CHAPTER 8

HABITUS FEATURES AND PALEOZOOGEOGRAPHY OF THE NEW CHIGUTISAURIDS

GENERAL TRAITS OF THE NEW CHIGUTISAURIDS

Chigutisaurids have been considered as an active predator and agile swimmer by Cosgriff (1984). Watson (1951) informally grouped several temnospondyls on the basis of their shape of the skull and noted that the brachyopids with their vaulted pterygoid and high skull might have had an edge over the forms having a flat skull. Panchen (1959) and Howie (1970) considered brachyopids, the closest allies of the chigutisaurids, as active predators. The slender and streamlined humerus of *Siderops kehli* has been considered as an evidence for a quick swimming habit of that animal (Warren and Hutchinson 1983). In fact *S. kehli* has more similarity with the recent salamanders with its elongate body, flat light tail and slender limbs. Its pectoral girdle is more posteriorly placed (Warren and Hutchinson 1983). The long flippery tail and narrow, elongate body must have helped in swimming. DeFauw (1989) considered chigutisaurids as semiaquatic forms.

*Compsocerops cosgriffi* has many similarities with *S. kehli* as far as
their postcranial bones are concerned. A similar kind of agility can also be attributed to *C. cosgriffi*.

*Kuttycephalus triangularis* did not have the dentition placed at the anterior half of the palate and upper jaw. Its parasphenoid is also flat and wide. But it had the vaulted pterygoid and nearly parabolic skull with a complete row of marginal and palatal teeth. The character state mentioned last could have helped *K. triangularis* to compete with *C. cosgriffi*. However, *K. triangularis* was probably restricted to the smaller fishes and with its small, numerous teeth in the maxilla and premaxilla, it could have developed into an efficient nibbler only. The possibility, that whether *C. cosgriffi* was in the habit of attacking *K. triangularis* remains uncertain. It is interesting to note that, at least in one locality, remains of both the animals have been noted to occur together.

The presence of various horns in the posterior part of the skull of *C. cosgriffi* remains another enigma. Later in this chapter, it will be argued that the brachyopoids could possibly raise their heads. In that case, the strongly developed projections could probably have come against the neck muscles. It is very unlikely for an advanced animal like *C. cosgriffi* to develop a feature which has no clear functional significance. All the specimens of *C. cosgriffi* collected, show the projections. The chances of their being the secondary sex characters remain low. There is, of course, a third possibility. *K. triangularis*, with no postparietal projections could represent different sex of the same species. In that case, the wide variation in the dentition which results into two different modes of feeding.
becomes unexplainable. The projections undoubtedly have given the posterior skull an extra strength. On the whole, *C. cosgriffi* seems to have redeveloped an archaic character of wild uncontrolled skull projections along with many advanced traits.

All the specimens of *C. cosgriffi* were discovered separately as isolated individuals. *K. triangularis* has only one skull specimen.

Certain important aspects of the skull and lower jaw movements of the short faced brachyopids while catching and holding a prey have been discussed by Howie (1970). Firstly, she figured that the lower jaw of the brachyopids must shoot forward when it raises its skull. Earlier, Panchen (1959) has also discussed this point. But to raise the skull, the depressor muscle requires the lower jaw to be rested on the ground. Howie (1970) postulated that the depressor, the occiputo-vertebral muscle and the cleidomastoideus muscle are responsible for the skull and jaw movements of the brachyopids. All the muscles are to be attached at the posterior most part of the skull. The vertebral part of the occiputo-vertebral muscles must attach on the neural spine and the posterior part of the cleidomastoideus muscle has its attachment usually on the dorsal process of the clavicle. If all of them act together, "The most obvious advantage of this system is that raising the skull against the occipital condyles as well---- and so the lower jaw will be freed from ground. Subsequent contraction of the depressor does not need ground support as it is lowering, not a raising action." The lateral movement of the tabular horn through time has been considered by Howie (1970) as to give more space to the occiputo-vertebral muscle. The dorsally upward curvature of the
retroarticular process has been attributed to a more spacious gape.

*C. cosgriffi* has a long dorsal process of the clavicle and a large depressed area in the squamosal-quadratojugal trough. Welles and Estes (1969) opined that this trough is the best place for the attachment of the depressor. The mechanism of skull and jaw movements of the brachyopids, as envisaged by Howie (1970), is a partial one. The modern day reptiles show a complex lower jaw and skull movements when they catch a prey. They have to counterbalance the various desperate movements of the prey. Moreover the phytosaurs had a strong pterygoideus muscles which controlled their lower jaw movements (Kutty personal communication). This need not require the ground support like the depressor. Wilson (1941), stated that the development of well defined coronoid process on the mandible indicates stronger masculinity used for the closure of the lower jaw. However, all the Howie's considerations have been based on the posterior position of the occipital condyles with respect to the quadrate condyles and the former's position on much higher planes than the latter's. Both *C. cosgriffi* and *K. triangularis* had the lastly mentioned character states and the paradigm must be valid for them also. If it works, at least *C. cosgriffi* could have been able to take maximum benefits out of that as it has got the maximum area for relevant masculinity attachments.

In the Maleri Formation metoposaurids have been replaced by the chigutisaurids from base to the top. The world wide distribution of those two temnospondyls also indicate some interesting aspects of paleogeography. Hence a brief comparison of their feeding habits seems
to be relevant as a significant interpretive criterion.

The temnospondyls are traditionally known as fish eaters. In the Triassic of Pranhita-Godavari valley several species of *Ceratodus* are found. The phytosaurs found in profusion in Maleri were also fish eaters. In the lower part of the Maleri Formation, metoposaurids managed to continue with the phytosaurs. The upper part of Maleri was dominated by the chigutisaurids as far as the temnospondyls are concerned. There must be something in the chigutisaurids which outwitted the metoposaurids. *Metoposaurus maleriensis* has a rather flat skull with strictly dorsal eyes. The dorsoventral flattening, disproportionate body and weakly developed limbs have been thought as indication of their bottom dwelling habit and they have also been considered as passive predators (Murty 1989a). The dentition is much posteriorly placed in upper and lower jaws. The anterior palatal vacuity occupies a considerable area of the snout region. The cultriform process of the parasphenoid is flat and wide. The dentition of the upper jaw extends posterior to the centre of the interpterygoid vacuity. The skull outline is elongate. In contrast, the chigutisaurids not only have more streamlined bodies but also show some modifications of the skull and dentition. Their skull is parabolic with more effective area for a bite. The dentition is restricted, both in skull and lower jaw in the anterior 1/2 of the skull and mandible. The posterior half is mostly vacuous with large subtemporal vacuity, narrow parasphenoid and large adductor fossa of the lower jaw. The dentition of the upper jaw does not extend beyond the centre of the interpterygoid vacuity or the usually narrow
cultriform process of the parasphenoid. The anteriorly restricted
dentition gives an extra leverage than many other temnospondyls. The
complete row of teeth in the palate probably offered better grip. It
is quite possible that they probably could hold the prey for a long
time at the anterior half of their mouth and then swallow it slowly
with the deep, mostly vacuous posterior half. Carroll (1969) envisaged
similar traits in the early reptiles. To hold the animal until death
was probably necessary for the chigutisaurids. The mid portion of
their skull and the palate with narrow, thin cultriform process, is
not very strong. Unlike the metoposaurids, they could not offer the
entire pressure of the skulls transferred through the flat palate. In
that case, a prey which could have still posed some resistance even
after the stabbing by the tusks and teeth, could cause damage to the
chigutisaurid palate. Hence chigutisaurids probably utilised their
skull height with deeply vaulted palate and the anteriorly placed
dentition to adopt a disadvantageous mode of feeding than the slow
metoposaurids. In this context, it is significant to note that in \textit{C.}
\textit{cosgriffi} at the underside of the prefrontal, squamosal and probably
the jugal there are thin supports or processes descending on the
palate. Chigutisaurids had a larger area for the otic notch and for
housing the otic capsule. They probably had the capability of better
hearing than many other temnospondyls. Their eyes were dorsolateral.
All of these attributes are found in \textit{C. cosgriffi} and some in \textit{K.}
\textit{triangularis}. Those advantageous conditions are, to some extent, also
noticed in the brachyopids and the plagiosaurids. A careful look at
the world wide distribution of the chigutisaurids and the
metoposaurids suggests that they are only found together in India. Other than the Indian occurrences, metoposaurids are found in North America, Europe and Morocco (RoyChowdhury 1965, Benton 1986, DuTuit 1976). Chigutisaurids are reported from India, Australia and Argentina. Australia and India have fair amount of similarity as far as their Triassic temnospondyl records are concerned. They are the two countries in the world with fossil records of brachyopids, chigutisaurids, rhytidosteids together. North American Triassic has metoposaurids in profusion which continue up to the end of Norian (see chapter 9). In Europe and India metoposaurids are short lived. Norian sequences of Europe has plagiosaurids and cyclotosaurids but the metoposaurids are absent. In India they are replaced by the chigutisaurids at the end of Carnian. Australia and South Africa have various brachyopoids, capitosaurids without the metoposaurids. Plagiosaurids have recently been noted from Australia (Warren 1985).

From the above pattern of distribution it seems that wherever metoposaurids had to compete with the brachyopoids or the plagiosaurids (a close group to the brachyopoids, see chapter 6) they were short lived and their places were taken over by the more agile groups mentioned above. The brachyopids, particularly, continued up to Middle Jurassic (Dong 1985, see Milner 1989).

In this context it is also interesting to note that two different types of chigutisaurid palate mentioned in the review of the chigutisaurids is also confirmed from the new chigutisaurids. Among the two new genera, Kuttycephalus - with the wide cultriform process and posteriorly extended dentition falls in the 'Chigutisaurus' -
Keratobrachyops' category and Compsocerops with its long narrow cultriform process, largely vacuus posterior part of the palate and anteriorly restricted dentigerous area resemble the 'Siderops - Pelorocephalus' type. The mode of feeding as it has been described above would clearly place the second group in an advantageous position than the first. It is also possible that they depended on different prey population for their survival. Presence of the two types together in the upper part of the Maleri Formation may thus be explained.

DISPERAL PATTERN AND SOME IMPORTANT ASPECTS OF PALEOGEOGRAPHY

Chigutisaurids are thought to have originated in Australia (Warren and Hutchinson 1983). They are so far found to be restricted in the Gondwanas. Metoposaurids, on the other hand, have a chiefly Laurasian distribution. The question is why these two groups could be found together only in India?

As far as the vertebrate fossil record of India is concerned, the absence of endemism in Indian tetrapods have long been known particularly in the Triassic. India has been noted by Colbert (1986), Tucker and Benton (1982) and Chatterjee and Hotton II (1986) to have both elements of 'Northern' and 'Southern' faunas. Cox (1974) noted that in the Early Permian and in the Triassic there were no major geographic or climatic barriers. Cox (1974) noticed that the similarity coefficient of Indian fauna with that of North America and Europe is quite high (59% and 81% respectively). On the other hand
that with Africa and South America is also not negligible (75% and 56%). The present study stresses on a similarity in temnospondyl types found in India and Australia. Cifelli (1980) also has envisaged a world-wide distribution pattern for the temnospondyls.

What was the possible dispersal route of the Laurasian fauna to India. In this context, two aspects that is the geographical barrier and the climatic barrier as noted by Cox (1974) are important. While the latter will be discussed separately the former aspect is discussed below:

The paleoposition of the continents from Late Permian to Late Triassic shows a continuous circum-Tethyan shore line (figure 37). The presence of this shore line has been shown by Tucker and Benton (1982). Smith and Briden (1977) have shown that in Early Triassic Australia is close to India and Europe and North America were also not far away (Map 13, p. 24). The circum-Tethyan shore line is short and curved and the position of Africa was such that the land distance between India and North America was minimum. The distance between India and North America as well as the length of the circum-Tethyan shoreline gradually increases and perhaps in the Late Jurassic Laurasia was separated from Gondwana. Irving (1977, figure 51, p. 308) has shown that in Early Permian and in Late Jurassic the distance of Laurasian block and India was greater than what was present in Triassic. The circum-Tethyan shore line was also short. All the paleoposition reconstructions of Triassic done by several authors indicated the above mentioned aspects without really specifying them. The presence of a cryptic circum-Tethyan shore line can be
reconstructed in the figures shown by Hay et al (1982) and Parrish et al (1982). Cosgriff (1974) has discussed that certain group of short faced temnospondyls of the Triassic could possibly move through the shore lines. The Early Permian temnospondyls of Kashmir (with European affinities) as well as the Late Triassic metoposaurids could have come from Laurasia via circum - Tethyan shore line (figure 37). Chigutisaurids came later, at the late stage of Carnian, probably from Australia and replaced the metoposaurids in India.

PALEOCLIMATIC IMPLICATIONS

As far as the paleoclimate of the entire Triassic deposits of Pranhita - Godavari valley is concerned an interesting aspect seems to be quite relevant. Robinson (1973) postulated a sharply seasonal rainfall in parts of North America, Europe, Africa and India in the Triassic (figure 10 in Robinson 1973). She also noted a high pressure maxima in Laurasian summer and a Gondwana winter in the Indian plate. The areas adjacent to the circum - Tethyan shore line have been shown to have similar kind of climate as well as similarity in overall wind directions. Australia in that sense showed difference as the winds radiating from the high went in an opposite direction around Australia. Following this model Hay et al (1982) have suggested a humid to subhumid climate in the above said shore line except a strip of aridity in the NE of Africa. Australia on the otherhand was included in the subhumid zone. Parrish et al (1982) have also shown that during Induan time a low pressure belt was located in Africa with
an adjacent high at the north of India and another one in Europe causing a similar type of wind flow in the circum-Tethyian region (figure 5, p. 39). In summer the high is shifted at south of India and the low in Europe. The wind direction of circum-Tethyian shore line changes but remains similar at the entire shore line. The lastly mentioned authors have also shown that the entire shore line had 100 to 200 units of rainfall. In Late Jurassic the pattern changed. Before that, roughly from Late Permian to the end of the Triassic, probably a similar type of climate prevailed along the circum-Tethyian shore line. Though details are lacking in this field, this can be noted as an additional evidence of faunal migration without facing any sharp change in the climatic condition.

Earlier workers (Pascoe 1959, Wadia 1970), while talking about climatic conditions during the deposition of the Maleri sediments, had built up an opinion in favour of extreme aridity. Triassic in India, particularly its later half, was thought to be increasingly arid. Previously, aridity of the Triassic deposits were considered chiefly from the presence of the red beds. Poor floral content has also been cited as a supporting evidence in favour of aridity. Robinson (1970) first noted that the Triassic beds of the Pranhita-Godavari valley need not necessarily had to be deposited in a desert-like condition. The Maleri fauna on the otherhand speaks about a well watered country. All the major lines of evidences are explored below to settle the controversy.
Evidences from the Maleri peloidal calcirudite/calcarenite and sandstone

Sarkar (1988) noticed that the peloids of the Maleri Formation imply their prolonged exposure in a dry terrain. The peloidal calcirudite/calcarenite present at the base of a storey in the ridge forming sandstones along with the mudclasts occasionally present in them indicate a channel lag facies (Reneick and Singh 1973). Their periodic occurrences in the channel sand may indicate short, cyclic period of aridity. Sengupta (1970) noted a channel fill mode of the Maleri sabdbodies. The parallelly laminated fine sands are not a pin pointing climate indicator.

Evidences from the clay

In the recent past, studies on the red beds echoed Robinson's (1970) view. Unlike what was thought earlier, the red colour is now believed to be related with the climate in a very general way (Pye 1983). The reduction and oxidation of iron responsible for the colouration is not the sole function of the climate. Yellow, brown and red colour, so common in the lime mud clasts and in the thicker clay bodies are the product of ferric form of iron in a finely divided form; non-ferric forms lead to a grey, green or bluish colour (Pye 1983). Sarkar (1988) observed that high smectite (48-75 %) content of the Maleri clay is indicative of low rainfall. On the other hand Tucker and Benton (1982), from a detailed study of the sediments and
fossils of the world's Triassic deposits, included Indian Triassic red beds in a facies association thought to have developed in a warm to hot climate with possibly extended humid time alternating with drier periods. The Maleri red clay contains fossils of aquatic and semiaquatic habitat. On the whole no detailed work on the Maleri clay is available to establish their origin in a dry terrain.

Evidences from vertebrate and plant fossils

The lungfish _Ceratodus_, the subholostean and xenacanths; the aquatic phytosaurs; the metoposaurids and chigutisaurids of the Maleri fauna prove that the fauna had witnessed a monsoon-type climate, atleast seasonally. The herbivorous rhynchosaurs, aetosaurids and cynodonts suggest the presence of vegetation. Sarkar (1988) ruled out the possibility of a 'forest canopy' (as visualised by Chatterjee 1978) from the sedimentological evidences. A savanna, according to him, could have supplied enough food for the herbivores. Turner (1981) and Tucker and Benton (1982) have used the absence of megaplants as an indicator of aridity. The former worker, however, noticed that Triassic megaplants are rarely found in direct association with the tetrapods. Large tree trunks are present in the thicker sandstones. These sandstones are mostly barren as far as the tetrapods are concerned. The clay–sand ratio is greater in Maleri than that of Dharmaram. This could be a probable explanation for the absence of tree trunks (which are seen to have a bias for the
sandstones) in Maleri. But Maleri is afterall not devoid of sandstones and the situation is somewhat puzzling and so far the absence of megaplants in Maleri is basically inferred from their absence as fossils. The herbivores had to survive anyway, hence be it a forest or a savanna, there was hardly anything which could ignore the necessary presence of vegetation in the food chain of the fauna of the Maleri Formation.

Other kinds of evidences are not of much help. Sporadic barytes found in the clays speak for aridity. Gypsum crusts attached with the fossil bones may indicate low rainfall. On the otherhand extensive mobility of calcium carbonate in Maleri climate suggests the presence of ample water. The only probable solution is to think about a climate of alternating dry and wet periods. The arid periods yielded the channel lag fecies when dry channels were exposed to a scorching sun and they were covered up by finer sediments in the time of monsoon. The aquatic members of the Maleri fauna, living in ephemeral rivers, had survived the drier situations by concentrating in the more permanent bodies of water (Robinson 1971, Chatterjee et al. 1987). Sudden drying up of some 'permanent bodies of water could also have led to a graveyard of the aquatic or semiaquatic fauna at that spot. A metoposaurid graveyard found in Lower Maleri clay could be a possible example of that.