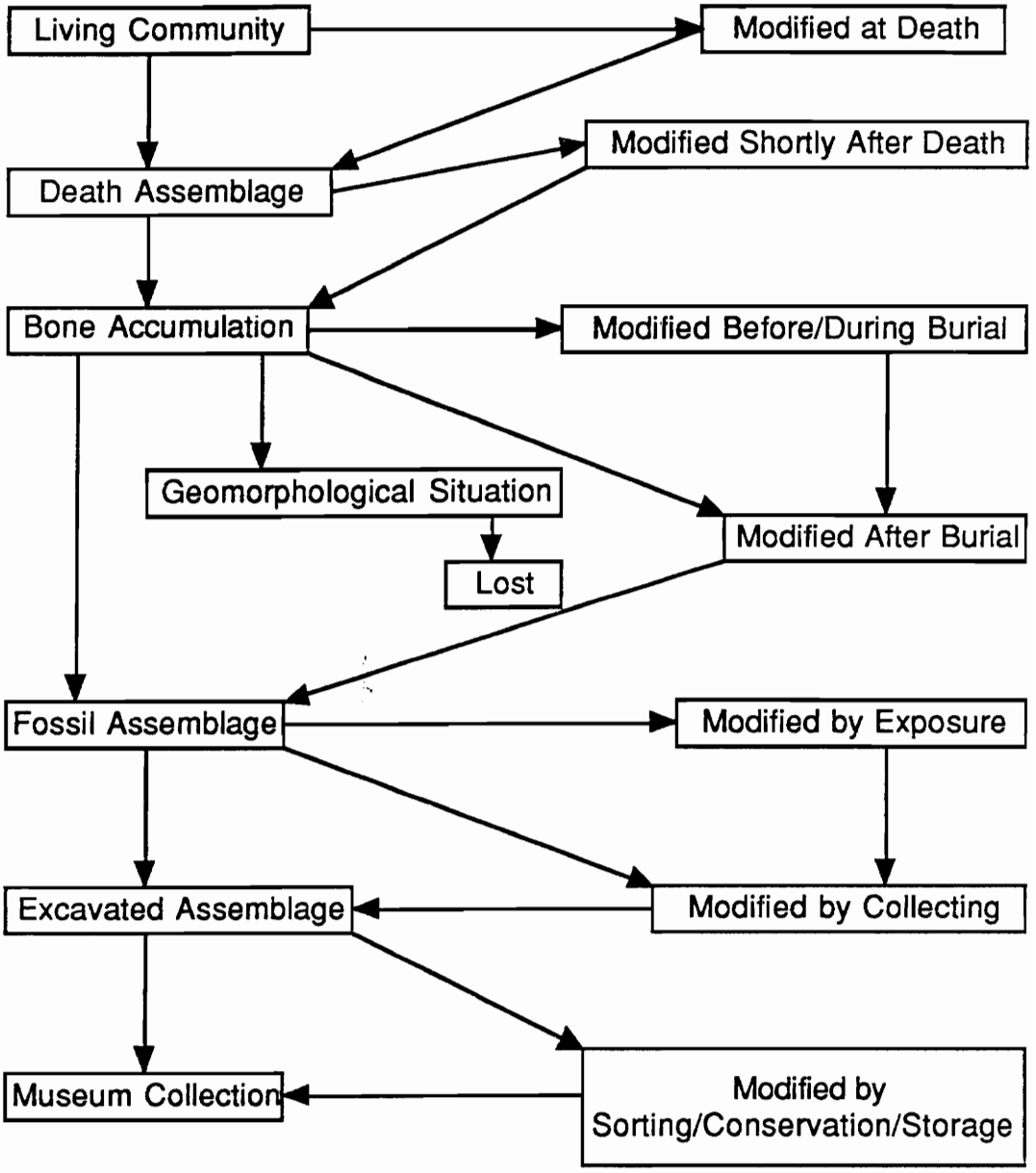



Figure 40

Stages in the formation and modification of bone assemblages. Formation stages are shown on the left and modification stages are to the right (from Andrews, 1990).

during the processing or curating of the Cromhall material. Based on personal observation and anecdotal evidence, it is only possible to state that this loss is minimal. The first five stages are much more likely to be involved in changing the faunal composition of a living community, and will be discussed in more detail.

Stage 1 - Means of Death

In general, death can occur either via "natural" causes (such as old age, starvation, disease, and drowning) or via predation (Andrews, 1990).

Animals whose deaths can be attributed to this first category may die at any time and in any place. There are, however, certain situations in which death is much more likely, such as during drought or flood conditions. Whatever the specific cause, animals that die of "natural" causes tend to show little skeletal modification at this stage.

Animals which die as a result of predation exhibit various degrees of skeletal modification depending on the method of prey ingestion utilized by the predator. Predators which use shearing tooth motions to break up their prey cause the greatest damage to the bone (Andrews, 1990). In the process of chewing, bones are shattered and disarticulated (Andrews, 1990). Other predators, which tear apart the carcass of their prey prior to ingestion, also disarticulate the skeleton, but do not break as many bones as "chewing" predators (Andrews, 1990). A final group of predators swallows their prey whole; causing the least amount of bone breakage (Andrews, 1990). In

general, bone modification via predation includes breakage, disarticulation, and bite/tooth marking. Skulls are rarely found intact, and the jawbones tend to show breakage of projecting processes and loss of teeth (Andrews, 1990). The lower jaw tends to be the most resilient of the jawbones, and is least damaged in predation (Andrews, 1990). In addition to damage caused during the prey ingestion period, the skeleton of the prey is further modified by the action of chemical digestion. The degree of acid etching to the bones is dependent on the physiology of the predator. Some avian predators, like owls, regurgitate bone and other indigestible segments of their prey in pellets (Andrews, 1990). Reptiles exhibit differing degrees of digestive activity. Bellairs (1970) noted that no bone material is found in snake faecal matter. In contrast, Fisher (1981) states that while crocodiles digest all the mineral matter in the bones and teeth of their prey, the organics which are voided are sometimes recognizable, especially in the case of the inner dentine core of the teeth. In mammalian carnivores, digestion occurs not only in the stomach, as in the previously mentioned predators, but also in the intestinal tract (Andrews, 1990).

Stage 2 - Processes Immediately Following Death

The remaining four stages can be considered as modifications superimposed on the primary changes associated with cause of death. Three processes that can act on the carcass immediately after death are decay, scavenging and trampling. Decay of the soft parts and the sinews of the carcass results in disarticulation of the skeleton (Andrews, 1990). Invertebrate

activity is important in decay, and carcasses partially or wholly immersed in water may take longer to decay as they are inaccessible to insects (Dodson, 1973). The carcass may be scavenged prior to, or during, the onset of decay. Since most predators are also opportunistic scavengers, it may be impossible to determine whether the individual died as a result of predation or was scavenged after a "natural" death (Andrews, 1990). Additional problems may arise when the bone modification associated with one type of predator is imprinted by the modifications of another predator in the process of scavenging the original kill (Andrews, 1990). During either decay and/or scavenging, the carcass may be trampled by other animals. Experiments to determine the effects of trampling on small mammal remains suggest that all the skeletal elements are less complete in trampled specimens (Andrews, 1990). The more fragile maxillae tend to break apart and the relative proportion of maxillae to lower jaws is much reduced (Andrews, 1990). Isolated teeth are more common in trampled remains (Andrews, 1990).

Stage 3 - Before/During Burial

The manner of death and circumstances immediately after death determine whether the carcass is affected by weathering and/or transport (Andrews, 1990). If the bone is exposed to surface conditions, it will be affected by the physical agents of sun, wind, rain, temperature fluctuation, and soil. While most studies have concentrated on the effects of weathering on large bones, some results for smaller bone are available (**Table 6**; Berhensmeyer,

| Stage | Berhensmeyer Large Mammal Categories | Range in Years | Exposure of Small Mammal Bones | Range in Years |
|---|---|---|---|---|
| 0 | no modification | 0-1 | no modification | 0-2 |
| 1 | cracking parallel to fibre structure; articular surfaces may have mosaic cracking | 0-3 | slight splitting of bone parallel to fibre structure; chipping of teeth and splitting of dentine | 1-5 |
| 2 | concentric flaking, usually associated with cracks; with loss of most of outer bone | 2-6 | more extensive splitting but little flaking; chipping and splitting of teeth leading to loss of parts of crown | 3-5+ |
| 3 | rough homogenous altered compact bone resulting in fibrous texture; weathering penetrates 1 -1.5 mm | 4-15 | deep splitting and some loss of deep segments or "flakes" between splits; extensive splitting of teeth | 4-5+ |
| 4 | coarsely fibrous and rough surface; splinters of bone loose on surface, with weathering penetrating inner cavities | 6-15 | | |
| 5 | bone falling apart in situ, with large splinters lying around | 6-15 | | |

Table 6

Weathering of large and small mammal bones in tropical and wet temperate climates, respectively (from Andrews, 1990).

1978). Transport of bone before burial is likely responsible for the majority of breakage modifications (Andrews, 1990). Degree of transport of bones from small animal assemblages is difficult to evaluate as Dodson (1973) discovered that very little energy, and very low water velocities, are needed to move small bones. The effects of hydrodynamic sorting are easily overcome by relatively small water speeds (Dodson, 1973). Korth (1979), looking at the effects of water transportation, subjected small bones to tumbling in a device containing water and fine sediments. The tumbled bones first exhibited disarticulation of the skull and loss of teeth (Korth, 1979). This was followed by gradual abrasive perforation of the thin bones of the skull, jawbones, pelvis, and scapula, and the attrition of the edges of the tooth enamel (Korth, 1979). When Andrews (1990) duplicated this experiment with larger sedimentary clasts, the tumbling yielded split tooth crowns and articular ends of long bones separating from the shafts. As Andrews (1990) notes, this pattern of breakage is controlled by the structural properties of the bones involved in the experiment.

Stage 4 - After Burial

After burial, bone may be affected by soil conditions or rock disturbance. Bones buried within soil may exhibit corrosion in the form of acid etching and root marks (Andrews, 1990). Once within rock, the bones are subject to any disturbances that effect their surrounding matrix. Cave roof and floor collapses, and/or tectonic shearing, may distort or shatter bones (Brain, 1981).

Stage 5 - Exposure

Bones may be exposed at the surface after burial. They then become subject to the actions of stages 2 to 4 once again. Additional transport may be recognized by the characteristic type of breakage it causes (Andrews, 1990). Fresh bone tends to break in jagged spirals (spiral fracture), dry bone breaks with uneven, but not spiralled, edges, and fossil bone breaks with straight transverse cuts across limb bone shafts (Andrews, 1990).

Preliminary examination, without quantification, of the Cromhall material analyzed in this thesis, indicates moderate bone modification. Most of the material is disarticulated and incomplete, suggesting that either the animals did not die from "natural" causes or, if they did, their carcasses were later subject to additional effects. While most of the bones are broken, the majority of the breakage is non-spiral in manner. In addition, there is no great disparity in numbers of lower to upper jawbones, with the exception of a single level in fissure 3 (Walkden and Fraser, 1993). No tooth marks are found on the bone, nor is there evidence of macroscopically determinable acid-etching. These factors suggest that predation/scavenging were either not modifying significant numbers of the Cromhall bones, or were so effective as to totally destroy those bones subject to modification. Differing degrees of abrasion are present on some of the bones, suggesting that transportation modification was occurring. Bone breakage after burial, during exposure, and during processing likely account for most of the bone loss.

Degree of bone modification becomes particularly important in assessing

the feasibility of Fraser's (1994) sphenodontian-based biostratigraphic scheme in that the jawbone data used in the relative abundance tallies may not be sufficiently accurate to tally the presence/absence of archosaurs.

In sphenodontians, the jawbones are robust and firmly fused, with the dentition ankylosed to the apex of the individual jawbone: acrodont dentition (Fraser and Walkden, 1983). Dentition, as derived from that of the extant *Sphenodon punctatus*, is subdivided into three tooth types that can be attributed to growth stages (Walkden and Fraser, 1983; Robinson, 1976; **Figure 41**). The hatchling dentition, present at hatching, is partially replaced anteriorly by larger successional teeth; the only tooth replacement to occur in *Sphenodon* (Robinson, 1976). Additional teeth are added posteriorly to each jaw as the animal grows (Robinson, 1976). Since there is no continuing tooth replacement in sphenodontians, the teeth of a mature individual may be partially or wholly worn away. In contrast, the jawbones of archosaurs tend to be less robust and a large lateral fenestra is often developed in the angular region of the lower jaw (Romer and Parsons, 1986). Archosaur dentition tends to thecodonty, with the teeth rooted by ligaments and soft tissue in deep sockets in the jaw (Romer and Parsons, 1986; **Figure 42**). The sockets act as areas of weakness in the jawbone. Sequential tooth replacement occurs throughout life, with teeth often shed during feeding (Edmund, 1962). As a result of the different morphology of the jawbones in sphenodontians and archosaurs, the numbers of identifiable jaw elements that are preserved may vary widely. Fraser (1988) noted that

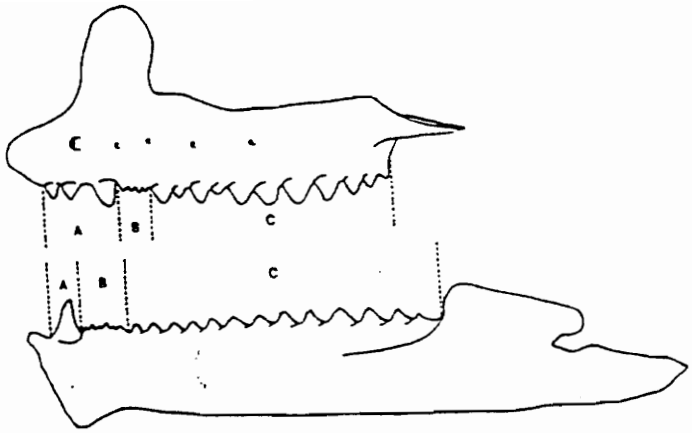



Figure 41

The three types of dentition found in Sphenodon: A, successional; B, remnant hatchling; C, additional (from Fraser and Walkden, 1983).

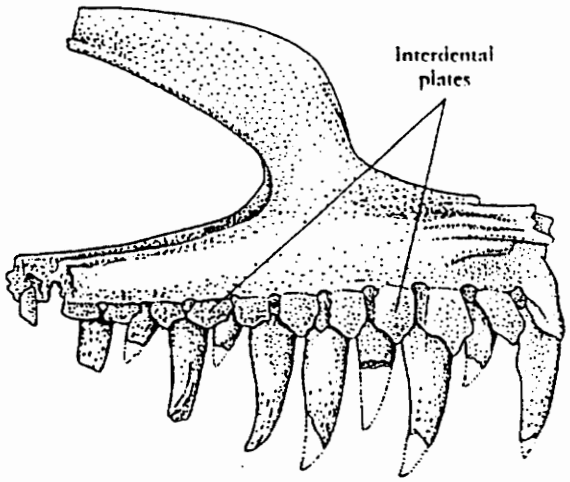



Figure 42

Medial surface of the maxilla of the dinosaur *Megalosaurus*. Note that the teeth are set into sockets in the jaw, with interdental plates securing the sockets lingually. While the presence of interdental plates is a specialization, this jaw serves to indicate the relative structural weakness of the thecodont tooth emplacement system in comparison to acrodont dentition (from Carroll, 1988).

when 1.5 tonnes of Cromhall material was processed at Aberdeen University, the approximately 10,000 identifiable bone fragments produced included 150 *Planocephalosaurus* maxillae and 120 premaxillae, and only 11 specimens of certain rarer archosaurian taxa. The material studied from sites 3, 4, 5, and 14 included 1284 jawbones; 1037 sphenodontian and 247 archosaurian. While this may only reflect differences in the relative abundance of these taxa in the biocenoses, it is also possible that archosaurs are being underrepresented due to the fragility of their jawbones and the methods used to take census. Other types of evidence from site 14 may be used to check this possibility: presence of landmark identifiable jawbone to jawbone fragments and presence of hypothesized tooth sockets to teeth.

In the site 14 material processed to date, level A contains seven archosaur dentary fragments, one landmark dentary, one maxillary fragment, one landmark maxilla, and one landmark premaxilla. Level B contains two archosaur dentary fragments and one landmark maxilla. This gives a site total of nine dentary fragments, one landmark dentary, one maxillary fragment, two landmark maxillae, and one landmark premaxilla **(Table 7)**. Using the landmark convention, four counts of archosaur presence are derived despite the fact that a further ten fragments, some representing a considerable portion of their individual elements, were also found at the site.

However, the ratio of archosaur teeth to jawbone presence suggests that the landmark system is accurate. Level A of site 14 contains 28 rooted and 71

| Element | Levels | | Site 14 Totals |
|---|---|---|---|
| | A | B | |
| landmark dentary | 1 | 0 | 1 |
| landmark maxilla | 1 | 1 | 2 |
| landmark premaxilla | 1 | 0 | 1 |
| landmark totals | 3 | 1 | 4 |
| dentary fragments | 7 | 2 | 9 |
| maxilla fragments | 1 | 0 | 1 |
| premaxilla fragments | 0 | 0 | 0 |
| total fragments | 8 | 2 | 10 |
| landmarks + fragments | 11 | 3 | 14 |

Table 7

Table indicating the relative abundances of landmark designated and fragment designated portions of archosaur jawbones in site 14.

unrooted archosaur teeth, and receives a landmark count of 3 archosaurs. Level B, with 1 landmark archosaur, contains 12 rooted and 71 unrooted archosaur teeth. If each of the landmark jawbones was reconstructed with 12-15 alveolar sockets (4 sockets for the premaxilla), this would lead to a ratio of 28-34 tooth sockets for 28 rooted (dislodged postmortem) teeth in level A and a ratio of 12-15 sockets for 12 rooted teeth in level B. Note that the choice of 12-15 alveoli per jawbone is an average number based on the types of jawbone and taxa present. The tooth to socket ratio obtained is close to 1:1.

Since cyclic tooth replacement patterns in the jaw result in a portion (close to 25 %, as determined by observation of figured jawbones and dentition) of the teeth being close to loss and close to rootless at any one time, discrepancies in the number of rooted teeth versus the number of hypothesized sockets may occur (Edmund, 1962). With this in mind, the presence, in level A, of 28 rooted teeth suggests that an additional 9 unrooted/close to rootless teeth would have to be included in the calculations. Thus, in level A there would be 28-34 hypothesized tooth sockets for 37 rooted and unrooted teeth. In level B, there would be 12-15 hypothesized tooth sockets for 16 (12 rooted and 4 unrooted/close to rootless) teeth. This is, again, close to a 1:1 ratio.

It could be argued that, if the jawbone fragments are also considered and reconstructed at 12-15 sockets each, and are also included in the count, then there are 124-154 sockets for those same 28 rooted teeth in level A, and 36-45 alveoli for 12 rooted teeth in level B. However, the reconstruction of these

fragments as whole and separate jawbones unassociated with the landmark elements is not necessarily warranted as the fragments may be portions of the landmarked elements for which the linking bone segments are lost.

In general, it appears that the number of tooth sockets available in archosaur jawbones derived from the landmark system tallies with the number of rooted archosaur teeth found in the same samples. Walkden and Fraser's (1993) "landmark" method of tallying taxonomic presence does not appear to greatly underestimate archosauromorph abundance.

It should be noted that, within level A (especially sample CR 93 38), there are several instances in which no landmark, or even fragmentary, archosaur jawbones are present, yet there are archosaurian postcranial remains in the form of vertebrae and highly fragmented long bones.

## PART II - PROCESSES AFFECTING BONE ACCUMULATION

In addition to these factors involved in bone modification, other processes are considered to account for bone accumulations found in caves. Andrews (1990) states that most bone concentrations found within caverns stem from four means by which carcasses may enter the system: individuals live (and die) in the caves, animals fall in accidentally, carcasses are introduced by predators, carcasses/bones are subject to postmortem transport into the cavern. The degree to which these factors operate in any one cave depend on the size and structure, especially of the cave entrances, of the cavern (Andrews, 1990). These factors, and their possible influence on the Cromhall accumulations, will be discussed individually.

Factor 1 - Animal Inhabits Cave

It has been suggested that fissure-fill material is composed of the remains of small animals that lived in the caves created by karstic collapse (Bambach, personal communication). Kermack (1984) felt that flash flooding could have drowned smaller reptiles that may or may not have lived in the fissure caves, and swept their bodies into the fills. Larger vertebrates would presumably either not need the shelter, or fit into, the caves in life, and their carcasses would be too big to be swept into the fissures in death.

In general, animals tend to inhabit either the interior, or an entrance to, the cave. Species which inhabit the body of a cave may be involved in hibernation/aestivation or may be colonial animals that live in large groups

(Andrews, 1990). Animals living in the entrance of a cave tend to select this area on the basis of individual requirements for access size and shelter (Andrews, 1990). Accumulations derived from cave inhabitants tend to contain large numbers of complete, undamaged, and often articulated, bone (Andrews, 1990). High concentrations, within the accumulation, of a single species are not unusual. However, these concentrations may result from occupation by only a few individuals spread over a long period of time, or by short term occupation of a large colony of animals (Andrews, 1990).

The morphology of the fissures at Cromhall (deep pits widening upwards to create doline cones a few meters across) does not suggest that they would provide adequate cave shelters for many species. Further, the lack of articulated materials in most of the fills suggests transport of remains to the fill sites. Also, in fissure 14, bone material from larger vertebrates (usually archosaurs) is abundant. However, the fissure area would have likely been the site of water drainage, hence an area with a regular water presence, and may have drawn animals to the general vicinity. Once in the area, they may have been introduced into the fills via the other three processes involved in bone accumulation.

Factor 2 - Animal Accidentally Trapped in Cave

Animals may become trapped in naturally occurring pits or caves. Experiments with natural and artificially created pitfalls show that up to 50 to 60 individuals may become trapped in a short amount of time (Armitage, 1985).

Natural pitfalls tend to provide accurate community samples of the surrounding fauna as those animals which are dependent on resources available in the immediate vicinity of the pit are the most likely to become trapped (Andrews, 1990). While high single species concentrations are not usual in accumulations derived in this manner, some animals are more prone to becoming trapped in pits than others. Andrzejewski and Rajska (1972) noted that younger individuals are more commonly found in pitfalls than are older individuals; suggesting an element of experience in avoiding these hazards. In addition, animals with poor eyesight are also more likely to be trapped (Armitage, 1985). Species with better developed jumping ability are less likely to stay trapped in pitfalls than those species with little or no jumping ability (Andrews, 1990). As with the previous factor, the accumulations produced by accidentally trapped animals tend to contain numbers of complete, undamaged, and often articulated, skeletons (Andrews, 1990).

Factor 3 - Carcass Introduced By Predator

As noted by Andrews (1990), predator activity is a common source of animal accumulation in caves, especially accumulation of small mammal remains. Predators may act to create bone concentrations by carrying prey to favoured eating places, storing excess meat in caches, and depositing pellets or scat in particular areas (Behrensmeyer, 1987; Andrews, 1990). Predator-derived bone accumulations tend to produce assemblages with size and species biases, according to the preferred type of prey (Andrews, 1990).

However, if the preferred food item is not available, they will take whatever other animals are in the area. The resulting prey diversity will then depend on the size and complexity of the habitats found within the predator's hunting territory (Andrews, 1990).

Evans and Kermack (1994), working on Jurassic fissure-fills in South Wales, believed that prey selection by larger theropods or morganucodontids was responsible for fissure bone accumulations. Kuhne (1956) cited tooth marks on fossil bone as proof that prey selection was operating in the creation of Jurassic fissure-fill deposits from South West Britain. While predator selection may have occurred in these other fills, Walkden and Fraser (1993) consider it unlikely at Cromhall as there is no sign of selective prey size and/or species preference, nor are there tooth marks or gastric acid etching on the bones. In situations where reptile, particularly archosaur, predation is suspected, the presence of shed tooth crowns may be sited as corroboration. Tooth replacement in the lower vertebrates is cyclic, such that adjacent teeth are not at the same stage of replacement at any one time, and continuous through life (Edmund, 1962). During the replacement stage, the tooth root is resorbed and a new tooth is grown in the soft tissue space that is produced (Edmund, 1962). When the unanchored mature tooth crown is lost, often during feeding, the new crown replaces it in the tooth row (Edmund, 1962). As a consequence of this process, unrooted teeth are commonly found in and around carcasses of prey or scavenged kills. Rooted teeth are usually found

still emplaced in the jawbones, or are dislodged after death of the archosaur. Walkden and Fraser (1993) did not consider this form of analysis, so no data on the relative frequency of rooted and unrooted archosaurian teeth is available for sites 3, 4, and 5. In site 14, level A produced 28 rooted and 71 unrooted archosaur teeth, while level B contained 12 rooted and 71 unrooted archosaur teeth, for a site total of 40 rooted and 142 unrooted archosaurian teeth. Pearson's chi-square goodness-of-fit test was applied to this distribution of unrooted to rooted teeth. Goodness-of-fit analysis tests the degree of correspondence between a sample and a theoretical frequency distribution i.e. observed and expected frequencies (Griffith and Amrhein, 1991). The data are analyzed with the the following inferential question in mind; does the observed frequency distribution conform to the expected frequency distribution? For site 14, the 182 (40 rooted and 142 unrooted) archosaurian teeth were treated as either/or events; the teeth were either rooted or unrooted. From this treatment, it was determined that 22 % of the teeth were rooted and 78 % of the teeth were unrooted. In this case, the expected frequency distribution is that of 75 % rooted and 25 % unrooted teeth. This distribution is derived from the fact that, given that multiple independent waves of tooth replacement are operating in the dentition at any one time and that each replacement wave consists of about half of the teeth developing and the other half of the teeth losing root tissue (Edmund, 1962), about three quarters of the teeth in any one archosaur should have visible root tissue and about one quarter will have no, or close to no, root

tissue. This ratio is taken from counts of rooted and unrooted teeth found in specimens illustrated in Edmund's (1962) paper. Therefore, the question asked in the site 14 Pearson chi-square goodness-of-fit test is formulated as: "is the distribution of rooted to unrooted teeth at site 14 consistent with the hypothesized frequency distribution of 75 % rooted and 25 % unrooted teeth, derived from Edmund's (1962) work?" Thus, the null hypothesis **Ho**: **p** equals .75 (where p is the hypothesized or expected proportion of rooted teeth) and the alternative hypothesis is **Ha**: **p** does not equal .75. After mathematical determination **(Figure 43)**, the chi-square term is determined as 298.385 with 1 degree of freedom. This term is applied to a table of critical values of the chi-square distribution for a goodness-of-fit test at the .05 significance level **(Table 8)**. Since the result of the site 14 test is greater than the critical value of 3.841 derived from the table, it is possible to reject the null hypothesis. The observed proportion of rooted teeth at the site is significantly less than the hypothesized (expected) value. This suggests that predation or scavenging may have been acting, at least at site 14, as a carcass-concentrating factor in the accumulation of vertebrate remains . While there is a tendency for the unrooted crowns to split along the midline axis, suggesting that the number of unrooted teeth may be artificially high, the numerical disparity between numbers of rooted and unrooted teeth is so large that it is hard to imagine that this is the only factor in operation.

Determination that predation or scavenging may have been acting on the

**Ho**: **p** is equal to .75

**Ha**: **p** is not equal to .75

| Category | Observed (o) | Expected (e) | o - e | $\frac{(o - e)^2}{e}$ |
|---|---|---|---|---|
| Rooted | 40 | (.75)(182) = 136.5 | 40 - 136.5 = -96.5 | 9312.25 /40 = 232.806 |
| Unrooted | 142 | (.25)(182) = 45.5 | 142 - 45.5 = 96.5 | 9312.25 /142 = 65.579 |

n = 182

$X^2 = 298.385$

Degrees of freedom
= number of categories (**k**) - 1
= 2 -1
= 1

**k** = 2

Figure 43
Calculations involved in determining the chi-square goodness-of-fit value for rooted and unrooted archosaur teeth from site 14, Cromhall Quarry.

| | Lower-tail critical values | | | | Upper-tail critical values | | | | |
|---|---|---|---|---|---|---|---|---|---|
| d f | $\chi^2_{.995}$ | $\chi^2_{.99}$ | $\chi^2_{.975}$ | $\chi^2_{.95}$ | $\chi^2_{.05}$ | $\chi^2_{.025}$ | $\chi^2_{.01}$ | $\chi^2_{.005}$ | d f |
| 1 | .0000393 | .000157 | .000982 | .00393 | 3.841 | 5.024 | 6.635 | 7.879 | 1 |
| 2 | .0100 | .0201 | .0506 | .103 | 5.991 | 7.378 | 9.210 | 10.597 | 2 |
| 3 | .0717 | .115 | .216 | .352 | 7.815 | 9.348 | 11.345 | 12.838 | 3 |
| 4 | .207 | .297 | .484 | .711 | 9.488 | 11.143 | 13.277 | 14.860 | 4 |
| 5 | .412 | .554 | .831 | 1.145 | 11.070 | 12.832 | 15.086 | 16.750 | 5 |
| 6 | .676 | .872 | 1.237 | 1.635 | 12.592 | 14.449 | 16.812 | 18.548 | 6 |
| 7 | .989 | 1.239 | 1.690 | 2.167 | 14.067 | 16.013 | 18.475 | 20.278 | 7 |
| 8 | 1.344 | 1.646 | 2.180 | 2.733 | 15.507 | 17.535 | 20.090 | 21.955 | 8 |
| 9 | 1.735 | 2.088 | 2.700 | 3.325 | 15.919 | 19.023 | 21.666 | 23.589 | 9 |
| 10 | 2.156 | 2.558 | 3.247 | 3.940 | 18.307 | 20.483 | 23.209 | 25.188 | 10 |
| 11 | 2.603 | 3.053 | 3.816 | 4.575 | 19.675 | 21.920 | 24.725 | 26.757 | 11 |
| 12 | 3.074 | 3.571 | 4.404 | 5.226 | 21.026 | 23.337 | 26.217 | 28.300 | 12 |
| 13 | 3.565 | 4.107 | 5.009 | 5.892 | 22.362 | 24.736 | 27.688 | 29.819 | 13 |
| 14 | 4.075 | 4.660 | 5.629 | 6.571 | 23.685 | 26.119 | 29.141 | 31.319 | 14 |
| 15 | 4.601 | 5.229 | 6.262 | 7.261 | 24.996 | 27.488 | 30.578 | 32.801 | 15 |
| 16 | 5.142 | 5.812 | 6.908 | 7.962 | 26.296 | 28.845 | 32.000 | 34.267 | 16 |
| 17 | 5.697 | 6.408 | 7.564 | 8.672 | 27.587 | 30.191 | 33.409 | 35.718 | 17 |
| 18 | 6.265 | 7.015 | 8.231 | 9.390 | 28.869 | 31.526 | 34.805 | 37.156 | 18 |
| 19 | 6.844 | 7.633 | 8.907 | 10.117 | 30.144 | 32.852 | 36.191 | 38.582 | 19 |
| 20 | 7.434 | 8.260 | 9.591 | 10.851 | 31.410 | 34.170 | 37.566 | 39.997 | 20 |
| 21 | 8.034 | 8.897 | 10.283 | 11.591 | 32.671 | 35.479 | 38.932 | 41.401 | 21 |
| 22 | 8.643 | 9.542 | 10.982 | 12.338 | 33.924 | 36.781 | 40.289 | 42.796 | 22 |
| 23 | 9.260 | 10.196 | 11.689 | 13.091 | 35.172 | 38.076 | 41.638 | 44.181 | 23 |
| 24 | 9.886 | 10.856 | 12.401 | 13.848 | 36.415 | 39.364 | 42.980 | 45.558 | 24 |
| 25 | 10.520 | 11.524 | 13.120 | 14.611 | 37.652 | 40.646 | 44.314 | 46.928 | 25 |
| 26 | 11.160 | 12.198 | 13.844 | 15.379 | 38.885 | 41.923 | 45.642 | 48.290 | 26 |
| 27 | 11.808 | 12.879 | 14.573 | 16.151 | 40.113 | 43.194 | 46.963 | 49.645 | 27 |
| 28 | 12.461 | 13.565 | 15.308 | 16.928 | 41.337 | 44.461 | 48.278 | 50.993 | 28 |
| 29 | 13.121 | 14.256 | 16.047 | 17.708 | 42.557 | 45.722 | 49.588 | 52.336 | 29 |
| 30 | 13.787 | 14.953 | 16.791 | 18.493 | 43.773 | 46.979 | 50.892 | 53.672 | 30 |

Table 8

Table of the critical values of the Chi-Square distribution (from Olson, 1988).

site 14 accumulations affects the conclusions regarding variation within this fissure. Earlier analysis of degree of bone modification within the fissure suggested that either predation/scavenging were not modifying many bones in the fissure, or that these processes were acting so effectively as to totally destroy those bones subject to modification. Ratio of unrooted to rooted archosaur teeth suggests that predation/scavenging were acting at site 14, and that the latter situation regarding degree of bone modification is correct. This, in turn, suggests that the relative abundances of taxa found in the fissures may reflect predator preferences, or prey with robust bones that make it through the effects of predation/scavenging, rather than actual abundance in the palaeocommunity. Note that earlier analysis of degree of representation of the relatively fragile archosauromorph jawbones, as indicated by a nearly 1:1 ratio between rooted (lost post-mortem) teeth found and hypothesized tooth sockets, is not affected by the number of unrooted (lost both ante- and post-mortem) teeth found in the site 14 deposit. Any level to level changes in fauna within fissure 14 may be more correctly attributed to changes in the predator/scavenger creating the accumulation, change in prey availability due to short-term ecologic stresses, and/or changes in local palaeoenvironment, rather than restructuring of the palaeocommunity over time. Additional problems in interpreing patterns of faunal change between fissures may be created if predation/scavenging is acting to create bone accumulations only in site 14 and not in sites 3, 4, and 5. If this is the case, then relative abundances

of taxa cannot be used as a basis to determine faunal similarities between different fissures as taxon abundance changes may be the result of different predators/scavengers, with different prey preferences, acting on accumulations in different fissures. Instead, simple presence/absence data might be best suited to determining faunal similarites as most predators/scavengers will occasionally take other prey if their preferred prey is not available. However, it is not possible to confirm whether or not this situation must be dealt with until the number of unrooted and rooted archosaur teeth in all of the other sites mentioned are tallied and analyzed.

One line of evidence suggests that the presence of large numbers of unrooted archosaur teeth in the site 14 deposits, or in any of the other faunal association B sites, indicates that predators/scavengers were not directly involved in creating bone accumulations in specific fissures. Bones in these sites often exhibit modifications related to transport, and it has been suggested that these accumulations represent surface lag deposits, developed over time, that were then introduced into the fissures. The bones in these lag deposits would be derived from surface-exposed carcasses which would be the product of the predation process and/or subject to postmortem scavenging. This surface predation/scavenging activity could have produced the skewed ratio between rooted and unrooted teeth. The ratio seen in the fissure-fills could then be attributed to the results of multiple, time-averaged, surface kills/scavenging by multiple carnivorous archosaurs rather than to the activity of a single type, or

individual, of predator/scavenger accumulating carcasses in a specific fissure.

It should be noted that the presence of any one predatory species within an assemblage is not proof that this particular species, or individual, is responsible for the bone accumulation.

Several extant cave-dwelling species that are not considered carnivores are also involved in creating bone accumulations. Mammals, such as the porcupine, may collect and store dry bones for gnawing purposes (Maguire *et al*, 1980).

Factor 4 - Carcass/Bone Subject to Postmortem Transport

Andrews (1990) does not consider bone transport into or within caves to be of significance in accumulation of small animal remains. Only one instance, an accumulation of bat bones in Nietoperzowa Cave, Poland, is cited as a transport-developed concentration of small animal bones (Andrews, 1990). Andrews (1990) further states that this accumulation is likely the result of secondary water transport of bones already within the cave. In general, water transport is considered a dispersal factor. However, Andrews (1990) does not consider the potential volume of water that could sweep into a cavern during periodic flooding, such as that seen in a monsoonal climate. Nor does he mention sporadic and violent sinkhole drainage, such as that cited in Walkden and Fraser (1993). It may be more accurate to state that postmortem transport can introduce animal remains into a cavern, but it is unlikely to concentrate those remains in any single area within the cave. Whether or not such transport

has occurred may have to be determined by looking at the microstratigraphy of the sediments within the cave.

There is evidence of low grade sedimentary sorting found in the fissure sediments from Cromhall Quarry. Small bones tend to be found as clasts in small grain sediments, calcite crystals protrude into the floors of the fissures and tend to act as long bone "baffles" (seen in the site 14 bone bed; **Figure 44**), and bone in crinoid sands (faunal association B) is often abraded/polished. Abrasion/polishing of bone may be the product of sedimentary transport or passage through the digestive track of another animal. The Cromhall material is more likely a product of the former than the latter as bones in faunal association B show differing degrees of attrition depending on whether they were contained within breccias/conglomerates or fine crinoid sands and marls (Fraser and Walkden 1983). Those bones in the coarser grained sedimentary rocks were further degraded than those in fine grained sediments.

As Fraser and Walkden (1993) note, evidence of time-lag transport, as seen in sedimentological effects, may mask the biological influences operating in the fissure-fills. The time required for crinoid grains to weather from the Carboniferous limestones, and to accumulate as crinoid sand (faunal association B) in amounts seen in the fissure-fills, may have stretched to thousands of years (Walkden and Fraser, 1993). Vertebrate remains contained within these sands would be subject to the same degree of weathering, mixing, and transport over this time period. The material deposited could therefore

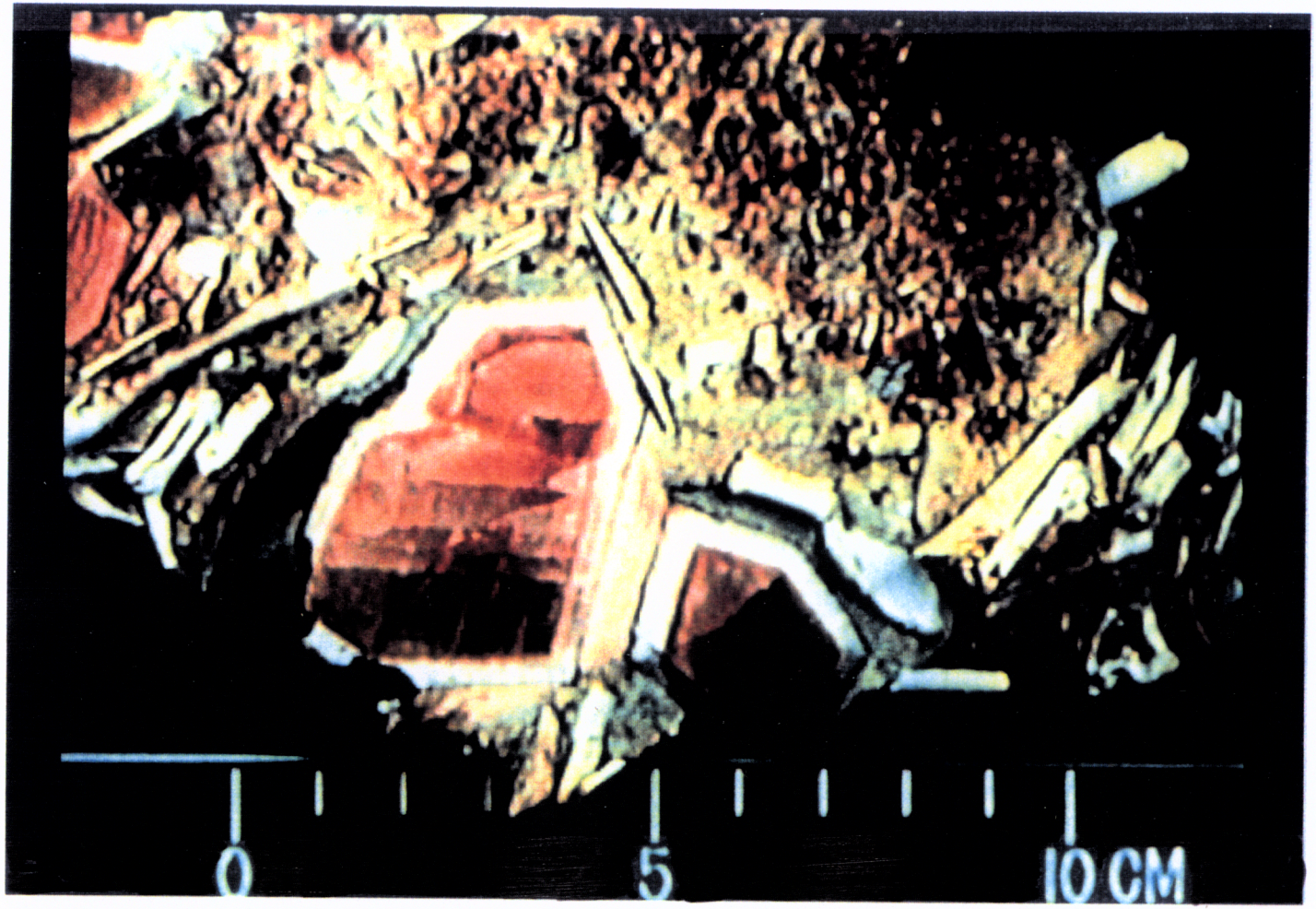



Figure 44

Colour print illustrating the "baffling" effect caused by calcite crystals protruding from the fissure walls. The bones trapped around the crystals in this sample (CBB 90) are oriented parallel to the sides of individual crystals.

stem from several different areas, time periods, and thanatocoeneses. In other words, the vertebrate assemblage could be time averaged. Faunal association A (site 14) rests on sediment association 2 (calcite crystals) in sediment associations 3 and, possibly, 4. The silts and muds of sedimentary associations 2 and 3 are felt to represent materials washed in from the surrounding areas over a period of time in which a mature terrestrial ecosystem was operating in the immediate region (Walkden and Fraser, 1993). Thus, time averaging may have also occurred in faunal association A. Contrastingly, faunal association C, from the fenestral limestones, exhibits fewer clues that sedimentological activity could skew any record of biological activity (Walkden and Fraser, 1993). Material from this association tends to be in pristine condition (sometimes even articulated), suggesting little or no transportation and/or quick burial (Walkden and Fraser, 1993).

## PART III - PROCESSES AFFECTING FAUNAL COMPOSITION

A third complicating factor may be acting at Cromhall Quarry. The general results of the statistical analyses suggest that sites with only a few levels, such as 3 and 14, tend to have those few levels cluster closely together while sites with numerous levels, such as 4 and 5, tend to show less distinct clustering. This trend may be random, in that the greater the number of samples, the more likely it is that they may diverge from each other in similarity. On the other hand, the trend may reflect the fact that sites with numerous samples may extend through more than one biostratigraphic zone. In this case, samples from the older levels in the site may contain a slightly, or considerably, different fauna from that found in the younger levels. A third possibility may be that changes in species distribution in the fissures are environment-related, and are not always abrupt and discontinuous. In other words, species may be distributed along a gradient that reflects environmental conditions, and changes in species distribution track changes in physical parameters: gradient analysis theory (Springer and Bambach, 1985). These last two possibilities seem most likely in that the levels which are clustering outside of their sites include the youngest level from site 5: 5j, and the oldest levels from site 4: 4b, 4f. This suggests that the faunal similarity in these levels is the result of overlapping temporal and/or physical conditions. In either case, the upper levels of site 5 must have been filling at the same time as the lower levels of site 4.

Further, the fact that, within any single fissure, there appears to be no

significant vertical change in the vertebrate assemblages despite vertical changes in sediments, suggests that differences in fauna between fissures are more likely due to temporal or spatial ecological variations than taphonomic conditions (Fraser, 1985).

Changing palaeoenvironmental conditions, and resultant changes in fauna, are difficult to dismiss. Fraser (1985) discusses the fact that the end Triassic in Britain is marked by general transgression. This transgression has been seen as the driving force behind the development of isolated "islands" of fauna in certain areas, as well as the migration of near-shore, upland, and other faunas in response to the relocating shoreline (Robinson, 1957; Marshall and Whiteside, 1980). However, transgression was not uni-directional, but was interspersed with periods of regression that would have allowed for mixing and redistribution of fauna (Fraser, 1985). In addition, extensive lake systems were present in Wales, and possibly Somerset and Avon, during the Norian (Tucker, 1978; Fraser, 1985). Large lakes can concentrate faunas in certain areas by acting as barriers to dispersal and/or providing narrowly defined nearshore niches. Habitat requirements, if strict, might limit the fauna to narrow, non-overlapping ranges even if no barrier to movement existed (Fraser, 1985). Any variations in fissure fauna, especially if the material shows little evidence of transport, may reflect different habitat requirements (Fraser, 1985).

However, it is important to note that most of the above factors that influence the accuracy of palaeoecological reconstructions based on fossil

assemblages become less important if the focus of the study of the fossil assemblages is changed from determining palaeoecology to creating a biostratigraphic framework. In other words, the potentially devastating effects of the multiple uncertainty factors are reduced in importance when there is no intention to determine very specific palaeoecological interactions. Biostratigraphic schemes are conceptual constructs organized in such a way as to allow for temporal linkage of a variety of locations. In fact, since biostratigraphic schemes based on wide-ranging taxa are more practical and useful, the inclusion of species from a large catch-basin may prove to be beneficial in extending the number of possible temporal/spatial correlations. The actual liklihood that changes in fissure faunas at Cromhall reflect different palaeoenvironments is very low. All the fissures analyzed occur within 120 metres of each other and it is very unlikely that, even in the case of the two fissures furthest from each other, there would be drastic differences in coeval palaeoenvironments within such a constrained space. Any changes in palaeoenvironment would affect all of the fissures analyzed and would take place, in this small area, over time. Therefore, in Cromhall Quarry, palaeoenvironmental change would also indicate temporal change.

## CONCLUSIONS

Several basic conclusions may be derived from this work:

1. Levels within any one fissure tend to contain faunas more like each other than like faunas seen in levels from any other fissure.

2. Levels from fissures that are hypothesized to be temporally sequential tend to contain faunas that are similar to each other.

3. There is an inverse relationship to the relative presences of *Planocephalosaurus robinsonae* and *Clevosaurus minor*. *Clevosaurus minor* is more abundant in the younger fissure material.

4. The bone material within the fissures is most likely modified/lost due to breakage after burial, during exposure, and, possibly, during processing/storage. It may also be modified in predation and transport.

5. The bone accumulations at Cromhall are most likely transport related. Predation may also be an accumulation factor.

6. It is impossible to totally resolve whether changes in the faunal distributions between fissures are exclusively temporal or palaeoenvironmental. However, give the small area sampled at Cromhall Quarry, any shifts in palaeoenvironment also indicate temporal change.

7. Walkden and Fraser's (1993) biostratigraphic framework may be accepted as the basis for further work.

8. Additional research, in the form of processing additional samples to expand the database, subjecting the new database to statistical analyses that do not

group taxa into the "Archosauromorpha" category, and quantification of degree and number of modified bone specimens, should be carried out in order to "fine-tune" the results presented in this thesis.

9. The biostratigraphic scheme should be compared with results from other fissure-fills in southwestern England and south Wales. Tytherington is an obvious choice for the first comparisons as Marshall and Whiteside (1980) have indicated that they believe that it may be close to the same age as the Cromhall deposits.

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## VITA

Anne L. M. Davis graduated, with a B.Sc. (Specialist - Vertebrate Palaeontology), from the University of Toronto in 1992. Born in March of 1966, she was fortunate to come into university with a little extra funding - being one of the last few people to receive monetary reward for finishing high school as an Ontario Scholar. During her undergraduate studies, she was an Imperial Oil Higher Education Scholarship recipient (2 years), an Arts and Science Faculty Scholar (3 years), and a Dr. James A. and Connie P. Dickson Scholar (3 years). In addition, she was a volunteer (later a paid position) with the Royal Ontario Museum Department of Vertebrate Palaeontology, and did summer field work with the Royal Tyrrell Museum, and the South Dakota School of Mines and Technology.

After graduation, Anne worked in the field with the Royal Ontario Museum, was a Palaeontology Intern at the South Dakota School of Mines and Technology, and travelled to Nepal as part of a high altitude waste management/solar energy initiative program in the Khumbu Himalaya region.

In 1993, Anne began a M.Sc. Program in the Department of Geological Sciences at Virginia Polytechnic Institute and State University. As a graduate teaching assistant at Tech, she was able to warp the minds of numerous undergraduates. During the two years she spent in Virginia, Anne did summer field work for the Virginia Museum of Natural History (and with any other

graduate student who asked) as well as taking part in V-QUEST (Virginia Quality Education in Science and Technology) training seminars. Results of her Master of Science studies were first presented as a talk ("Remains of Small Vertebrates and Their Implications for Late Triassic Faunal Composition") at the 1995 Southeastern Section meeting for the Geological Society of America.