An approach to the phylogeny of gomphodont cynodonts based on dental characters

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Gomphodonts are a heterogeneous group of omnivorous-herbivorous cynodonts with a nearly world-wide distribution. They are known from all continents excepts Australia, and range from the Early to Late Triassic (King, 1993). Among gomphodonts, the Diademodontidae and Trirachodontidae show little diversity, being probably monogeneric (Hopson, 1991). The Traversodontidae are remarkably more diverse and well documented, especially in South America where they are typical representatives of the Argentinian and Brazilian Triassic continental fauna (Barberena, 1974; Bonaparte, 1978). When considering cranial and postcranial anatomy, gomphodonts form a heterogeneous group. However, they are generally characterised by a transversely expanded crown in the postcanines, and a crown to crown occlusion (Crompton, 1972; Hopson, 1991).

Controversies exist regarding the phylogenetic nature of the gomphodonts. It has been postulated that tritylodontids are the sister group of traversodontids (Crompton, 1972; Sues, 1985; Hopson and Barghusen, 1986; Hopson, 1991; Battail, 1991). However other researchers (Kemp,1983; Rowe,1993; Wible, 1991; Martinez *et al.*, 1996) postulate tritylodontids as a sister group of mammaliaformes (i.e. basal mammals), and thus outside of gomphodonts. Luo (1993) considered tritylodontids to lie outside of gomphodonts as the sister group of tritheledontids plus mammaliaformes. Rowe (1993) postulated gomphodont cynodonts as a paraphyletic assemblage, implying that similarities in dentition between gomphodonts would be homoplastic.

Even when the monophyly of gomphodonts was supported by ambiguous characters in a recent phylogenetic analysis of eucynodonts (Abdala, 1996), they are considered here as monophyletic group but without the inclusion of tritylodontids.

In this contribution an analysis of relationships for 11 gomphodont taxa, using 13 characters of upper and lower dentition, is presented. This analysis includes representatives of the three families; the trees were rooted with *Diademodon*.

Eight most parsimonious trees were found with an exact solution using the program NONA (Goloboff, 1993b), and one using the program Pee-Wee, for parsymony analysis under implied weights (Goloboff, 1993a).

Under equal weights, *Cricodon* and *Trirachodon* fall into a basal position in all the cladograms but without forming a monophyletic assemblage between them. In most of the trees, *Pascualgnathus* is the basal traversodontid, followed by *Andescynodon*. But in two trees, the position of these taxa are reversed. In the consensus tree of the NONA analysis (Fig. 1a), *Exaeretodon* forms a crown group with *Gomphodontosuchus*, while the other traversodontids form a politomy. In four of the eight cladograms *Luangwa* holds a basal position, after *Pascualgnathus* or *Andescynodon*, and in five of them *Massetognathus* appears as a sister group of *Exaeretodon* and *Gomphodontosuchus*.

The cladogram obtained using the Pee-Wee program (Fig. 1b) shows *Pascualgnathus* as a basal traversodontid, followed by *Andescynodon*. Contrary to most of the resolutions with NONA, *Traversodon*, and not *Massetognathus*, appears as the sister group of *Exaeretodon* and *Gomphodontosuchus*.

The relationship hypotheses presented here agrees with that of Hopson (1985) on the derived position of *Gomphodontosuhus* and *Exaeretodon* (*Scalenodontoides* is not included in this analysis), but differs in *Massetognathus* showing a more derived condition than *Scalenodon*.

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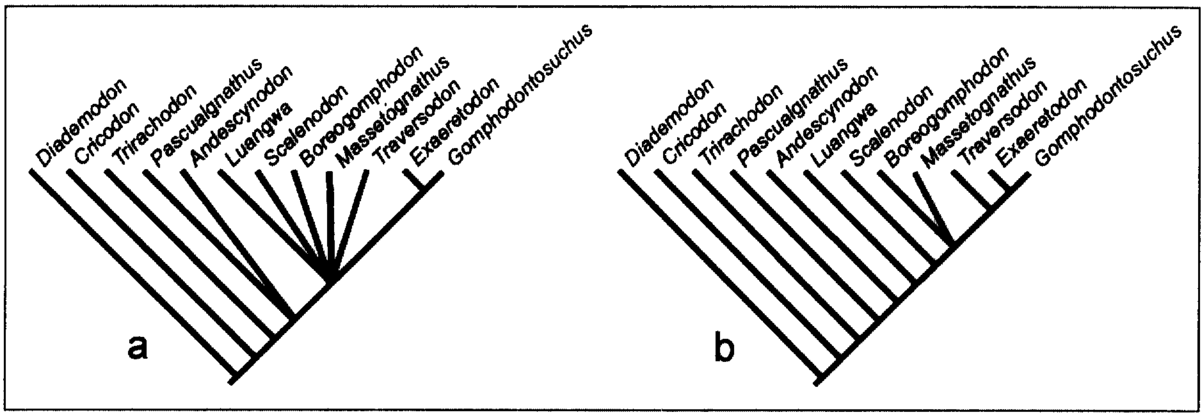

Figure 1. Consensus tree of the eight most parsimonious trees using (a) NONA analysis and (b) Pee-Wee analysis

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Break-up of the East Gondwana Indo-Australian continent: dispersal and accretionary history of continental blocks

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Continental blocks of different sizes were rifted out during Palaeo-Mesozoic times, in phases, from the northern margin of the East Gondwana Indo-Australian continent. The South China and Indo-China Blocks possibly rifted during the Early Palaeozoic, whereas, the Tibetan and the Thai-Burma-Sumatra (SIBUMASU) Blocks were rifted during the Permo-Carboniferous when the margin was under glacial or cool climatic conditions. Gondwana basins developed in the Indian continent since earliest Permian along favoured sites of Precambrian structural weak zones, craton junctions and reactivated mobile belts. The Late Palaeozoic lithic fill and mafic volcanics in the Himalayan Belt are closely similar to those in the Tibetan and SIBUMASU Blocks, but represent a failed rift setting. The latter blocks instead drifted northward to warmer position during mid-Late Permian. The Palaeo-Tethyan arm located to the north of these blocks closed during Late Permian-Triassic as these blocks were accreted to the South China and Indo-China Blocks. The amalgamation of these blocks formed the Cathayasia land.

The Indo-Burma-Andaman (IBA), Sikule and Lolotoi Blocks were rifted from the same continental margin during the Late Jurassic, followed by the break up of the Ind an and the Australian continents during the Early Cretaceous, initiating opening of the Indian Ocean. The Seychelles and Madagascar Blocks were rifted from the west coast of the Indian Peninsula during the Late Cretaceous, followed by jumping of the spreading axis to the Carlsberg Ridge located between India and Seychelles since the beginning of the Tertiary (Bhattacharya *et al.*, 1994). As the Indian Plate moved northward, traces of the Reunion and Kerguelen hotspots produced Chagos-Laccadive and 90°E ridges in the Indian Ocean and extensive flood basalt extrusion; Rajmahal (110 Ma) and Deccan (65-70 Ma) in the Indian continent. The 85°E ridge instead was possibly caused by compression and volcanism during Early-mid-Cretaceous plate re-organisation.

The Neo-Tethys, separating India from Tibet and the IBA from the SIBUMASU Blocks expanded during major parts of the Mesozoic, however the opening of the Indian Ocean was linked up with the closing of the poly-islandic Tethyan Ocean. The Palaeo- and Neo-Tethyan sutures in Tibet, Yunnan, Myanmar, Laos-Thailand and Vietnam reveal the complex opening and closing history of Tethys (Acharyya, 1996, 1997a). The IBA block rotated clockwise from its earlier east-west orientation because of 90°E and adjacent dextral transcurrent fault movements which ensured faster northward movement of the Indian Plate relative to the Australian Plate during Late Cretaceous-Early Eocene. The India-Tibet terminal collision during Early-Middle Eocene was a mega-tectonic event. Contemporaneously, there was laterally extensive tholeiitic-alkalic and acid volcanism (Abor and equivalents) in the Himalayan foreland basin at the leading edge of the Indian continent (Sengupta *et al.*, 1996). There was post-Deccan ultrapotassic dyke intrusion in central India flanking the Narmada-Son mega-lineament (Datta *et al.*, 1991; Acharyya, 1998). Deep seated dislocations related to terminal collision possibly provided channel ways for the alkaline magma. Post-collisional northward movement of the Indian Plate caused Himalayan orogenesis, neotectonically reactivated east-west orientated Narmada-Son geofracture, east-west trending open folds and thrusts in the central Indian Ocean Basin and induced clockwise rotation of the southeast Asian Cathayasian Block. Dislocations in the 90°E ridge indicate main compression during the Early Eocene, which was followed by later events since Late Miocene.

The dismembered and flat-lying ophiolite train on the IBA does not represent the eastern suture of the Indian Plate. Mesozoic-Early Eocene ophiolites, their mid-Eocene cover and trench sediments occur as klippe on the IBA, emplace during Late Oligocene oblique collision between the SIBUMASU and IBA. An east dipping subduction and Benioff zone, N-Q magmatic arc and back-arc opening developed along the western margin and east of the IBA due to oblique convergence between the IBA and the Indian Plate. The northeast prolongation of the Indian continent appears to have collided against the northern end of the IBA during Mio-Pliocene, uplifting and overthrusting the Shillong Massif over the Bengal Basin located over its passive margin to the south, whereas Eocene distal shelf sediments of the IBA were overthrusted over the Tertiary shelf cover of the Indian continent. The inferred suture at the northern end of the active subduction zone is concealed under cover (Acharyya, 1997b).

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