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MORPHOMETRICS OF SOME TRIASSIC TEMNOSPONDYLS

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ABSTRACT: Various simple techniques of shape analysis have been tied together to provide a composite study of the late temnospondyls of mainly the Triassic Period. The "skeletons" of the late temnospondyls suggest that the forms with vaulted pterygoid and anteriorly placed dentition preferentially thrived beyond the Triassic. Another important late temnopsondyl, the metoposaurids, also have some minor variations of the shape of the skulls. This fact is always camouflaged by the overall similarity of their skull shapes. Factor analysis performed on some measured distances between different landmarks of metoposaurid skulls has brought out important shape variabilities within the family.

INTRODUCTION

In recent years some late temnospondyl families, hitherto known from nonmarine Triassic deposits, are increasingly being recovered from post-Triassic sediments. This negates the idea that temnospondyls are restricted to the Triassic (Milner, 1989; Warren, 1991). The late temnospondyls of the Triassic are significant as they may hold the key to their survival in the post Triassic. The relationships among temnospondyl families have been attempted by several workers (Colbert, 1947; Watson, 1956, 1962; Welles and Cosgriff, 1965; Welles and Estes, 1969; DuTuit, 1976; Coldiron, 1976; Bonaparte, 1978; Cosgriff and Zawaskie, 1979; Warren and Black, 1985; Jupp and Warren, 1986; Shishkin, 1987; Milner, 1990, among others). Colbert and Imbrie (1959), Welles and Cosgriff (1965) and Welles and Estes (1969) used quantitative methods by measuring some skull parameters to study the systematics of several temnospondyl families. On the other hand, several workers (Howie, 1970; Cosgriff, 1974, 1984; Defauw, 1989) have worked on the functional morphology and habitat of the late temnospondyls. However, no attempt has been made so far to compare the forms on the basis of the changing position of some skull landmarks both within a group and among some groups. Landmark-based analysis has now become a subject in itself and is widely used in paleontology (see Bookstein, 1978, 1986; Thonston et al., 1992 and Temple, 1992). The skulls of the temnospondyls are the most diagnostic part and are usually low and flat. This makes them quite suitable for two dimensional morphometrics. In this paper we have attempted a landmark-based comparison of late temnospondyl skulls. We have derived some simple "skeletons" (*sensu* Bookstein, 1978, Fig. 1) which represent the skull shapes. The "skeletons" are drawn from the overall shape as well as from some landmarks on the skulls. Some type "skeletons" are noted. From such a mechanical model we tried to establish the *"form - function"* relationship". The soft parts of a temnospondyl skull, associated with the brain-case and other sense organs, are usually positioned in a manner which reflects the total skull form. Thus a "skeleton" type may also throw some light on functional morphology and habitat. It is interesting to note here that all post Triassic temnospondyls are either chigutisaurids or brachyopids (Warren and Hutchinson, 1983; Dong, 1985; Nessov, 1988; Shishkin, 1991). We have also tried to explain that with the aid of the "skeletons."

Within a single family we have also tried to differentiate several morphs based on the works of Chapman (1981, 1990). While the "skeletons" have been drawn geometrically, Chapman's method was based on numerical methods. We have selected metoposaurids to analyze the change of the shape of the skulls within a family. Metoposaurids have a very flat skull and they are a compact group with certain minor shape variations of their skulls. The flatness of the skulls offers two dimensional data and thus makes it easily measurable. On the other hand, the minor differences present within the group make them ideal for a stiff but good test of landmark-based analysis.

THE BASIC TYPES OF LATE TEMNOSPONDYL SKULLS

A simple "skeleton" diagram (see Bookstein 1978) can be erected for the major late temnospondyl families such as the Metoposauridae, Capitosauridae, Rhytidosteidae, Brachyopidae, Chigutisauridae and Plagiosauridae (Fig. 1). Ideally a "skeleton" is the minimum possible, streamlined structure conceived within a particular form. In two dimensions, a "skeleton" line will be just at the middle of the external form, or in other words all the points lying on that line will be equidistant from the corresponding points on the boundary line of the external shape on the both sides. If the external form is considered, the palate and the skull roof will have only one "skeleton". In that case the important aspects of the palate will be difficult to depict. On the skull roof mere consideration of the external form may lead to the omission of important landmarks like the position of the orbit. Hence the "skeleton" diagrams used here are based on both the external outline and some important landmarks like the anterior- and posteriormost points of the orbit and maximum width in the skull roof and the posterior boundary of the dentigerous area as well as the shape of the interpterygoid vacuities in the palate. In the occiput, the central occipital structure and the vault of the lateral flange

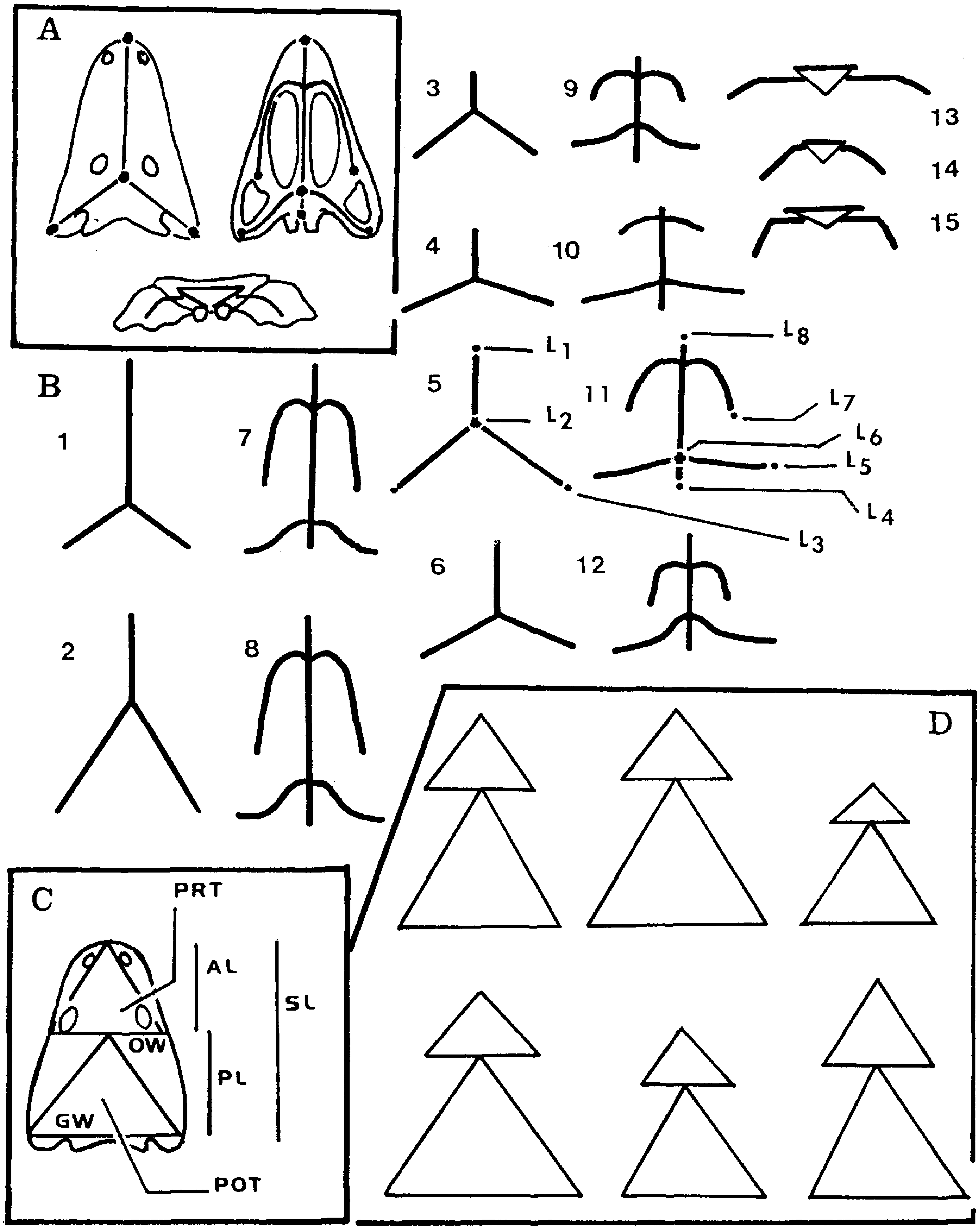

FIGURE 1. A. Key to the "skeletons". B. Skull roof "skeletons" of *Cyclotosaurus, Metoposaurus, Batrachosuchus, Plagiosaurus, Chigutisaurus, Deltasaurus* (1-6 respectively). Palate "skeletons" of *Cyclotosaurus, Buettneria, Batrachosuchus, Plagiosuchus, Chigutisaurus* and *Deltasurus* (7-12). All the outlines of the skulls are after Romer (1947) except *Chigutisaurus* (Rusconi, 1951) and *Deltasaurus* (Cosgriff, 1965). L1 - anteriormost point on the skull roof, l2 - Middle point of the line joining the posterior boundary of the orbit, L3 - points on the maximum width of the skull roof, L4 - posteriormost point on the palate, L5 - point on the maximum width on the palate, L6 - middle point on the line joining posterior boundary of the interpterygoid vacuities, L7 - posterior limit of the dentition of the upper jaw, L8 - anteriormost point on the palate (= L1). C. Key to the measurements on the metoposaurid skulls. D. the pre and post orbital triangles of the Indian metoposaurid morphs (x 1/10).

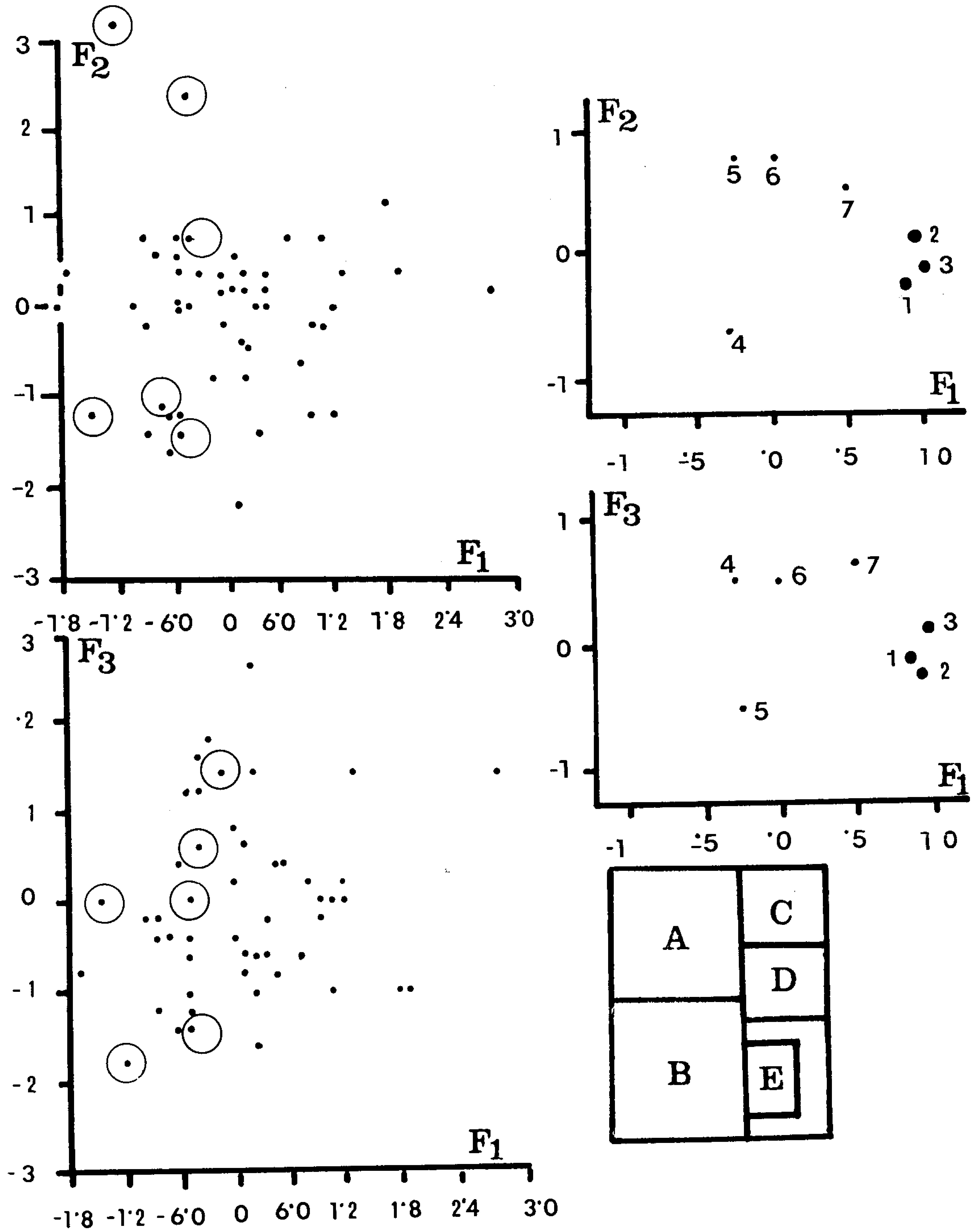

FIGURE 2. Plots of factor scores (A & B) for factor 1 vs. 2 and 1 vs. 3. (Small circles and large circles represent American and Indian morphs respectively) C & D are the plots of factor loadings for 1vs. 3. (1=SL, 2=GW, 3=OW, 4=PL/GW, 5=GW/OW, 6=PL/AL, 7=OW/AL.

have been considered (Fig. 1A). This simple idea of depicting the temnospondyl morphs through a "skeleton" can provide models of some basic types (Fig. 1B). It seems that in the late temnospondyls the total number of parameters involved are not many (which makes the "skeletons" simple). Though more in-depth study is required to say anything definitely, lack of variations in the basic "skeletons" could be the reason of the repetition of characters in different combinations in the late temnospondyls.

Among several late families, the Plagiosauridae and the Chigutisauridae will not look very different from the Brachyopidae in the "skeleton" diagram, and the same can be stated for the Indobrachopydae and the Rhytidosteidae (Fig. 1B). It is interesting to note that Warren and Black (1986) grouped the plagisaurids, brachyopids and chigutisaurids together and Cosgriff and Zawiskie (1979) noted that indobrachyopids and rhytidosteids are so close as to form a superfamily. The capitosaurids and metoposaurids look a little different in the occiput "skeleton" as the former has more flat skulls. In the roof "skeleton" the position of orbits is different but the palate "skeletons" of the above two families are almost similar. The cyclotosaurids differ from the capitosaurids by their otic notch. However, it is not possible to differentiate them with the "skeletons". The brachyopids are differentiated from the rhytidosteids by the depth of their skulls noted in occiput "skeleton". If the noises generated from small variations are ignored (we shall later discuss the smaller aberrations within a family), two distinct types of morphs are noticeable in the late temnospondyls (Fig. 1B). One is the capitosaurid - metoposaurid type and the other is the brachyopid - chigutisaurid type. The key to the success of the latter may lie in their "skeletons". The "skeletons" suggest that chigutisaurids had a vaulted pterygoid and their dentigerous area was restricted to the anterior two-thirds of the skull length (Fig. 1B) and consequently had more room for maneuvering food, when compared to the flat-skull-bearing metoposaurids. The chigutisaurid's feeding habit seems to be more advanced and may have been more like the reptiles (see Carroll, 1969 for the mechanism involved). Warren and Hutchinson (1983) also noted that brachyopids and chigutisaurids are basically the two families which lasted beyond the Triassic. They connected this achievement of the chigutisaurids and brachyopids with the absence of large agile reptiles - at least in Australia. In India the chigutisaurids competed with advanced phytosaurs which were quite agile. It seems that the brachyopoids (*sensu* Warren and Hutchinson, 1983) were more advanced than other temnospondyls, and their "skeleton" type is completely different.

VARIATION OF SKULL SHAPE WITHIN A FAMILY

Within a family, mere geometric comparison of the "skeletons" may not show much variation among the morphs. Davidow-Henry (1989) recently has shown that the shapes of different specimens of metoposaurids collected from a single locality show some variations in skull width, length, position of orbis and position of the pineal foramen. The shape and size of the otic notch is also variable. She followed the graphical method of D'Arcy Thompson (1942). To show the variations within the metoposaurids is extremely difficult due to the compactness of the elements on one hand and the presence of "mosaic" variation on the other. The overall similarity of the metoposaurid morphs also clouds the "signals" indicating differences. Clustering operations based on some skull roof parameters may also indicate false grouping, as it is difficult to define the proper weight of the parameters. Chapman (1981, 1990) performed factor analysis (principal components) on the distances between a few landmarks of several dinosaurian morphs. We have used an improvised version of the method followed by Chapman (1981, 1990).

The total length (SL), maximum width (GW), and orbital width (OW) along with the ratios of postorbital length and maximum width (PL/GW), orbital width and maximum width (OW/GW), postorbital and preorbital lengths (PL/AL) and orbital width and preorbital length (OW/AL) were considered as the important parameters which control the size and the shape of the skulls. Thus a data set is developed comprising the North American and Indian specimens of the metoposaurids (after Colbert and Imbrie, 1959). Indian morphs, though only six or so in number, have been considered for two reasons. Firstly, those six specimens show considerable shape variations. Secondly, both Romer (1947) and Roychowdhury (1965) considered the Indian forms to be very close to the North American ones.

	FACTOR1	FACTOR2	FACTOR3
1.SL	0.898	-0.243	-0.139
2.GW	0.947	0.150	-0.228
3.OW	0.975	-0.186	0.067
4.PL/GW	-0.309	-0.578	0.554
5.GW/OW	-0.242	0.747	-0.528
6.PL/AL	0.028	0.777	0.522
7.OW/AL	0.474	0.503	0.642
VP*	3.033	1.863	1.346

* variance explained by the factors.

TABLE 1. Factor loadings.

A principal component based factor analysis has been carried out on the North American and the Indian data using BMDP (4M) software. The factor dominantly loaded by the variables AL, PL and GW is considered as a size factor. On the other hand the factors dominantly loaded by the ratios (e.g. PL/AL, PL/GW etc.) are treated as essentially shape factors (Davis, 1973) (Table 1, Fig. 2 C, D). Hazlehurt and Rayner (1992) found similar "size" and "shape" factors for the wings of pterosaurs. One of those was highly loaded by absolute values and the other by the ratios.

The plots of the individual morphs with respect to factors (size and shape) show that the Indian morphs occupy the peripheral parts of each scatter (Fig. 2 A, B). Though the highly dissimilar size of the two populations (American and Indian) restricts direct comparison between the two, it can be stated with some amount of confidence that the available Indian morphs have more variable shapes than their American counterparts. Especially the position of the orbit (PL/AL) and the widening at squamosal (GW/OW) (mainly represented by the factor 2), are much more variable in Indian morphs than American morphs. On the other hand, the shape of the antorbital and postorbital triangles (mainly represented along factor 3) vary widely both for the Indian and the American morphs (Fig. 1D). Roychowdhury (1965) and Sengupta (1991) suggested that all the Indian specimens are of same species. It thus appears from this study that the intraspecific variation is high among the Indian metoposaurid species. This fact usually remains hidden by the overall similarity of the morphs. This may alert the workers on metoposaurid taxonomy who are trying to stress small shape differences.

It has been noted that there are two types of morphs within the metoposaurid population; one with expanded squamosal and the other without. Whether this is due to sexual dimorphism or not is difficult to infer. Unlike the two types of otic notches noted by Gregory (1980), these two types occur within a population restricted to a single locality. The relationship between the triangularity of the preorbital part of skull and the expansion of the squamosal forms a true mosaic. Probably, this is responsible for the complexity of the loadings on the shape factor(s) (Table 1).

The other important shape changes of the skull, like the shape of the otic notch, have not been considered so far. This is an important aspect as not only the different metoposaurids but also the brachyopids are differentiated from the chigutisaurids with the aid of that character. The cyclotosaurids are also differentiated by the otic notch. To incorporate this aspect into landmark analysis, one has to simply put some additional strategic points on the curvature of the notch.

CONCLUDING REMARKS

We hope that this idea of two dimensional cephalometrics will be helpful for paleontologists particularly interested in the temnospondyls. The variation in shape of the skulls, the minor variations within the skulls in a "population", some special characters showing important shape changes and some aspects of studies of functional morphologies of the late temnospondyls are discussed here in the light of that method. A simple understanding of the changing positions of some landmarks on the skull may lead to a better understanding of the animals. Proper selection of characters which are shape dependent as well as taxonomically important may lead a step further to change a morph into a taxon. The shape of the otic notch, for example, has been used by evolutionary taxonomists (Gregory, 1980; Watson, 1962) as well as utilized in the cladograms (Warren and Hutchinson, 1983) to differentiate various groups. But to do so most of the workers use words like "larger", "more curved" and similar descriptive terms. In that case a simple diagram showing the displacements of the landmarks plotted on that character may provide more objective pictures.

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