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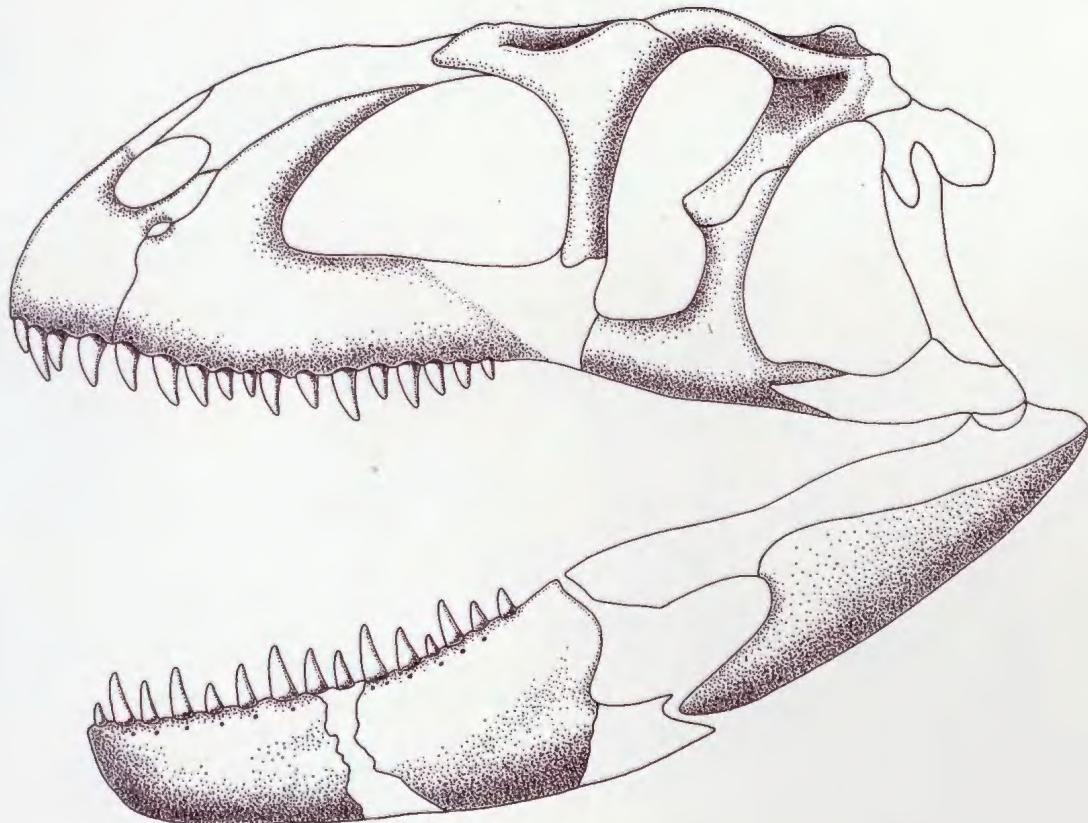
KT EVENTS IN INDIA: IMPACT, RIFTING, VOLCANISM AND DINOSAUR EXTINCTION

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For more than a decade, a number of impact sites have been linked to the mass extinction at the KT (Cretaceous/Tertiary) boundary. The prime candidate today is the Chicxulub Crater in Yucatán Peninsula, Mexico. Recently another potential KT impact scar — the Shiva Crater — has been identified from subsurface data at the India-Seychelles rift margin. The crucial evidence in support of this impact structure comes from the Bombay High field, a giant offshore oil basin in India, and associated alkaline intrusives within the Deccan Traps. The KT boundary age of the crater is inferred from its Deccan lava floor, Palaeocene age of the overlying sediments, isotope dating (~65Ma) of presumed melt rocks, and the Carlsberg rifting event (chron 29R) within the basin. Seismic reflection data and India-Seychelles plate reconstruction at 65Ma reveal a buried oblong crater, 600km long, 450km wide and 12km deep, carved through Deccan Traps and into underlying Precambrian granite. It represents the largest impact structure of Phanerozoic age. The crater shows the morphology of a complex impact structure and basin, with a distinct central uplift in the form of a series of peaks, an annular trough and a slumped rim. The oblong shape of the crater and the asymmetric distribution of fluid ejecta indicate oblique impact in a SW-NE trajectory. We speculate that a 40km diameter meteorite crashed on the western continental shelf of India around 65Ma, excavating the Shiva Crater, shattering the lithosphere and inducing the India-Seychelles rifting. The crater appears to narrow in the form of a teardrop to the NE or downrange where the ejecta melt rocks were emplaced radially outward by the impact shock. The shape of the Shiva Crater and the asymmetric ejecta distribution mimic those of artificial craters produced by oblique impacts in laboratory experiments. The synchrony and near-antipodal positions of the Shiva and Chicxulub Craters may indicate two alternative modes of their origin. Either, both craters originated from splitting of a larger diameter meteorite, or, large impact on one side of the Earth produced a similar signature on the far side by axial focusing of seismic waves. Since India was ground zero for both an impact and Deccan volcanism, their causal relationships and biotic effects were assessed. It appears that Deccan volcanism began 1Ma before the KT event and was not triggered by the impact. Its origin is attributed to the Deccan-Reunion hotspot. The extensive areal distribution of Deccan Traps is owing to intercanyon flows along the drainage of the Narmada, Godavari and the Cambay basins. During the early stage of Deccan eruption, sauropods, theropods and ankylosaurs flourished in India, but they died out suddenly at the KT impact boundary. Although both impact and Deccan volcanism are hypothesized as contributing to the deleterious environmental consequences leading to biotic crisis at the KT boundary, the impact is suggested as having played the major role as the killing mechanism. □ *Impact, Cretaceous-Tertiary boundary, India, dinosaur, extinction, volcanism.*

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Since its emergence and subsequent eruption of diversity, life has shown a tenacious and wildly successful hold on this planet. But the rich history of life has been repeatedly punctuated by equally awesome displays of its destruction. It is estimated that 99% of plant and animal life that have ever lived on Earth are now extinct (Wilson, 1992). The history of life is replete with major episodes of biotic catastrophes or mass extinctions, when 50% or more of the unrelated species died out fairly rapidly. All mass extinctions, however, have been followed by at least a partial evolutionary recovery in which the number of species on Earth has increased again.

There are five major episodes of mass extinctions during the past 600 million years: Late Ordovician (440Ma), Late Devonian (365Ma), Late Permian (245Ma), Late Triassic (210Ma) and Late Cretaceous (65Ma). Of these mass extinctions, the one that has captured the greatest
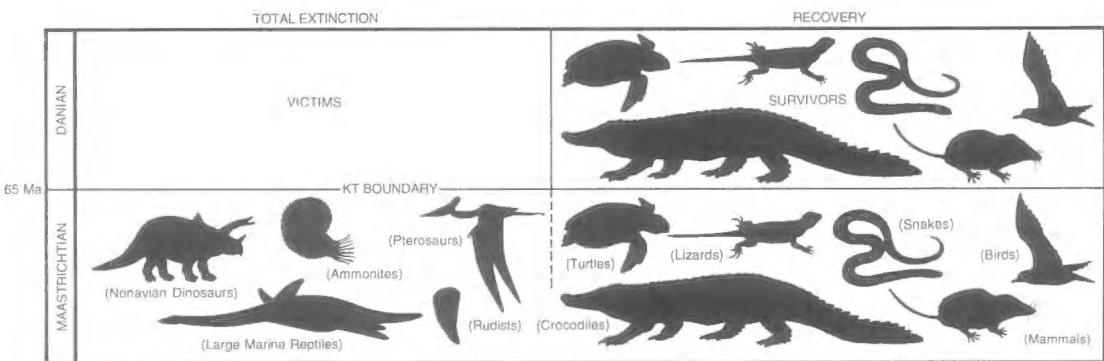
FIG. 1. Victims and survivors after the KT extinction. The primary victims were nonavian dinosaurs, pterosaurs, large marine reptiles such as plesiosaurs and mosasaurs, and various invertebrates such as ammonites and rudists. Lizards, snakes, turtles, crocodiles, birds and mammals endured this catastrophe and rebounded. Both birds and mammals underwent explosive evolutions after this crisis.

attention of earth scientists has been the KT (Cretaceous/Tertiary) extinction when the dinosaurs and two-thirds of all marine animal speices were wiped out. The sudden extinction of dinosaurs has puzzled both scientists and public for more than a century. Having survived for 160 million years, dinosaurs seemed indestructible. Not only the dinosaurs died out during that relatively brief period; all land animals weighing more than 25kg disappeared from the planet. All pterosaurs, plesiosaurs, mosasaurs as well as several families of birds and marsupial mammals, and hundreds of plants were also suddenly wiped out at this time. The small calcareous plankters that float at the ocean surface and the ammonites and rudists from the depths also vanished. The Earth was devastated. Life was ravaged by one of the worst catastrophes.

There were survivors, of course, after the KT disaster (Fig. 1). Neornithine birds, placental mammals, crocodiles, turtles, lizards and snakes all survived as groups — despite the extinction of some species. From this catastrophe, opportunities arose for the survivors. The KT extinction had opened the door for the age of mammals and the rise of birds and changed the course of evolutionary history. What triggered this catastrophe that led to such an unprecedented ecological crisis? Over the years, many theories, some bizzare and some plausible, have been offered to explain the mystery behind the extinction of dinosaurs. There is no shortage of murder suspects. Any explanation of the causes of biotic crises must focus on finding agents of destruction that affected environments, climates, ecology and organisms.

By the end of the Cretaceous, harsh changes of environments were taking place as a result of plate movements, mountain buildings, volcanic emissions and sea regressions. Exactly what caused the biotic crisis remains highly controversial. Currently two competing models have been proposed to explain this apocalyptic disaster at the KT boundary: meteorite impact hypothesis and volcanic hypothesis. The impact theory postulates that the environments were lethally altered or destroyed at the end of the Cretaceous by the collision of a large meteorite leading to biotic crisis. The volcanic theory argues that the pollution in the atmosphere and oceans by the massive outpourings of Deccan flood basalt in India had devastating effects on ecology.

In 1980, the Alvarez group proposed that the KT extinction was caused by the impact of a 10km meteorite. This proposal has generated a great deal of interest among scientists and the public. But the key piece of evidence was still missing. If a huge meteorite had indeed crashed into the Earth, where was the crater? Critics searched for alternate explanation. The end of the Cretaceous was also a time of massive continental flood basalt volcanism, especially the Deccan Traps in India. Many palaeontologists believe that such cataclysmic volcanism may have been the culprit in the KT extinction (McLean, 1985; Officer et al., 1987). Over the past 15 years, exciting new insights have poured in from virtually every branch of earth and planetary sciences to understanding the effects of these catastrophic events — impact and volcanic — on earth's ecosphere and the evolution of life. Recently the Chicxulub structure in the northern coast of Yucatán Peninsula of Mexico has

emerged as a prime candidate for the KT impact site (Hildebrand et al., 1991). In this paper we describe another buried KT impact structure — the Shiva Crater at the India-Seychelles rift margin, and its relevance to the Chicxulub structure, Deccan volcanism and mass extinction (Chatterjee, 1992; Chatterjee & Rudra, 1993).

THE IMPACT MODEL

Like other planets in the solar system, the Earth resides in a swarm of asteroids and comets. It is now apparent that the Earth has been heavily bombarded during its history by meteorites of various sources, sizes and compositions (Clube & Napier, 1982). The incontrovertible evidence for large cosmic collisions is the occurrence of circular craters associated with considerable local structural disturbance and shock metamorphism (French & Short, 1968). Because of the dynamic nature of the terrestrial lithosphere where such forces as erosion, volcanism, deposition, orogeny and plate tectonics constantly restructure the surface, impact craters are often erased or obscured, unlike the more static surfaces of the Moon, Mercury and Mars. To date over 150 impact craters have been recognized on the Earth's surface and the list is growing. They range in size from approximately 100m to 200km and in age from Precambrian to Recent (Grieve, 1987; 1990; Grieve et al., 1988). The spatial distribution indicates concentrations in cratonic areas. Other craters may be submerged under oceans and remain inaccessible or undetected. Scientific interest in the role of impact in geological and biological evolution has been enhanced by several developments in recent years. Among the most prominent of these are the hypotheses of Alvarez et al. (1980) concerning terminal Cretaceous extinction and lunar and planetary exploration by manned and unmanned spacecraft. As interest in bombardment mounts, previously unknown or cryptic impact sites are recognized with increasing frequency. As a grim reminder that the threat of impact on our planet is a real possibility, the world's attention was focused during late July, 1994, on the spectacular collision of comet Shoemaker-Levy 9 on the surface of Jupiter, leaving scars the size of Earth on the giant planet (Levy et al., 1995; Weissman, 1955).

Hypervelocity impacts can have a large range of effects that depend on the strength and density of the projectile and the nature of the target material. The most obvious result of larger collisions is seen in the spectrum of crater sizes and morphologies. The recovery of meteorite fragments and shock effects within or surrounding a crater are the most persuasive evidence for an impact origin, but when large craters are deeply eroded or buried, the evidence of impact is obscured or blurred. Such evidence may be identified indirectly from shock-metamorphic effects on the target rock and ejecta components, as well as distinctive geochemical signatures attributable to a particular type of meteoritic projectile (Grieve, 1990). These signatures may be preserved locally near the impact site, or globally at a particular stratigraphic level containing the ejecta fallout. Together they may provide clues to the nature of the target material and the impactor. Impact craters of this obscure nature are the most controversial and require additional information for verification.

In 1980, the Alvarez group advanced a startling theory to explain the sudden demise of dinosaurs — the most succesful land animals ever to arise on Earth. They discovered an abnormally high concentration of iridium (about 30 times more than the surrounding rocks) at the KT boundary level of Gubbio, Italy. Soon a comparable iridium anomaly was found globally at different KT boundary sections (Orth, 1989). Since iridium is a very rare element in the earth's crust, but fairly abundant in chondritic meteorites, the Alvarez team proposed that the iridium spike at the KT boundary is cosmic in origin, implying the strike of a large meteorite. There was enough iridium in the KT boundary, they calculated, to equal a 10km-diameter asteroid. They proposed that this giant asteroid crashed into the Earth with a velocity of 90,000km/hour to cause the worldwide catastrophic event. This impact lofted so much debris into Earth's atmosphere as to creater a 'nuclear winter' that caused much of the life on Earth to perish. A blackout of sun would kill plants and destory the food chain. The global distribution of the iridium layer was caused by the impact and vaporization of the bolide. The impact theory was reinforced by additional evidence such as shocked quartz (Bohor et al., 1984; 1987; Owen & Anders, 1988), stishovite (McHone et al., 1989), micro-diamonds (Carlisle & Braman, 1991), impact glasses (Izett et al., 1990), osmimium isotope ratios (Turekian, 1982), Ni-rich spinels (Robin et al., 1994), rhodium (Bekov et al., 1988), carbon soots (Wolbach et al., 1988), tsunami deposits (Bourgeois et al., 1988), and extraterrestrial amino acids (Carlisle & Braman, 1993) in the KT boundary layer at different sites.

Among all this cumulative evidence, the shocked quartz is a distinctive signature of impact event as it can form at a force more than 10 gigapascal (GPa) that travels through quartz-bearing grains of the target rock to porduce microscopic shock lamellae (Grieve, 1990). Pressures and temperatures produced by a large body impact are much greater than those generated by other geologic processes, such as volcanic activity, mountain building and earthquakes.

However, the strongest evidence in favor of the KT impact event would be to locate a crater marking the point of collision. Such a crater should be 150km or more in diameter (Grieve, 1982). The search for an impact site of the right age (~65Ma), and the right size (150km) has continued, including reassessment of many enigmatic structures. Now, after a decade-long search, the Chicxulub structure on the Yucatán Peninsula of Mexico (Hildebrand et al., 1991) and the Shiva Crater at the India-Seychelles rift margin (Chatterjee, 1992) appear to be two potential candidates for the long-sought KT impact scar.

THE VOLCANIC MODEL

Although the impact hypothesis is very compelling, not everybody believes that impacts killed the dinosaurs and other organisms at the KT boundary. Critics have advanced a volcanic alternative. The end of the Cretaceous was also a time of massive continental flood basalt volcanism, especially the Deccan Traps of India. Recent radiometric dating suggests that the main pulse of Deccan volcanism may have occured close to the KT boundary at 65 million years ago (Duncan & Pyle, 1988; Courtillot, 1990). Many palaeontologists argue forcefully that such cataclysmic Deccan volcanism may have been the main contributing factor for the biotic crisis at the KT boundary (Clemens, 1982; Officer et al., 1987; Hallam, 1987; Keller, 1989; Stanley, 1987; Zinsmeister et al., 1989; Courtillot, 1990). Other contemporary episodes of volcanism at the KT boundary such as in Cameroon and the Coral Sea have been linked to the KT event (Sutherland, 1994). The proponents of the volcanic model argue that the KT extinction was neither global, nor instantaneous, but occurred over an extended period of time, because different organisms disappeared at different levels at or near the KT boundary. Such step-wise extinction pattern could be best explained by prolonged emissions of volcanic pollutants. Large amounts of iridium have been discovered to be spewing from the Hawaiian and Reunion volcanoes, suggesting that the iridium anomaly at the KT boundary could have also had a volcanic origin (Olmez et al., 1986). There is no doubt that such a massive volcanic outburst over an extended period would have deleterious environmental consequences. Proponents of the volcanic model claim that many of the supposed impact signatures at the KT boundary layer, such as iridium enrichment, shocked quartz, microspherules, clay mineralogy and carbon soot, could have volcanic explanations (Officer, at al., 1987; Courtillot, 1990). The impact proponents disagree. They point out that the Deccan volcanism was not of an explosive type and could not account for the global distribution of the iridium anomaly, shocked quartz and tektites at the KT boundary layer (Alvarez, 1986; Alvarez & Asaro, 1990). Moreover, the lamellar features in quartz grains associated with explosive volcanism show curvatures contrary to the planar and parallel lamellae in impact-related shocked quartz recoved from the KT boundary (Izett, 1990). The gradual extinction pattern seen among organisms may be an artifact of preservation and poor sampling quality. Others argue that because Deccan volcanism had little effect on the diversity of local Indian biota, its catastrophic role in global life is questionable (Prasad et al., 1994).

SEARCH FOR THE KT IMPACT SITE

Since Alvarez et al (1980) presented their geochemical evidence for an impact event at the KT boundary, the search for the proposed impact crater has   continued. There are a number of candidates for the KT impact site, none of which are very compelling at present. The 35km Manson structure in north-central Iowa is such a candidate (French, 1984; Anderson & Hartung, 1988), but new work suggests that this crater is older (~74mya) and played no role in the KT mass extinction (Izett at al., 1993). Twin impact structures in the Kara Sea in the former USSR, the Kara (diameter, 60km) and Ust-Kara (diameter, 25km), have been proposed as possible impact sites (Koeberl et al., 1988), but recent geochronologic data suggest that these structures are also older than the KT boundary event (Koeberl et al., 1990).

Even the general location of the KT impact, whether continental or oceanic, remains controversial. Trace element and isotopic studies of the highly altered KT boundary-layer components tend to support the oceanic impact

hypothesis (Gilmore et al., 1984; Hildebrand & Boynton, 1990). On the other hand, the presence of shocked quartz at several KT boundary sites would indicate a continental site (Bohor at al., 1987). The apparent contradiction can be reconciled if the single impact occurred at a continental margin involving both oceanic and continental crust, or multiple impacts at different sites.

It was soon realized that the size and abundance of the ejecta, such as shocked quartz grains and tektites, may give some clues as to the location of the impact crater. Bohor et al. (1987) and Izett (1990) concluded that the largest sizes and greatest abundance of shocked quartz grains in KT boundary sediments occur in western North America, suggesting that the impact occurred on or near the continent. The discovery of tsunami deposits at the KT boundary sections on the Brazos River, Texas (Bourgeois et al., 1988), near Braggs, Alabama, (Smit et al., 1994), in the Caribbean (Hildebrand & Boynton, 1988), and Deep-Sea Drilling Program holes 536 and 540 in the southwestern Gulf of Mexico (Alvarez et al., 1992) as well as the identification of tektites at Beloc, Haiti (Izett et al., 1991; Maurrasse & Sen, 1991) and Arroyo el Mimbral, northeastern Mexico (Smit et al., 1992), narrowed the search further to the Caribbean region. Impact breccia has been recovered from Albion Island of Belize, near the Mexican border (Ocampo & Pope, 1994). At least four possible Caribbean sites have been suggested, including the Colombian Basin, western Cuba, Haiti and the Yucatan Peninsula.

Hildebrand & Boynton (1990) placed the KT impact location in the Colombian Basin between Colombia and Haiti on the basis of seismic data and DSDP core samples, but the putative crater is not only under water but buried under 1,000m of sediment and is subject to other interpretations, such as tectonic origin or a change in the thickness of the oceanic crust. Bohor & Seitz (1990) speculated that the impact site was near Cuba, about 1,350km from the site proposed by Hildebrand and Boynton, on the basis of a boulder bed interpreted as ejecta components, but the boulder bed is found to be of local, weathering origin and the Cuban site has been rejected (Dietz & McHone, 1990). The Massif de la Hotte on the southern peninsula of Haiti, a mountainous region with Cretaceous sediments, has also been proposed as the KT impact site (Maurrasse, 1990), but closer examination of the area clearly indicates that it is not an impact site (Officer et al., 1992).

The most promising KT impact site appears to be the Chicxulub Crater on the northern margin of the Yucatán Peninsula, Mexico (Penfield & Camargo, 1982; Hilderbrand et al., 1991; 1995). It is a circular structure about 180km in diameter, buried under 1,100 m of carbonate strata, extending out under the Gulf of Mexico, and defined by magnetic and gravity anomalies (Fig. 2A).

THE CHICXULUB CRATER

The subsurface stratigraphy of the Chicxulub structure is known primarily from petroleum exploration bore holes drilled by Pemex, the Mexican national petroleum company, in the 1950s (Lopez-Ramos, 1975; Meyerhoff et al. 1994). Unfortunately, most of the critical core samples were destroyed in a warehouse fire. At present, samples of the Chicxulub structure are limited; as a result, the subsurface stratigraphy is open to various interpretations. In hindsight, it is ironic that drilling and exploration were stopped as soon as the andesitic bodies at a depth of 1500-2000m were encountered; these may have provided the critical evidence for the impact. Penfield & Camargo (1982) suspected an impact origin for the Chicxulub Crater on the basis of concentric geophysical anomalies with associated extrusive material such as andesitic bodies. Recently located samples from the old Pemex wells, including brecciated carbonates, andesites and crystalline basement have been studied extensively and inferred to support the impact scenario for this site. For example, Hildebrand et al. (1991) reported shocked quartz within Chicxulub breccias and documented chemical and isotopic similarities between andesites and tektite deposits from the KT boundary sections of Haiti and Mexico. These findings indicate that the Chicxulub Crater may be the source for the Haitian and Mexican tektites. Kring & Boynton (1992) interpreted the rocks initially thought to be andesites as probable impact melts, whereas Blum et al (1993) found an isotopic match between the Haiti glass and the Chicxulub melt. Subsequently, Sharpton et al. (1992) recognized that the breccia above the melt rock is suevite breccia, a distinct signature of an impact crater. They recognized that the Chicxulub melt rocks show high levels of iridium and their age corresponds well with the KT boundary. Single crystal $^{40}Ar/^{39}Ar$ dating places the melt rock at 65Ma (Swisher et al., 1992). All this combined evidence suggests that the Chicxulub
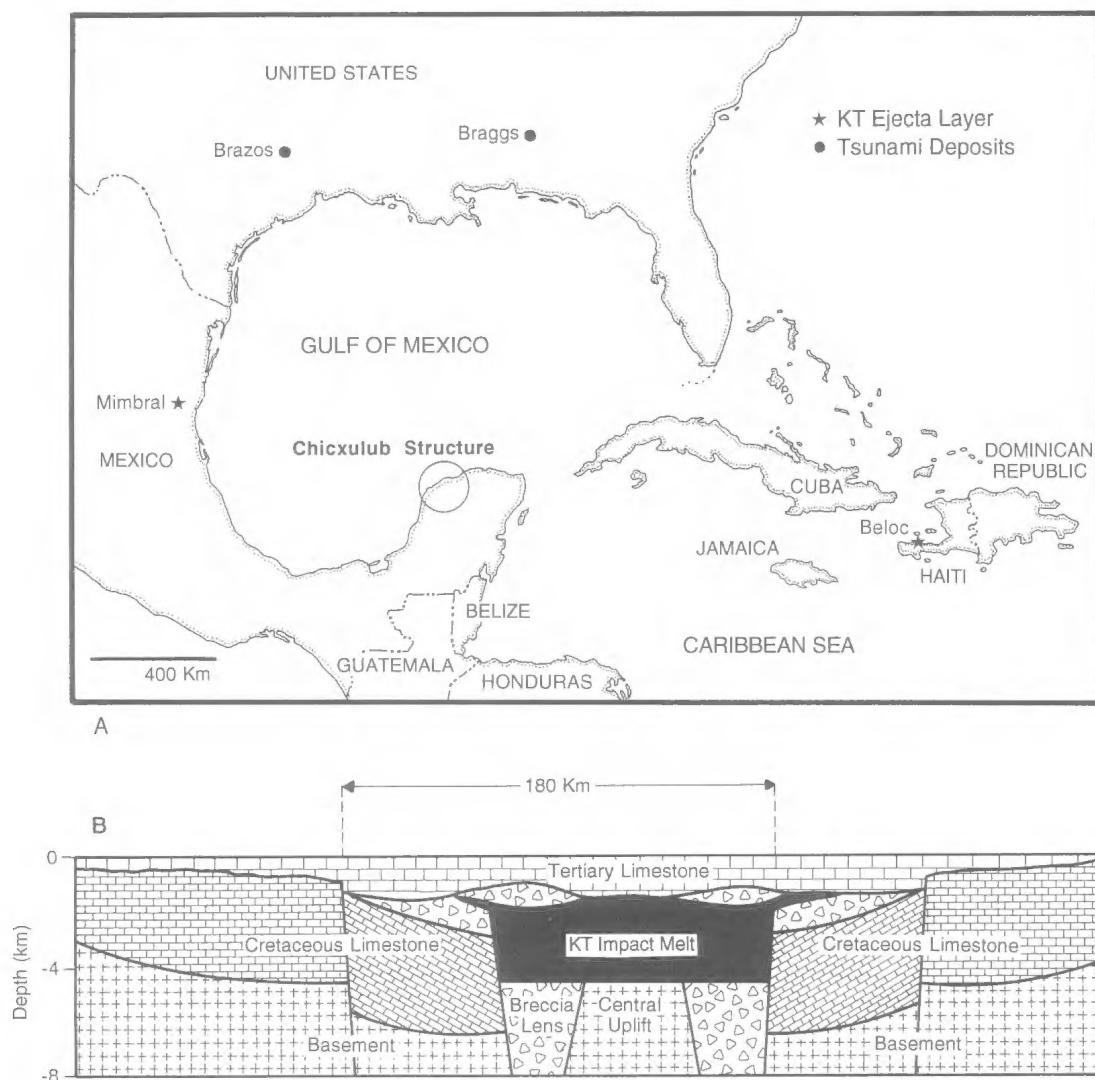
FIG. 2. A, Location of the Chicxulub structure on the northern edge of the Yucatán Peninsula, Mexico, showing distribution of proximal impact deposits. B, Cross-section; estmated crater diameter is 180km (simplified from Hildebrand et al., 1994).

structure may be a prime candidate for the long sought KT impact crater (Fig. 2B).

It appears from the above discussion that two lines of evidence support the impact scenario for the Chicxulub structure: evidence of shock metamorphism, iridium enrichment, brecciation and impact melt within the crater itself, and the distribution of proximal ejecta components at the KT sections in Haiti, Mexico, Texas, Alabama, the Caribbean and adjacent areas (Fig. 2A). However, in recent times both interpretations have faced strong criticisms. For example, some

workers dispute the impact origin of the Chicxulub structure and interpreted it as a buried volcanic complex of Late Cretaceous age (Officer et al., 1992; Meyerhoff et al., 1994). Their counterargument is based on the original subsurface correlation proposed by Lopez-Ramos (1975) and the unpublished well log for the Yucatán No. 6 well, drilled in 1966 over the Chicxulub structure. One of the authors, Dr Arthur A. Meyerhoff, was a consulting geologist to Pemex at the time Yucatán No. 6 was drilled and had first-hand information on the biostratigraphy

of the site. This well penetrated a superimposed sequence of Pliocene-Miocene, Oligocene, Eocene-Palaeocene and Maastrichtian-Campanian sediments, and bottomed in andesitic rocks and Cretaceous limestone, dolomite and anhydrite. The most damaging evidence against the impact origin is the inverted stratigraphy of the Cretaceous horizon in relation to the andesite. These dissenters point to the presence of 350m of undisturbed Late Cretaceous sediments with index fossils (foraminifera) overlying the andesitic body. If the andesitic rocks were indeed impact melt from KT boundary time, the overlying strata must be Palaeocene or younger in age. Palaeontologic evidence indicates otherwise; these strata are of Campanian and Maastrichtian age lying conformably over the andesite. Swisher et al. (1992) explained this stratigraphic inversion as fallback breccia of Cretaceous limestone infilling the crater. However these overlying Cretaceous strata are not disturbed, brecciated and shocked, and thus pose a problem for the KT impact age of the andesite body.

Meyerhoff et al. (1994) indicated the following additional discrepancies in the impact origin hypothesis of the Chicxulub structure:

1) The Chicxulub structure is too shallow (~2000m) for an impact of this dimension; expected excavation depth would be around 10km or greater (Melosh, 1989).

2) Several layers of bentonitic breccia occur interbedded with the Cretaceous limestones without any structural disturbance or obliteration, so their impact origin is suspect.

3) If the andesite were of impact origin, one would expect highly homogeneous composition with appreciable thickness; in contrast, chemical analysis suggests that the Chicxulub andesite is thin, chemically inhomegeneous with a wide range of major oxide compositions (Sharpton et al., 1992).

4) In an impact structure, the impact melt represents the aggregate composition of the target rock (Engelhardt, 1984); in Chicxulub, on the other hand, the target country rock is metamorphosed quartzite and rhyolite, whereas the presumed impact melt is andesite.

5) The anhydrite at the bottom of the Yucatán No. 6 well would have been completely vaporized at the point of collision, if there was an impact; its presence below the putative melt rock is anomalous.

6) Unlike the planar and parallel lamellae in shocked quartz associated with an impact site, the lamellar features in quartz grains in Chicxulub breccia show curvatures typical of volcanic origin.

7) Later thermal events in the Chicxulub volcanic sequence might have reset the radiometric age of the andesite; these authors indicated that out of ten samples analyzed by Sharpton et al. (1972), nine gave spurious results; accordingly, the correlation between the KT impact event and the presumed andesite melt is tenuous at best.

8) The Chicxulub volcanics are not local impact melt, but part of a well-known Late Cretaceous igneous province surrounding the Gulf of Mexico.

Not only the impact origin of the Chicxulub structure, but also the interpretation of proximal deposits of ballistic ejecta and impact-wave disturbances in the Caribbean and Gulf Coast is in dispute. Recent studies have shown that many of these so called impact-generated deposits may in fact represent gravity-flow or turbidite deposits occurring over an extended period of time, whereas supposed impact droplets are altered volcanic particles (Lyons & Officer, 1992; Keller et al., 1993; Stinnesbeck et al., 1993; Beeson et al, 1994; Adatte et al, 1994).

The presumed connection between the Haitian glasses and Chicxulub has been questioned by Koeberl (1993) on the basis of geochemical evidence. He pointed out that, at the time of impact, the Chicxulub area was covered by evaporitic and carbonate deposits several kilometers thick. Yellow glasses found in the KT section of Haiti are not tektities and cannot be linked to evaporitic target rocks of the Chicxulub. Similarly, the interpretation of some breccias within Chicxulub as impact breccias may be wrong. However, proponents of the Chicxulub Crater have dismissed most of these criticisms (Alvarez et al. 1994; Hildebrand et al., 1994).

Thus, the Chicxulub impact is open to question, and more study is needed before a final assessment can be made. The only way to settle this question decisively is by drilling new holes into the Chicxulub structure, as in the case of the Manson Crater, to determine more precisely when and how it formed.

THE SHIVA CRATER

Although the Chicxulub structure has emerged as the leading candidate for the KT impact scar, another promising KT impact site has been identified at the India-Seychelles rift margin in the northwest Indian Ocean, almost antipodal to the Chicxulub structure. Hartnady (1986) suggested
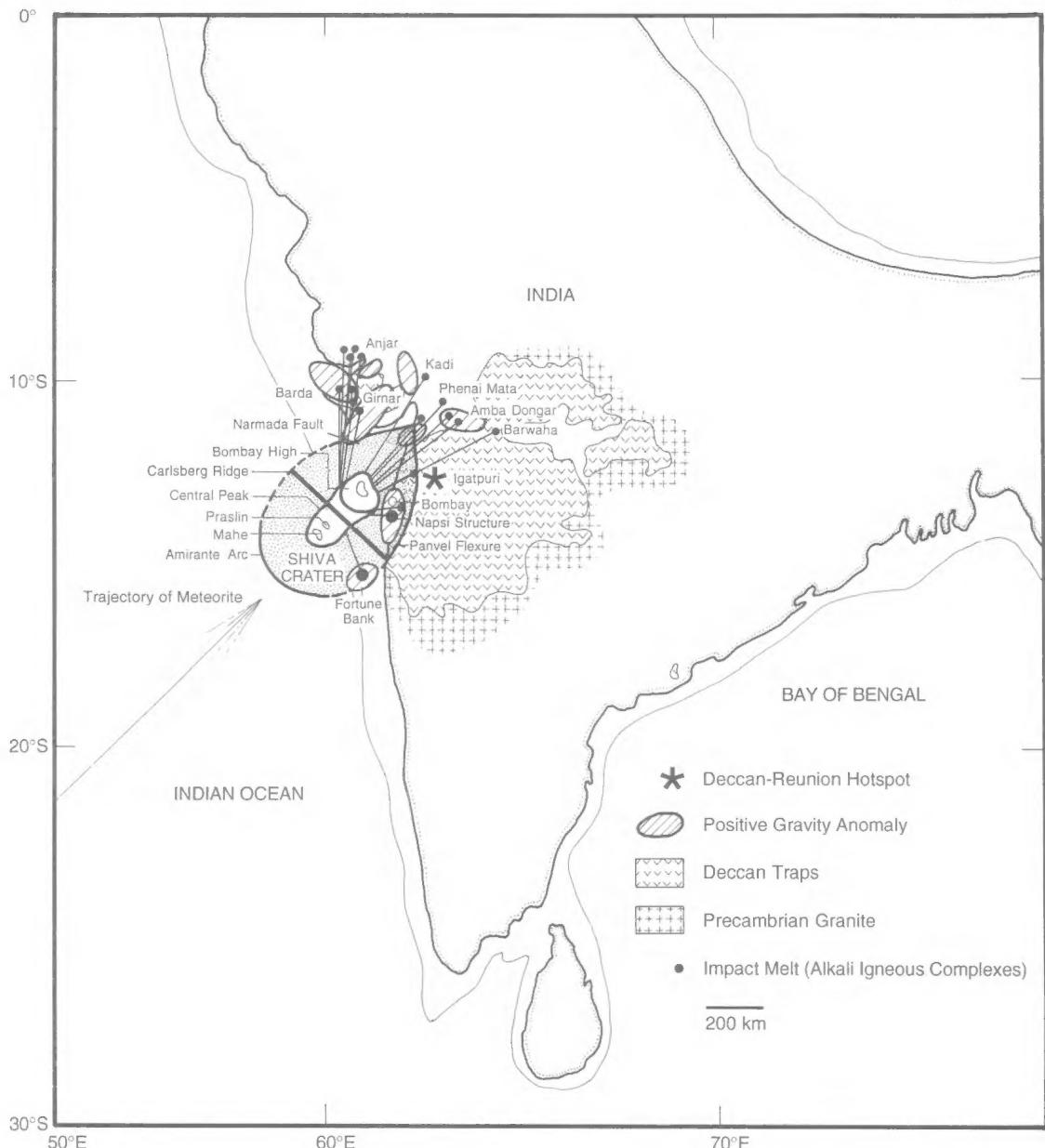
FIG. 3. Location of the Shiva Crater at the India-Seychelles rift margin during KT boundary; arrow indicates trajectory of meteorite; radial, asymmetric distributions of alkaline igneous complexes (impact melt rocks) downrange of the Shiva Crater are shown by closed circles (data from Bose, 1980); areas of positive gravity anomaly (data from Biswas, 1988) coincide with the ejecta melt distribution; asterisk indicates location of the Deccan-Reunion hotspot.

that the Amirante Basin, south of the Seychelles Island, may be a possible KT impact site. The basin has a subcircular shape of about 300km in diameter, bounded on the northeast by the Seychelles Bank and partially ringed on the southwest by the structure of the Amirante Arc. Sediments from the adjacent Amirante Passage have yielded Late Maastrichtian foraminifera *Abathomphalus mayorensis* (Johnson et al., 1982), while basalt samples dredged from the

Amirante Arc look like Deccan Trap and have a similar radiometric age (Fisher et al., 1968). Both palaeontologic and radiometric age indicate that the arc was formed near the KT boundary. However, its arcuate structure is enigmatic. It does not appear to be a recent or ancient trench, as it lacks volcanic activity, seismicity, and any significant accretionary sedimentary prism on its 'landward' side (Johnson et al., 1982). Thus the interpretation of the Amirante Arc as a crater rim is a distinct possibility. The proposed impact also may explain the puzzling jump of the Carlsberg Ridge at the KT boundary during the rifting of India and the Seychelles. Hartnady noticed that the Carlsberg Ridge between the Seychelles and Madagascar jumped more than 500km to the northeast to lie between India and the Seychelles and initiate rifting between these two landmasses. He could not find any evidence for plate reorganization in the Atlantic or Pacific Oceans during this time. He attributed this major plate tectonic adjustment to the enormous force of a large meteorite. As additional evidence, he pointed to massive tsunami deposits in the KT boundary section of Somalia and Kenya, which may be linked to this impact event.

Although Hartnady's model initially had attracted wide attention, one major problem of his idea is the enigmatic morphology of the Amirante Basin. It is semicircular in outline, preserving half of a supposed crater rim. What happened to the other half of the crater? Although circularity is not diagnostic of impact origin, there must be evidence of some structure off the coast of Seychelles. Is it possible to find the missing rim?

Alt et al. (1988) remedied the deficiency of the Amirante Basin model as the point of collision. They argued that during KT boundary, the Seychelles was adjacent to the west coast of india. They concurred with Hartanady (1986) that the western rim of the crater survives in the Amirante Arc, but the eastern rim lies along the west coast of India, hidden by the overlying Deccan Traps. They speculated that the impact was forceful enough to create not only the enormous crater approximately 600km in diameter, but also to cause pressure-release melting in the asthenosphere. Basalt then filled the crater basin to form an immense lava lake, the terrestrial equivalent of a lunar mare. The synchrony of initiation of spreading along the Carlsberg Ridge, the emplacement of the flood basalts at the Deccan plateau, Saya de Malha bank and Amrante Basin, as well as close spatial association around the crater basin, indicate that the array of simul-

taneous tectonic and volcanic features might have been triggered by a single physical cause — an enormous impact.

Chatterjee (1990; 1992) elaborated upon this KT impact scenario at the India-Seychelles rift margin, and identified the eastern rim of the crater along the Panvel Flexure, near the Bombay coast (Figs. 3-6). The Panvel Flexure is an arcuate segment of the crater about 120km long on the Deccan Traps, and it is difficult to explain in terms of conventional tectonics. It is marked by a line of hot springs, dikes, deep crustal faults and seismicity (Kaila et al., 1981; Powar, 1981). Since the Indian shield is usually aseismic, the seismicity along the flexure is unusual, indicating tectonic instability. The geothermal gradient is abnormally high along this flexure ($36\text{-}78°C/km^{-1}$) with evidence of thinned lithosphere (31-39km), suggesting melting conditions at shallow depths (Negi et al., 1992). The Panvel Flexure may represent the eastern rim of the crater in the form of a collapsed rim structure. It exercises tectonic control on the attitude of the Deccan lavas. To the east of the flexure, the basaltic flows are horizontal; to the west of the flexure, the basaltic flows dip west to west-southwest at 50° to 60° toward the coast. The abrupt change of dip along the flexure axis may indicate the slope of the eastern crater wall, which is now concealed by Deccan lavas. Seismic data indicate that the basement topography below the Deccan lava west of the flexure has a crater-like depression (Kaila et al., 1981). Completing the oval by combining the Amirante Arc and the Panvel Flexure, the extent of the crater can be extrapolated. It is a giant oval crater, 600km long and 450km wide, showing the morphology of a complex impact scar. Chatterjee (1992) named this impact structure the Shiva Crater, after the Hindu god of destruction and renewal (Fig. 3). However, the Shiva Crater is difficult to interpret because it is submarine and largely concealed by the Deccan lava. Many of the impact signatures are thus erased or obscured. Moreover, the rifting of the Seychelles from India, which occurred along the width of the crater, has obliterated the geomorphology of the structure. A series of geodynamic and volcanic events that occurred near KT boundary time must be untangled and put into proper chronologic order to unveil the crater morphology. Recent exploratory data from the Bombay High, a giant offshore oilfield located 160km west of the city of Bombay, has produced a wealth of infomation supporting an impact origin for the Shiva Crater.
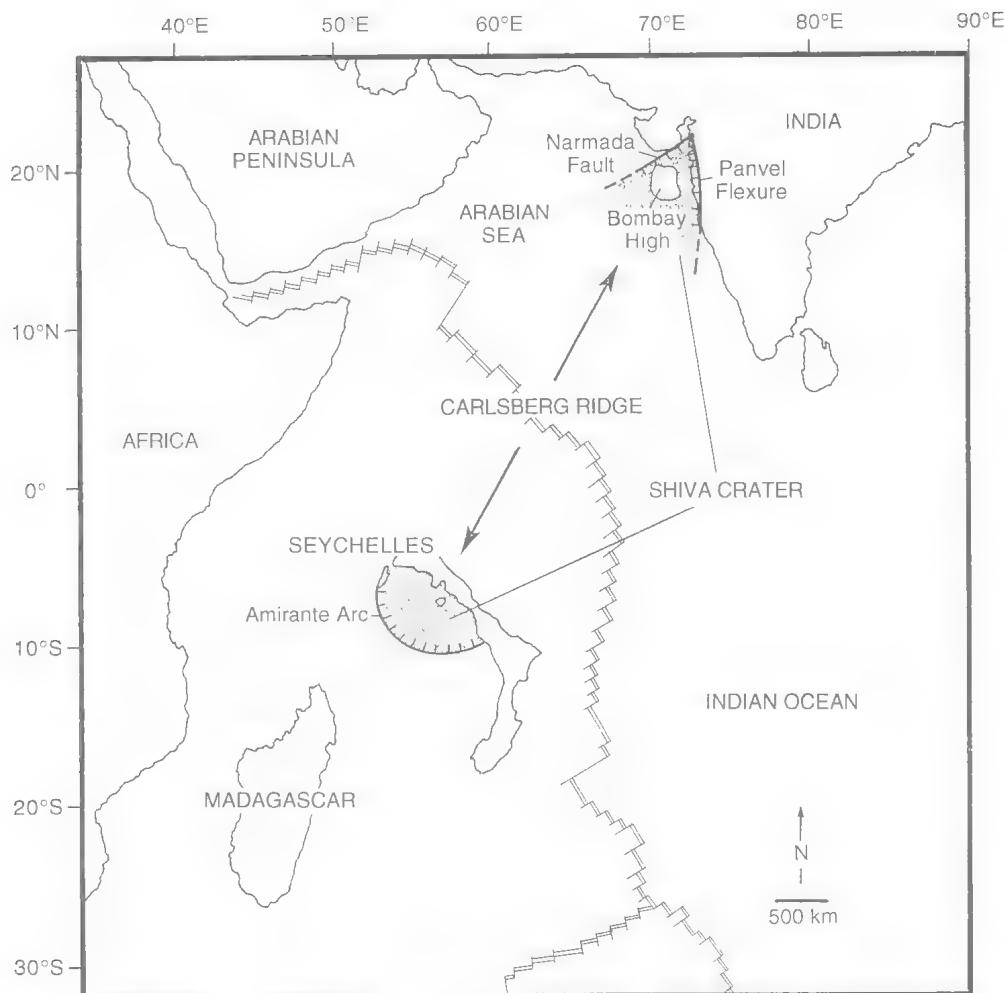
FIG. 4. Present day location of the split Shiva Crater in reference to India and Seychelles on either side of the Carlsberg Ridge. Today, part of the Shiva Crater is attached to the southern part of the Seychelles, the other-half to the western part of India. The crater was joined 65 million years ago when the Seychelles was part of India before the spreading of the Carlsberg Ridge.

INIDA-SEYCHELLES FIT. Today, the Seychelles microcontinent is separated from the western coast of India by 2,800km because of spreading along the Carlsberg Ridge (Fig. 4). This midoceanic ridge shows symmetrical magnetic anomalies of 5, 23, 24, 25, 26, 27, 28 and 29 on either side of the ridge axis between India and the Seychelles (Norton & Sclater, 1979; Naini & Talwani, 1982). Using both palaeomagnetic and palaeontologic evidence Chatterjee (1992) has restored the India-Seychelles fit for the KT boundary time (Figs. 3 & 8). The reconstruction places the western coast of India against the Seychelles-Saya de Malha Bank at about the time

of Deccan volcanism and shows matching geological provinces. The largely submerged continental block that bears the Seychelles Islands contains enormous flood basalt deposits in the submarine plateau of the Saya de Malha Bank, which are inferred to be an extension of the Deccan volcanism (Meyerhoff & Kamen-Kaye, 1981; Backman et al., 1988), especially the Bushe Formation of the Upper Deccan Basalt Group (Devey & Stephens, 1992). The link between KT magmatism on the Seychelles and India is emphasized by matching the geochemistry and geochronology of alkaline rocks (White & Mc-Kenzie, 1989; Devey & Stephens, 1992). Similar-

ly, the Late Proterozoic Mahe Granite on the Seychelles (Baker & Miller, 1963) is isochronous (70050Ma) with the Siwana-Jalor Granite (Auden, 1974) of western India, the crystalline basement below the Deccan lava. Various tectonic and volcanic features, when restored for the Indo-Seychelles block at 65Ma, reveals the presence of a large oval, oblong structure, the Shiva Crater (Figs. 3, 5).

ANATOMY OF THE SHIVA CRATER. Since the Shiva Crater was spilt by the Carlsberg Ridge and each half is now buried under a thick pile of lava flows, and because the structure is largely submarine, geophysical exploration and drilling data are essential to understanding its morphology and structure. Morever, overlying lava flows and thick sediments obstruct a direct examination of various impact signatures such as shock metamorphic effects, breccia and impact melt that are generally associated with complex craters. Today, one part of the crater is attached to the western coast of India, the other to the Seychelles (Fig. 4), but of course both parts were joined at the KT boundary (Fig. 3).

The most critical evidence regarding this impact structure comes from recent oil exploration in the Bombay High offshore basin, which represents the eastern-half of the crater. Bombay High is a giant offshore oilfield ($\sim 120,000^2$km) located 160km west of Bombay in the Arabian Sea at a depth of about 75m (Fig. 5). The structure is 60km long and 20km wide, trending WNW-ESE with a faulted eastern flank. The stratigraphy of this enigmatic structure is known from extensive drilling and seismic data by the Oil and Natural Gas Commission (Rao & Talukdar, 1980; Basu et al., 1982; Bhandari & Jain, 1984). The Bombay offshore basin shows part of the crater rim (Panvel Flexure and Narmada Fault), annular trough (Surat Basin, Dahanu Depression, and Panna Depression) and the central uplift (Bombay High) (Fig. 5A). The morphology of the western-half of the Shiva Crater around the Seychelles microcontinent is also known from oil exploration data (Meyerhoff & Kamen-Kaye, 1981; Kamen-Kaye, 1985; Devey & Stephens, 1992). Here we see part of the crater rim (Amirante Arc), annular trough (Amirante basin) and the central peaks (Mahe and Praslin granitic cores). When the Shiva structure is restored to KT boundary time (Fig. 5), it shows the structure and morphology of a giant, complex crater, oval in outline with: 1, a collapsed outer ring, 600km long and 450km wide; 2, an annular trough, presumably filled with KT melt rocks; and 3, a distinct central core in the form of linear uplifted peaks of older Precambrian granite.

The Shiva Crater is defined by a collapsed outer ring, which is partially preserved in the form of the Amirante Arc, Panvel Flexure and the Narmada Fault (Figs. 3 & 5). The outer rim is surrounded by a gravity high, especially in both the Panvel Flexure and Narmada Fault areas (Biswas, 1988) and may be linked to the distribution impact melt. Part of the outer ring along the northwest and southeast edges was obliterated by spreading of the Carlsberg Ridge. The outer ring is followed by the annular trough which was largely filled with ponded Deccan lava (and possibly by suevite and impact melt). Part of the trough is preserved in the Surat Basin, Dahanu Depression and Panna Depression around the Bombay High, and the Amirante Basin, southwest of the Seychelles. The uplift in the center is represented by a large peak followed by two small irregular peaks, all composed of older Precambrian granitic cores: the Bombay High on the western coast of India and the Praslin and Mahe Islands of the Seychelles. Jansa (1993) pointed out that the central uplift in oceanic impact sites is generally cylindrical in shape, as is the Shiva Crater. The lateral continuity of the central peaks was disrupted by the Carlsberg Rift and may indicate a collapse structure. The central uplift associated with the 600km Shiva Crater is estimated to be 150km wide, about one-fourth of the crater's final diameter, as is expected in a complex crater (Melosh, 1989). Figure 5B is a geologic cross-section of the 600km diameter Shiva structure along the longitudinal axis. The depth of the crater can be estimated from the thickness of the sedimentary basins around the annular trough as well as from the height of the central peaks. The sedimentary fill around the trough of Bombay High consists of shallow marine Tertiary sediments exceeding 5,000m, overlying the Deccan basalt floor (Bhandari & Jain, 1984). Such thick sediments indicate that the crater basin is more than 5km deep above the Deccan floor. The thickness of the Deccan lava, and the presence of impact melt within the crater are unknown, but Meyerhoff and Kamen-Kaye (1981) have described a well log on the Saya de Malha Bank which penetrated 832m of basalt overlain by 2400m of upper Palaeocene to Quaternary sediments. Based on their seismic work, Shor & Pollard (1963) suggested that approximately 2km of Deccan basalt overlie the granitic basement some 80km southwest of the
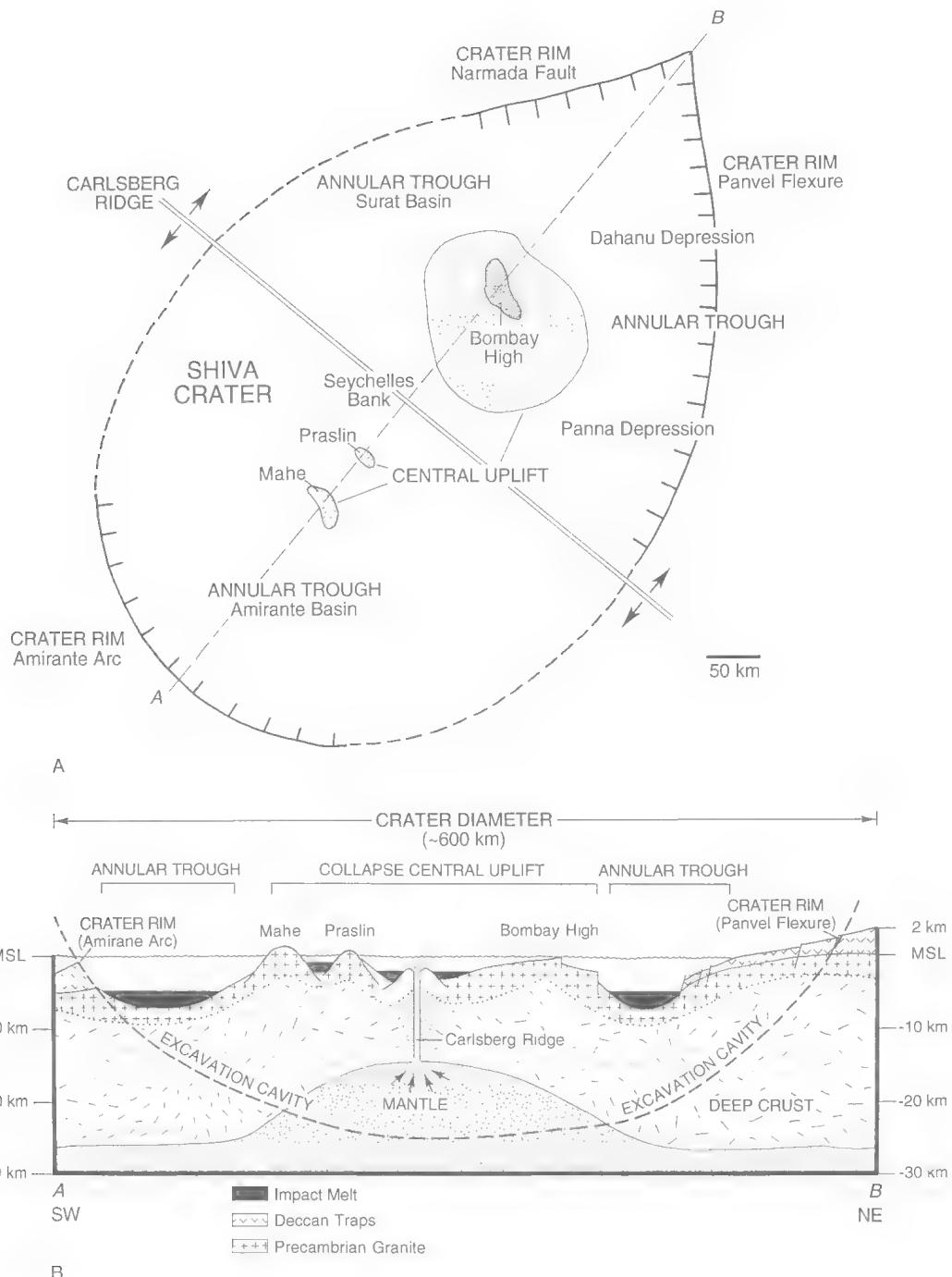
FIG. 5. Morphology of the Shiva Crater. A, plan view showing a central uplift (Bombay High, Praslin and Mahe granitic core); an annular trough (Surat Basin, Dahanu Depression, Panna Depression and Amirante Basin); and a slumped outer rim (Narmada Fault, Panvel Flexure and Amirante Arc). The oblong crater is about 600km long, 450km wide and more than 12km deep; it is bisected by the Carlsberg Ridge. B, schematic cross-section along the line AB; the post-impact Deccan lava flows are removed to show the morphology of the crater and possible sites of impact melt sheets; (seismic profile data from Rao & Talukdar, 1980; Kaila et al., 1981).

Mahe Peak. If we now add to this the 2km thick lava pile in the Western Ghats section near the Panvel Flexure, the depth from rim to actual floor may exceed 10km (Fig. 5B).

AGE OF THE SHIVA CRATER. Although the age of the Shiva Crater is not precisely known, combined evidence from various components of the structure, such as the formation of the rim, biostratigraphy of the annular trough, age of the melt sheets, timing of the central uplift, association of Deccan volcanics and the Carlberg rifting event suggests that the crater formed at the KT boundary. As discussed earlier, the preserved rim of the Shiva Crater, such as the Amirante Arc (Hartnady, 1986; Alt et al., 1988), the Panvel Flexure (Auden, 1949; Chatterjee, 1992) and the Narmada Fault (Biswas, 1988) evolved at KT boundary time. Seismic stratigraphy has identified the basement rock as reflection-free or chaotic Precambrian granite in the form a central uplift with a thin veneer of Deccan lava at the base (Rao & Talukdar, 1980; Basu et al., 1982; Bhandari & Jain, 1984). The oldest sediment overlying the Deccan Trap or crystalline basement is the Panna Formation of Palaeocene age (Fig. 6). The upper boundary of the Panna Formation coincides with H-4 seismic horizon. The Panna Formation is composed of poorly sorted, angular sandstone, claystone and trap fragments at the bottom, followed by shale and coal sequence. This unit is relatively thin on the uplift, but attains a large thickness (75m) on the flank. Seismic data indicate that the formation may be as thick as 500m in the annular trough region, but wells have not penetrated the bottom layer. Although the formation is mostly unfossiliferous, it has yielded *Globorotalia pseudomenardii* from the middle of the sequence corresponding to P4 planktic foraminiferal zone of Late Palaeocene, indicating a short palaeontologic hiatus after the KT event. Since the impact took place in a shallow-marine setting, the hiatus may be linked to erosion by a megatsunami generated by the impact. The KT boundary section lies farther down at the bottom of the sequence. Jansa (1993) suggested that in oceanic impacts most of the fall-out breccia is reworked back into the crater cavity. If so, the lowest unit of the Panna Formation, if recovered in future, should be investigated for an iridium anomaly and shock metamorphic minerals (Fig. 6B). The crater floor is composed of younger Deccan flows from the adjoining Western Ghat section that took place around ~65Ma (Couirtillot, 1990; Duncan & Pyle, 1988). The Deccan floor at the annular trough and the overlying Panna Formation narrow down its age to close to the KT boundary. Recent isotopic dating of the Shiva melt rock, as discussed in the following section, has yielded an $^{40}Ar/^{39}Ar$ date of 65Ma (Basu et al., 1994). Finally, the Carlsberg rifting within the crater basin was formed during the magnetic chron 29R (Naini & Talwani, 1982).

Although it is generally believed that the Bombay High was formed during the breakup of India-Seychelles at the KT boundary (Basu et al., 1982), no tectonic mechanism has been offered to explain this spectacular uplift (~ 10km high) of the Precambrian granite with a thin veneer of Deccan Traps at the passive margin of the Bombay shelf (Fig. 6B). We propose that this structural high represents one of the central peaks of the Shiva impact that originally underlay the transient crater. The other two central peaks, Praslin and Mahe Islands in the Seychelles (Fig. 5A), also rebounded upward at the same time as they contain similar Precambrian granites and younger KT intrusive rocks (Devey & Stephens, 1992). These central peaks are composed of deformed and fractured rocks that have been stratigraphically uplifted distances comparable to the crater depth (Melosh, 1989). The fractured nature of the central peak of the Bombay High can be seen in Figure 6B. The crystalline rocks beneath the Shiva Crater are shattered, as in the Ries Crater of Germany, as inferred from the low seismic velocity beneath the H4 horizon (Rao & Talukdar, 1980). Similarly, Baker (1967) reported a 'megablock zone' — a chaotic assemblage of gigantic blocks of granite, each up to 13m high, often marked with surface fluting at the Mahe uplift in the Seychelles. Evidence from drill holes, geochronology and seismicity suggest that the magmatism at the Seychelles Bank occurred at the KT boundary, producing both Deccan lavas and alkaline igneous complexes (Devey & Stephens, 1992).

IMPACT MELT ROCKS. The Shiva impact must have produced enormous volumes of impact melt, breccias and shocked materials between the central structure and the rim. Yet, these impact signatures are difficult to interpret because of mobilization and mixing of thick lava flows from Carlsberg Ridge, subsequent burial by the Deccan lava, as well as lack of drilling and seismic data below the Deccan floor. However, there is some indirect evidence that indicates a lava-like impact melt was emplaced radially within and outside the crater.
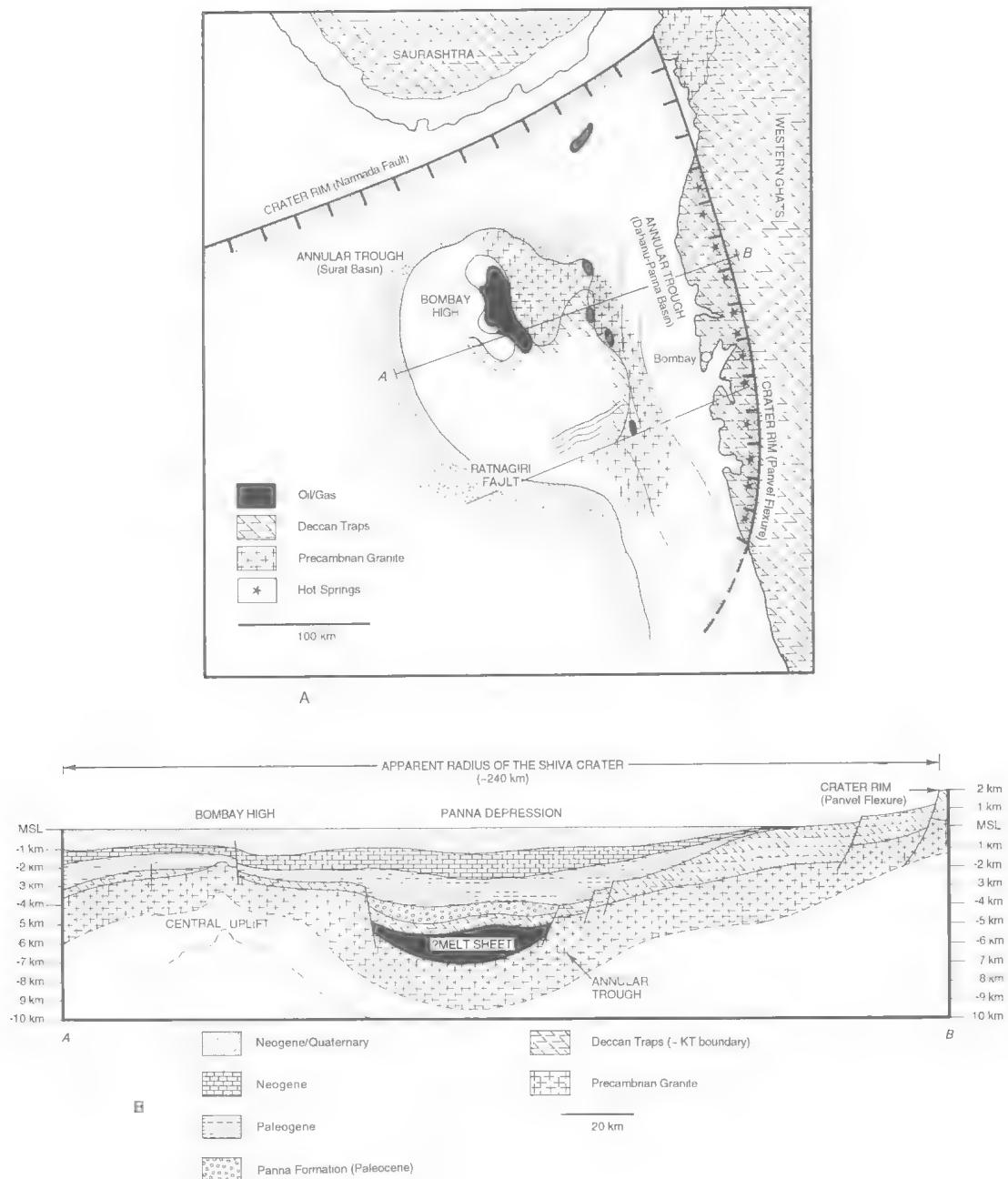
FIG. 6. A, Location and tectonic framework of Bombay High in relation to India representing the eastern-half of the Shiva Crater (simplified from Rao & Talukdar, 1980). B, seismic cross-section along the line AB to show the central uplift (Bombay High), annular trough (Panna Depression) and the crater rim (Panvel Flexure) (simplified from Rao & Talukdar, 1980).

One of the most intriguing features following the Deccan flood basalt volcanism is the occurrence of several post-tholeiitic alkali igneous complexes of nepheline-carbonatite affinities, along the radii of the Shiva Crater (Figs 3, 7). They are manifested in plug-like bodies and minor intrusions in the western and northwestern part of the Deccan volcanic province and are

limited in space and volume compared to the vast expanse of tholeiitic lavas (Bose, 1980; De, 1981). They are clearly defined by zones of gravity highs (Biswas, 1988). Extrusive rocks are relatively rare except in the Kutch rift zone, indicative of fissure eruption. Devey & Stephens (1992) described contemporary alkaline intrusives in several islands in the Seychelles microcontinent, especially in Mahe, North Island and Silhouette Island within the Deccan lavas. Geochemically they are very similar to the Murud alkaline dikes of Bombay. Recent $^{40}Ar/^{39}Ar$ dating of these alkaline complexes indicates 65Ma, precisely coinciding with the KT boundary (Basu et al, 1993; Pande et al, 1988; Devey & Stephens, 1992). In the Anjar section of the extrusive alkaline complexes, cosmic iridium and osmium anomalies have been reported from the interbed (Bhandari et al., 1994). Their distributions are shown in Figures 3 & 7A.

Two spectacular volcanic plugs within the Shiva Crater need discussion. One is Fortune Bank igneous center south of the Seychelles, the other is a newly discovered buried structure near Bombay. The Fortune Bank is an unusual submarine volcanic center, about 15kms high and 50km across, with anomalous magnetic and gravity signatures within the Deccan volcanics (Girling 1992). Devey & Stephens (1992) interpreted this structure as a large alkaline intrusion contemporary with similar volcanics around the Seychelles. Negi et al. (1993) identified a large volcanic cone-like intrusive, about 12km high and 35km in diameter, buried 6km below the Deccan Trap near Bombay, east of the Panvel Flexure. It is defined by a high gravity and thermal anomaly. They found that the crustal thickness in this site is half of the normal Moho depth, and the granitic basement is almost missing in this region. They interpreted the structure as a large fossil conduit, formed at the point of collision of a large KT meteorite. For ease of description, we designate this igneous complex the *Napsi structure* after the last names of the discoverers (*N*egi, *A*grawal, *P*andey, *Si*ngh). Since alkaline intrusives are known from this area, and they show high gravity anomalies relative to the surrounding Deccan Trap, we interpret the Napsi structure as a massive alkaline complex similar to the Fortune Bank (Fig. 7A).

The origin of these alkaline igneous complexes within the Deccan volcanics has been debated for many years. They have been linked to fractional crystallization of parent tholeiitic magma (West, 1958), an early stage of Carlsberg rifting

(Thompson & Nelson, 1972; Devey & Stephens, 1992) and a late stage of Reunion mantle plume (Bose, 1980; De, 1981; Basu et al. 1993). How is it possible to derive from the same mantle source large volumes of tholeiite extrusives followed by limited occurrences of alkaline intrusives? Why are the alkaline rocks so heavy relative to the Deccan Traps and so easily demarcated by gravity anomalies? How can we explain the abundance of these alkaline rocks in and around the Shiva Crater in the form of volcanic cones? Some of these buried volcanic cones, such as Napsi structure and Fortune Bank even dwarf Mount Everest. Alkaline igneous complexes are commonly found as melt sheets associated with several Canadian craters (Grieve, 1987). The spatial and temporal correlations of these alkaline igneous complexes with the Shiva Crater are intriguing, making a causal relationship likely. All these alkaline igneous complexes show the following features indicative of impact origin:

1, The centers of alkaline magmatism are clustered around the Shiva Crater in radial fashion but conspicuously absent in other parts of the Deccan province (Figs 3 & 7A);

2, Their age matches exactly with the KT impact event;

3, They are all defined by positive gravity anomalies;

4, They have restricted distributions and occur within the Deccan volcanics as post-tholeiitic intrusives or plugs;

5, Their parent melt composition was homogeneous, but later differentiation within the plug has produced varieties and compositional layering as in the case of impact melts in several Canadian craters such as Brent and Manicougan;

6, They show higher alkali content than the country rock;

7, They show evidence of crustal contamination.

This evidence suggests that the alkaline igneous rocks around the Shiva Crater were formed by crystallization from impact melted country rocks. We hypothesize that these alkaline rocks represent melt ejecta produced by impact-induced mixing and melting of the target rocks, and were emplaced radially on downrange side of the trajectory (Fig. 7A). The close isotopic and age relationship of the impact melt with the younger Deccan volcanics such as the Ambenali Formation (Pande et al., 1986; Devey & Stephens, 1992) indicates remelting of these rocks. We believe three groups of rocks, younger Deccan volcanics, platform carbonates and evaporites, and
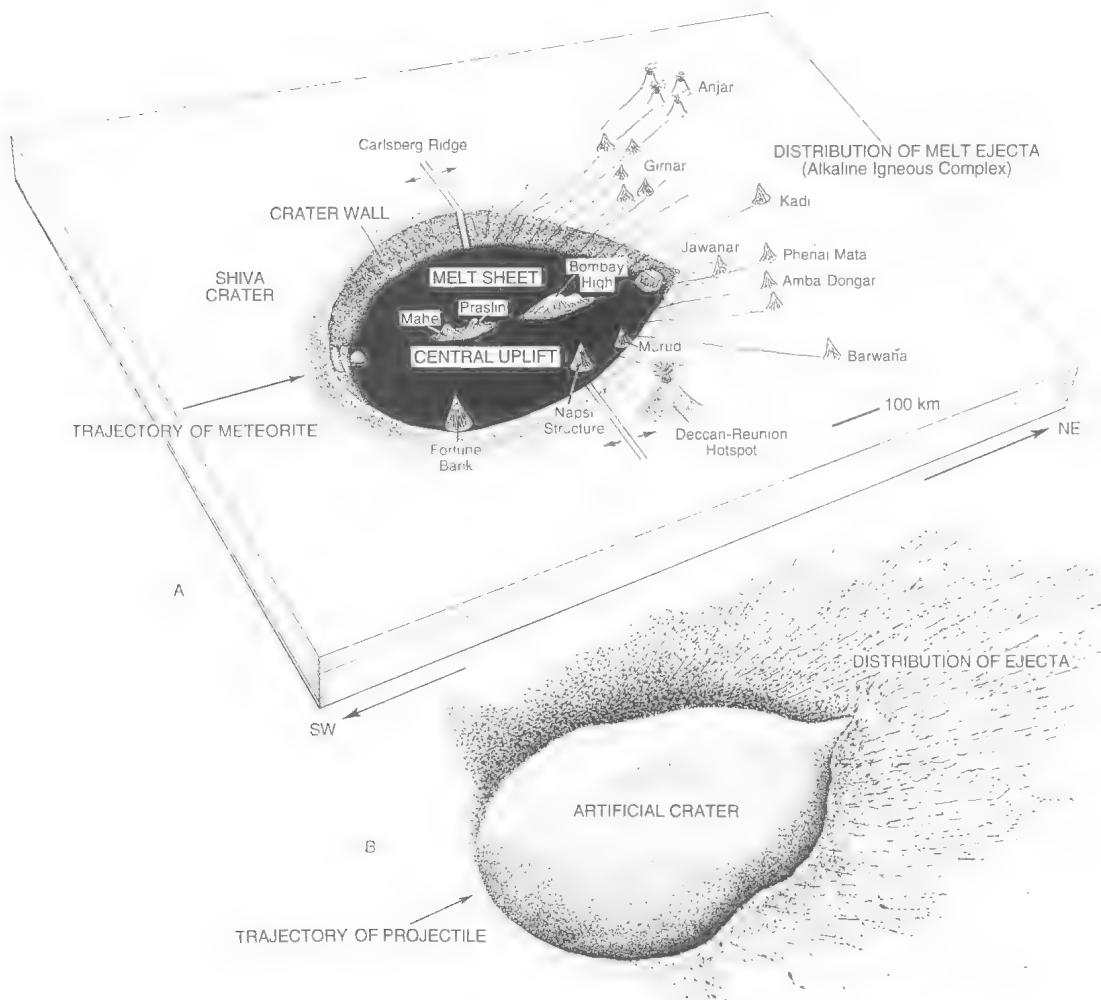
FIG. 7. A, Schematic three-dimensional view of the Shiva Crater showing the radial distribution of the impact melt rocks in the form of volcanic plugs; younger Deccan volcanics are removed to show the morphology of the crater; oblong, teardrop shape of the crater and the asymmetric distribution of the melt rocks consistent with an oblique impact event along the NE downrange direction. B, Artificial crater produced by low-angle (~15°) oblique impact in the laboratory mimics the shape and ejecta distribution of the Shiva Crater (simplified from Schultz & Gault, 1990).

Precambrian basement were involved in the genesis of the melt rocks of the Shiva Crater. The younger Deccan volcanics covering the Precambrian basement of the Bombay and Seychelles region at the KT boundary were the main target rocks. However, the Precambrian granite itself was also involved in the impact, as indicated by the unusually thin crust in the Bombay area with missing granitic layer (Negi et al., 1993) as well as by evidence of crustal contamination in the alkaline suites (Paul et al, 1977; Basu et al., 1993). The Shiva Crater was also

inferred to have been excavated on a shallow sea platform containing thick carbonate and evaporitic rocks such as we see today around the Bombay High and Rann of Kutch. Thus the melt rock can be interpreted as the mixing product of Deccan Traps, Precambrian granite and the thick Late Cretaceous sequences of carbonate/evaporite-rich sediments. These Cretaceous sediments are still preserved in the adjacent Kutch, Saurashtra and Rajasthan areas, covered by the Deccan Traps, and are encountered by subsurface drilling (Biswas, 1988). However, the alkaline rocks are

TABLE 1. Large Earth-crossing and Earth-approaching asteroids (diameter > 10km; after Wetherill & Shoemaker, 1982).

NUMBER	NAME	CLASS	DIAM. (Km)
1866	Sisyphus	Apollo	11.4
433	Eros	Amor[3]	19.6
1036	Ganymed	Amor[3]	39.6

generally undersaturated with a high K_2O/NaO ratio relative to the Deccan tholeiites (Bose, 1980). Such an 'anomaly' is not unusual with an impact event. Alkaline volcanic rocks are commonly present as impact melt in most of the Canadian craters. Grieve (1987) discussed the compositional variation of these alkaline melt rocks, where melt sheets have a higher K_2O/NaO ratio than the target rock. The reason for this alkali enrichment is not clear; he believed that either it is caused by selective elemental vaporization and condensation during the melt and vapor formation, or hydrothermal alteration. Since the impact was largely oceanic, the latter explanation of enrichment of alkali from sea water is likely. The gravity high of the alkaline igneous complexes most likely reflects mass concentration associated with dense impact melt and uplift of the silicate basement rock along the crater rim (Figs. 3, 7A).

The radial distribution of melt sheets in the down-range direction of the Shiva Crater is intriguing (Fig. 7A). They might have developed either during the passage of the shock waves when fluid ejecta was emplaced downrange, or during the collapse of the transient crater when radial fractures were formed. Melosh (1989) discussed the mechanism by which radial fracture patterns develop during the collapse of a large, multi-ring crater. Radiating fractures from the central uplift to the rim are known from the Manicougan Crater of Canada (Grieve et al., 1988) and the Wells Creek Structure of Tennessee (Stern, 1968).

SIZE AND TRAJECTORY OF THE IMPACTOR. Throughout its history the Earth has been impacted by countless meteorites. There are two broad categories of meteorites with orbits that bring them close to the Earth: comets and asteroids. Comets are composed in large part of water, ice and other volatiles and therefore are more easily fragmented than rocky or metallic asteroids. Although smaller meteorites pose little threat, impacts by large objects (diameter > 1km) constitute the greatest hazard, with their potential

for global environmental damage and mass mortality. The most famous large impact on planet Earth is the KT event that killed the dinosaurs and other contemporary biota. Wetherill & Shoemaker (1982) have summarized the current knowledge of Earth-crossing and Earth-orbiting asteroids and their probability of impacting the Earth. They estimate that out of 1,000 near-Earth asteroids (NEA) that have diameters greater than 1km, three exceed the 10km range. These are 1866 Sisyphus (11.4km), 433 Eros (19.6km) and 1036 Ganymede (39.6km) (see Table 1). Both Eros and Ganymede can be perturbed into Earth-crossing orbits by close encounters with Mars. They speculate that asteroids as large as 20km in diameter probably have struck the Earth in the last few billion years, and 10km diameter bodies apparently may impact every 40 million years. Recently Paola Farienella of the Universty of Pisa in Italy and colleagues simulated eight computer models to calulate the probability of colliding the 20km-wide asteroid Eros with the Earth. One forecast of this catastrophic impact is alarming; it could happen in the next 1.14 million years (Desonie, 1996). Because of this continued threat from space, NASA has organized an International Spacegurad Survey Network to detect and monitor near-Earth-objects. In February 1996 NASA sent its Near Earth Asteroid Rendezvous (NEAR) spacecraft to examine Eros from a close distance. The spacecraft is scheduled to arrive in close proximity to this asteroid in 1999 to scrutinize its surface in great detail for the understanding of its origin (Bell, 1996).

Although hypervelocity impacts normally create circular craters, impacts at a low angle ($\leq 15°$ from the horizontal) often generate elongate craters such as the Messier and Schiller Craters of the Moon (Wilhelms, 1987) and the Rio Cuarto Crater in Argentina (Schultz & Lianza, 1992). Craters formed by artificial oblique impact are generally oblong (Moore, 1976; Gault & Wedekind, 1978). The shape of an artificial crater formed by oblique impact at 15° (Schultz & Gault, 1990) is like a teardrop, where the pointed end indicates the downrange direction (Fig. 7B). In an oblique impact, the crater and its ejecta are bilaterally symmetrical about the plane of the trajectory, but the distribution of ejecta is concentrated asymmetrically on the downrange side. The shape of the Shiva Crater and the distribution of melt ejecta are almost identical to those of the artitificial crater (Fig. 7A). If so, the impact that produced the Shiva Crater was probably oblique along a SW-NE trajectory as evident from the

direction of the longer diameter of the oblong crater; the tip of teardrop indicates that the downrange direction was NE. Howard & Wilshire (1975) described flows of impact melt of large lunar craters both outside on crater rims and inside on crater walls, where asymmetric distribution of this melt sheet can be used to determine impact trajectory. The rim pools tend be concentrated on the inferred downrange side. The asymmetric concentrations of sheet melts on the NE side of the Shiva Crater indicate the downrange direction (Fig. 7A).

We estimate that a 40km diameter asteroid, about the size of the Amor object Ganymed, could have created the Shiva Crater, initiated the Carlsberg rift and excavated the crustal materials into mantle reservoirs resulting in basaltic volcanism (Fig. 5A). An impact of this magnitude may be a rare event, but seems possible, because of the presence of even larger craters on the Moon and Mars. Currently there are at least three known craters which are close to 200km across: Vredefort in South Africa (2,000Ma), Sudbury in Canada (1,849Ma) and Chicxulub (65Ma) in Mexico. The Shiva Crater is not unique, but nearly so. The only older similar structure in its size range is the eastern shore (Nastapoka Arc) of Hudson Bay in Canada: this 600km wide depression is believed to be an impact scar of Archean age (Dietz, 1993). If properly understood, the Shiva Crater is the largest impact structure produced in the Phanerozoic and is consistent with the environmental havoc wreaked at the KT boundary.

A new model of lithosphere thinning by meteoritic impact is proposed here to explain the origin of the Carlsberg ridge, rift volcanism and the Shiva Crater. In this model the lithosphere could be excavated and shattered by a projectile of considerable size (~40km) to initiate a midoceanic ridge. Asteroids strike the Earth at an average speed of 25km/sec and transfer considerable kinetic energy to the target rocks (Shoemaker, 1983). The pressures exerted on the meteorite and target rock can exceed 100GPa; temperatures can reach several thousand degrees Celsius; and impacting energy would generate a 100-million megaton blast (Grieve, 1990). Such a hypervelocity impacting body penetrates the target rocks to two or three times its radius (Grieve, 1987). An asteroid of 40km diameter would produce cratering and associated tectonic rebound-collapse effects sufficient to shatter the 80km thick lithosphere that could form plate boundaries and continental rifts. This concept opens up a new field of research to investigate whether plate tectonics may be influenced by impacts of large bodies.

NEW LINKS BETWEEN THE CHICXULUB AND THE SHIVA CRATERS.

A Multiple-impact Model. If both the Chicxulub and Shiva Craters are real and were formed at KT boundary time, is there any genetic link between them? Hartnady (1989) suggested that if a low-angle, oblique primary impact occured in the Southern Hemisphere near India, then bolide ricochet may have resulted in secondary impacts a few minutes later in the Northern Hemisphere. However, since the trajectory of the Shiva Crater is from SW to NE, Hartnady's model fails to explain the origin of both the Shiva Crater and the Chicxulub Crater by oblique impact ricochet process. However, the recent crash of 21 fragments of comet Shoemaker-Levy 9 (S-L 9) on Jupiter inspired scientists searching for similar multiple impacts on other bodies in the solar system. Crater chains were soon discovered on Jupiter's satellites and on the Moon (Levy et al., 1995). The cometary fragments of S-L 9 did not collide simultaneously on Jupiter but spread in time over 5 days. If the original KT meteorite broke into several fragments, as in the case of Shoemaker-Levy, and the larger one formed the Shiva Crater, the second impact, almost after 12 hours (or odd multiple thereof), could create the Chicxulub as the Earth rotated anticlockwise around its axis. If the collisions of two fragments were spread over 12 hours, two antipodal craters could be formed by meteorite fragments around a great circle. If so, one can predict that additional KT impact scars, if discovered in future, should lie on this great circle joining the Shiva and the Chicxulub structures. This great circle is named here the *Alvarez Impact Belt* in honor of Luis and Walter Alvarez for their pioneering work (Fig. 8A).

There may be signs of this 'string of pearls' effect along the Alvarez Impact Belt in the form of a crater chain. Various authors have predicted a third KT impact site on the Pacific plate which surprsingly lay along the Alvarez Impact Belt. Frank Kyte (pers. comm.) made a dramatic discovery of a tiny fragment (~ 3mm) of the KT bolide in a drill core from DSDP site 576 in the western North Pacific. The bolide chip held micrometer-size metallic grains that are up to 87% nickel and rich in iridium. From the geochemical signature of the chip, Kyte speculates that the KT projectile is probably an
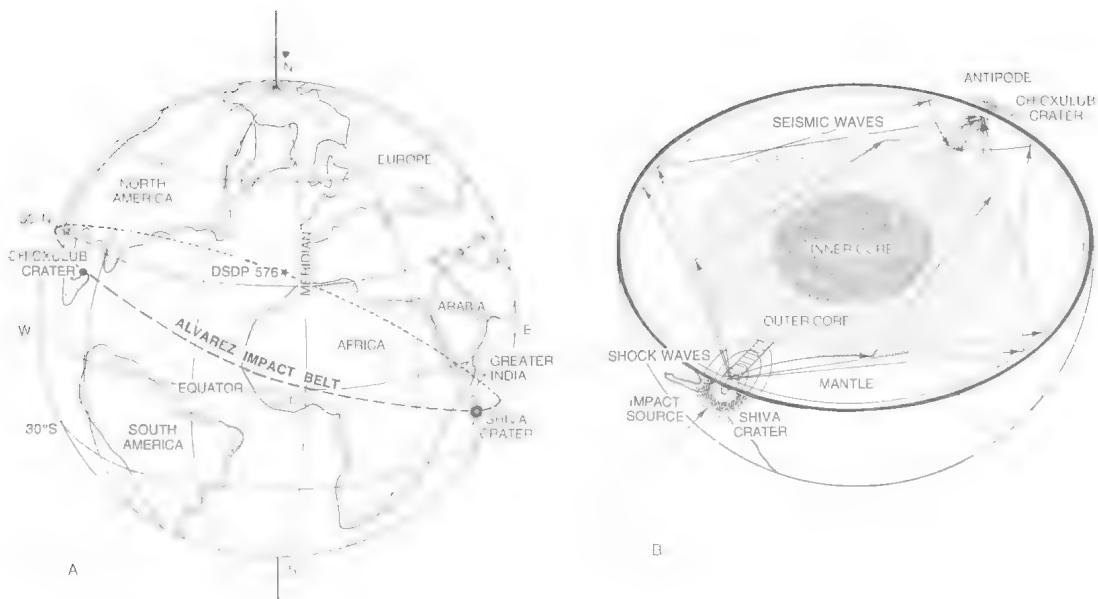
FIG. 8. Possible links between the Shiva and Chicxulub Craters. A, locations of the Chicxulub and the Shiva Craters along the 'Alvarez Impact Belt' at KT boundary time; note, impact debris and extinction events are concentrated along this belt. Both craters may have originated when two fragments from a larger meteorite crashed on a rotating earth over the course of 12 hours. B, near-antipodal positions of the Chicxulub and the Shiva Craters may also indicate alternative scenario that a large impact on one side of the Earth (near India) might have produced a similar signature on the far side (near Mexico) by axial focusing of seismic waves (modelled after Boslough et al., in press).

asteroid, not a comet, that slammed into Earth at a shallow angle. This is the first direct evidence regarding the carrier for iridium. The chip may have broken off of the asteroid before it crashed on the Pacific plate. At 65Ma, the Pacific impact site was located midway between the Chicxulub and the Shiva Craters right on the Alvarez Impact Belt (Fig. 8A). Kyte et al. (1994) also identified additional five KT boundary sites on the Pacific Plate around 576, characterized by an iridium anomaly, spherules and shocked quartz; they all cluster along this DSDP site 576. The point of collision of the KT projectile on the Pacific plate is further supported by other evidence. Robin et al. (1994) concluded from spinel compositions at the KT boundary sites of the Pacific plate that multiple impacts might have occurred from a single disrupted bolide, where the largest objects would have impacted in the Pacific and Indian Ocean. Their spinel distributions and proposed impact site at the Pacific fit nicely with the Alvarez Impact Belt. Finally, all the known localities with an iridium anomaly and shocked quartz related to the KT impact event (see Alvarez

& Asaro, 1990) cluster symmetrically on either side of the Alvarez Impact Belt. Distribution of impact-related minerals and trace elements along this belt coincides nicely with biogeographic selectivity of extinction at low latitudes (Keller, 1994). The high latitudes probably served as a refuge for many organisms, especially for plants. If so, the distribution of several impact sites and variation of composition of impact-generated minerals along the Alvarez Impact Belt could be explained by multiple impact events on a rotating Earth, around the equator, rather than by a single large impact. Such a latitudinal gradient, with most extinctions occurring in the tropics, is exactly what is to be expected by a chain of three impact sites in India, Mexico and Pacific plate respectively. These sites were formed when a large parent body broke apart into a string of smaller asteroidal fragments in the inner solar system and crashed into the planet.

Recently, Alvarez et al. (1995) raised three paradoxes in KT boundary sediments which are apparently difficult to reconcile in a single impact hypothesis. 1) In North America the KT boundary

reveals the double layer of ejecta: the lower layer consists mainly of iridium spike and altered spherules, whereas the upper contains shocked quartz. 2) Shocked quartz is more abundant and coarser grained at longitudes west than east of the Chicxulub Crater. Various KT boundary sites in Europe, Africa and Asia show little or no evidence of shocked quartz and may represent a 'forbidden zone' for shocked quartz distribution. 3) The proposed impact energy (>100GPa) released by collision of a 10km diameter asteroid at Chicxulub Crater would produce impact melt, not the moderate-pressure shock lamellae. Alvarez et al. linked all these three anomalies to differential timing of emplacement of target rocks. However, we speculate that the double layer ejecta at KT boundary sediments reflects two different sources of impact events: the lower iridium spike and impact spherules layer might have come from the earlier Shiva impact, whereas shocked quartz layer was emplaced during the Chicxulub event. This travel time sorting at two different impact sites may explain stratigraphic superposition of the double layer ejecta in North America and lack of upper layer in the distant areas of Europe, Asia and Africa. We propose that the energy released at the Shiva impact site was hundreds of gigapascals through the collision of a larger bolide fragment that produced mainly impact melt, emplacing it around the crater vicinity. From this impact site, spherules and iridium spikes were emplaced distally and globally. The high impact pressure would explain why we could not detect any shocked quartz grains at the KT boundary sections in India after repeated searches, as well as a general lack of shocked quartz in adjacent landmasses in Asia, Europe and Africa. On the other hand, the impact energy at the Chicxulub site was moderate to the tune of a few tens of gigapascals, producing mainly shocked quartz ejecta that were emplaced on the western side of the crater as the Earth rotated anticlockwise. Occurrence of multiple iridium spikes at some KT boundary sections (Officer et al., 1987) may be attributed to different timing of arrival from separate sources of impact sites.

Antipodal Crater Pairs Model. The antipodal locations of the Chicxulub and Shiva craters at the KT boundary are intriguing and suggest an alternative scenario (Fig. 8B). A hypervelocity impact is now known to have important geomorphic effects at its antipode. For example, Watts et al. (1991) documented unusual surface features such as 'disrupted terrains' antipodal to crater

basins on the Moon, Mercury and icy satellites. Similarly, Rampino & Caldeira (1992) proposed that antipodal focusing of impact energy may lead to Deccan volcanism and hotspot activity. Boslough et al. (1994) proposed a new model to explain how energy from a large impact on the Earth's surface would couple to its interior and focus axially at its antipode. However, their model is based on a vertical impact, whereas most impacts occur obliquely (Schultz & Gault, 1990). Because the Shiva Crater is much larger than the Chicxulub, it is likely that the Shiva Crater is the primary impact event at the KT boundary, whereas the Chicxulub may be its antipodal effect (Fig. 8B). The oblique impact may explain the departure of a few hundred kilometers from the true antipodal position. However, the presence of an iridium anomaly at the Chicxulub antipode is difficult to explain by the axial focusing mechanism. Similarly, the Pacific site of collision is anomalous in this model. The multiple-impact model is preferred here because of an unusual concentration of impact deposits and biogeographic selectivity of extinction at low latitudes along the Alvarez Impact Belt.

DID THE SHIVA IMPACT TRIGGER DECCAN VOLCANISM?

DISTRIBUTION AND EXTENT OF DECCAN VOLCANISM. The close of Cretaceous time was marked by the outpouring of the enormous Deccan lava flows, spreading over vast areas of western, central and southern India (Fig. 9). The Deccan Traps cover 800,000km^2 of west-central India and extend seaward along more than 500km of Arabian sea coastline, reaching as far as the continental shelf and beyond (Devey & Lightfoot, 1986). Deccan lava flows also spread across the Seychelles-Saya de Malha Bank, implying that their original extent may be more than 1.5 million km^2 (Krishnan, 1982; Devey & Stephens, 1992). They are extremely flat, with most dips less than 1, and rest mainly on the Precambrian granitic basement. Significant departures from horizontal occur, in particular, in the Western Ghats, west of the Panvel Flexure. Deep-seismic sounding studies reveal that the thickness of the Deccan Traps varies from about 100m in the northeastern part to about 2km along the west coast (Kaila, 1988). Deccan volcanism is considered to be one of the largest continental flood basalt deposits in the Phanerozoic (Courtillot et al., 1986).

STRUCTURAL FEATURES. Four important structural lineaments are associated within the Deccan volcanic province: the east-west trending Narmada Rift (Choubey, 1971); north-south trending Cambay rift (Biswas, 1982); northwest-southeast trending Godavari Rift (Qureshy et al., 1988); and the arcuate Panvel Flexure (Auden, 1949) (Fig. 9). The Narmada, Cambay and Godavari Rifts are older geofractures (Biswas, 1987), and may have influenced the distribution of the Deccan lava basalts. The Panvel Flexure, on the other hand, is syntectonic with the younger flows (Wai subgroup) of the Western Ghats Deccan volcanism (Auden, 1949) and is interpreted here as the faulted outer rim of the Shiva Crater (Chatterjee, 1992). Three volcanic subprovinces are identified within the Deccan associated with these rift systems: the Narmada subprovince, north and south of the Narmada Rift including the outlier of Rajahmundry in the Godavari Basin; the Saurashtra subprovince, covering the Deccan exposures in Saurashtra, west of the Cambay Rift; the Western Ghats subprovince, including the thick volcanic sequence east and west of the Panvel Flexure. The boundary between the Narmada and Western Ghats subprovinces is somewhat diffuse and can be demarcated in the field by mineralogy and the nature of the lava flow. A combination of field mapping with petrochemical and isotopic studies permits division of the thick lava pile of the Western Ghats section into 3 subgroups (Kalsubai, Lonavala & Wai) and 12 formations, with a progressive decrease in age from north to south (Beane et al., 1986; Hooper et al., 1988). Similarly, Subbarao et al. (1988) recognized 3 new formations in the Narmada region (Narmada, Manpur & Mhow), but their relationships with the Western Ghats section is not clear.

TIMING AND DURATION OF DECCAN VOLCANISM. The temporal coincidence of the main pulse of the Deccan volcanism with the KT boundary led many authors to believe that a major asteroid impact might have initiated this massive volcanism (Alvarez et al., 1982; Rampino, 1987; Alt et al, 1988; Negi et al., 1993; Chatterjee & Rudra, 1993). However, critics have pointed out that the Deccan volcanism started at least a million years before the impact event, making the causal relationship less likely (Courtillot, 1990; Sutherland, 1994; Alvarez et al., 1994; Bhandari et al., 1995). The possible link between the KT extinction and the Deccan flood basalts has spurred detailed analyses to determine the timing

and duration of Deccan volcanism from radiometric, palaeomagnetic and palaeontologic constraints. We have also sampled various Deccan stratigraphic sections to determine the KT boundary event layer. Here we synthesize all available data to estimate the absolute age and age span of the Deccan volcanism in the context of its origin and subsequent influence on the biotic crisis at the KT boundary.

Geochronology. Because of the altered nature of the Deccan basalt, previous attempts to determine its age by K/Ar method were unsatisfactory, with results ranging from 102 to 30Ma (Alexander, 1981). However, recent $^{40}Ar/^{39}Ar$ dates of the stratigraphically controlled thick sequence of the Western Ghats section cluster around a narrow span of age from 69 to 64Ma, with a major eruptive phase around 65Ma (Duncan & Pyle, 1988; Courtillot et al, 1988; Venkatesan et al., 1993; Baksi, 1994). Although a close temporal correspondence between the main pulse of Deccan volcanism and the KT boundary is indicated by isotope dating, early phases of eruption may have started at least 1Ma before the KT event.

Palaeomagnetism. Recent palaeomagnetic studies indicate that only 3 magnetic chrons (30N, 29R, & 29N) are represented in the thick Deccan lava pile, where the main eruptive phase in the Western Ghats section corresponds with chron 29R (Gallet et al., 1989; Courtillot, 1990; Vandamme & Courtillot, 1992). This normal-reversed-normal (NRN) magnetostratigraphy appears to be a powerful tool in correlating widely separated Deccan basalt provinces. Palaeomagnetic results support a shorter span of Deccan volcanism, from 67 to 64Ma, centered around chron 29R (65Ma). In this case, the whole eruptive history would cover only 1-2Ma.

Palaeontology. Palaeontologic evidence comes from thick fossiliferous sedimentary beds associated with the basaltic flows. These interbeds are traditionally named according to their physical position relative to the basal Deccan flow; they may underlie the flows (infratraps, such as the Lameta Beds) or they may be intercalated within the flows (intertraps). Stratigraphically infratraps are believed to be older than the intertraps (Krishnan, 1982, p. 415). This distinction is not clear-cut in regional biostratigraphic analysis. Local infratrappean beds may appear intertrappean in large-scale mapping. Sahni & Khoshla (1994) proposed a neutral term, 'Deccan basalt volcano-sedimentary sequence' (DBVSS) for these trappean beds. These sedimentary beds occur marginal to the Deccan outcrops in the

Narmada and Saurashtra subprovinces, indicating that these vast thicknesses of lava flows were not extruded all at once; volcanic activity was punctuated periodically. In between the flows are fluvial or lacustrine deposits of trappean beds that contain abundant remains of plants, invertebrates, dinosaurs and their eggs. We made extensive sampling of these trappean beds in search of the iridium anomaly, shocked quartz and tektites to detect the KT boundary layer, but the results were negative, reinforcing the palaeontologic observations that most of these trappean sediments are older than the KT boundary. Palaeontologic evidence drawn from palynoflora *Aquilapollenites*, charophytes, non-marine ostracods, the selachian *Igdabatis*, pelobatid frogs, anguid lizards, booid snakes, pelomedusid turtles, abelisaurid, titanosaurid and ankylosaurid dinosaurs and palaeoryctid mammals indicate a Maastrichtian age for these trappean beds, but the upper limit is unknown (Sahni & Bajpai, 1988; Chatterjee, 1992). More precise data comes from oil-exploration wells in the Godavari Basin, where the Narsapur well has encountered KT boundary flows (Govindan, 1981). Here the lower marine intertrap has yielded the planktonic zone fossil *Abathomphalus mayaroensis* of Late Maastrichtian age, whereas the upper post-trappean bed contains *Globorotalia praecursoria* of the P2 planktonic foraminifera zone of Early Palaeocene age. Palaeontological data define broad limits of Deccan volcanism from 67.5 to 60.5Ma in the Godavari Basin.

Stratigraphic Calibration. A schematic correlation of Deccan Trap sequences between the western Ghats and the Narmada/Saurasthra subprovinces is shown in Fig. 10, combining radiometric, palaeomagnetic and palaeontologic data. The following observations can be made:

1) The volcanism north of the Narmada Rift started somewhat earlier than the southern part. The Lameta beds are restricted to the north of this lineament and provide palaeontological control on the onset of volcanism. So far, only one magnetic chron, 30N, has been identified in this region associated with the infratrap (Sahni & Bajpai, 1988). In the Bara Simla section of Jabalpur, north of the rift zone, the Deccan flow overlying the dinosaur-bearing Lameta Group shows normal polarity (30N). This flow has not yet been dated by the Ar-Ar technique. Dinosaur bones, nesting sites, microvertebrates, palynoflora *Aquilapollenites* and the selachian *Igdabatis* suggest a Maastrichtian age for the Lameta Beds (Chatterjee, 1992; Jaeger et al., 1989; Sahni &

Bajpai, 1988; Sahni et al., 1994). Sauropod nesting sites occur in a specific lithotype, a pedogenically modified sandy carbonate that forms a distinct marker bed. This egg-bearing bed can be traced for almost 1,000km, from Balasinor, Dohad and Hathni to Jabalpur in the northern part of the Narmada Rift (Mohabey, 1984, 1987; Srivastava et al., 1986; Sahni et al., 1994).

2) The 670m thick volcanic sequence at Kalghat-Mhow region, north of the Narmada lineament, lacks infratraps but shows three trap formations (Narmada, Manpur and Mhow) with normal (30N) and reverse (29R) chrons (Subbarao et al., 1988; Vandamme & Courtillot, 1992) and can be equated with the Western Ghats section.

3) The Saurashtra subprovince is not well constrained in age by palaeontological and palaeomagnetic analysis. Here the Deccan Traps overlie the 50m marine sequence of Late Cretaceous Wardhan Member and can be correlated with the volcanics of the northern part of the Narmada Rift (Biswas, 1988).

4) South of the Narmada lineament, in the Nagpur-Umrer-Dongargaon intertrappean beds, a thick sequence of reverse polarity (29R) is followed by a normal sequence (29N) (Sahni & Bajpai, 1988). In these intertraps dinosaur bones, fragmentary eggshells and microvertebrates of Late Maastrichtian are common. In Dongargaon the basal flow has yielded a precise Ar-Ar plateau age of 66.4±1.9Ma (Duncan & Pyle, 1988).

5) Vadamme & Courtillot (1992) reported a 29R-29N reversal chron from the Rajahmundry outcrop. Geochronological studies suggest an age of ~64Ma coeval with 29N chron (Baksi et al., 1994). In the Narsapur well, trappean beds can be tied to two foraminiferal zone boundaries in the type KT boundary sections of Italy (Alvarez et al., 1987; Govindan, 1981): the lower, infra-trap bed correlates with the *Abathomphalus mayorensis* zone (Maastrichtian), while the upper, post-trap bed corresponds with the *Globorotalia praecursoria* of P2 zone (Early Palaeocene).

6) The thick flows of Deccan volcanism in the Western Ghats sections show three subgroups (Kalsubai, Lonavla, and Wai) and are well-constrained by radiometric and palaeomagnetic data; volcanic activity was short-lived and reached its major peak of activity during chron 29R (~65Ma), followed by a short interval of chron 29N. Lack of trappean beds makes it impossible to estimate the age of Western Ghat sections by palaeontological methods.

7) A definite KT boundary section with iridium anomaly has been identified recently in the inter-trappean beds of Anjar in Kutch, where radiometric ages of the traps cluster around 65Ma (Bhandari et al., 1994). As discussed earlier, we believe this section of alkaline basalt flows is directly related to the impact event.

8) The duration of Deccan volcanism may range from 67.5 to 60.5Ma (palaeontologic constraints), from 69 to 64Ma (geochronologic constraints), or from 67 to 64Ma (palaeomagnetic constraints). Thus the minimum age range of eruption may be around 67Ma to 64Ma, about 3My in duration.

9) Because of the presence of foraminiferal zones and magnetic reversal chrons, the Deccan stratigraphic sequence can be equated with the magnetostratigraphic type section of the KT boundary at Gubbio, Italy (Alvarez et al., 1987).

ORIGIN OF DECCAN VOLCANISM. A cause-and-effect connection between impact and Deccan volcanism has been the subject of extensive discussion and speculation. If the Deccan volcanism started 1Ma before the KT boundary event, and extended over 3Ma, as combined evidence of isotopic dating, magnetic anomalies and palaeontology suggests, then the Shiva impact did not initiate the Deccan volcanism. Deccan volcanism predated the impact event (Courtillot, 1990; Sutherland, 1994; Bhandari et al., 1995). Impact and Deccan volcanism are independent, having occurred by chance at about the same time. Deccan volcanism was already active when when the KT mpact occured near the Bombay coast. However, the impact might have shaken the Earth's mantle violently to enhance the spectacular Deccan outburst precisely at the time of the KT boundary.

The spatial and temporal coincidence of Deccan volcanism with the Carlsberg Rift and the Reunion hotspot activity at the KT boundary sheds critical insights into its origin. The enormous thickness of the lava pile in the Western Ghats sections associated with compound flows and ash beds indicate that the major eruptive source for Deccan volcanism must be located near the Bombay area, where evidence of both hotspot and rift magmatism are present. There has always been controversy as to whether the plume or rifting was the initiating factor for the Deccan volcanism. This conflict can be resolved if we can determine accurately the timing of initial eruption and duration of Deccan volcanism. Morgan (1981) proposed that the Deccan flood basalts

were the first manifestation of the Reunion hotspot that subsequently produced the hotspot trails underlying the Laccadive, Maldive and Chagos islands; the Mascarene Plateau; and the youngest volcanic islands of Mauritius and Reunion. Recent DSDP data confirm that the age of the volcanism decreases from north to south, from the Deccan to the Reunion hotspot (Backman et al., 1988). Thus the geometry and the age range of these volcanic provinces, islands and submarine ridges are consistent with the rapid northward motion of the Indian plate over a fixed hotspot (Morgan, 1981; Duncan & Pyle, 1988).

Although the hotspot model is very attractive in explaining the Deccan flood basalt volcanism and linear volcanic chains of the western Indian Ocean, there are distinctions in both trace element and isotope geochemistry between present-day Reunion eruptives and those of the Deccan province; the likely source of the Deccan volcanism is similar to rift volcanism rather than the Reunion hotspot (Mahoney, 1988). Further geochemical and geothermal evidence suggests that Deccan magmas were generated at relatively shallow (35-45km) depth in Mid-Ocean Ridge Basalt (MORB) mantle and rules out the possibility of its origin by a deep mantle plume (Sen, 1988). However geophysical evidence indicates that the continental crust was extremely thin in the Western Ghats section under the plume (Negi et al., 1993). Morever, Ellam (1992) showed convincingly that the thinned lithosphere of Western Ghats is the reason for this trace element discrepancy between the Deccan volcanism and the Reunion hotspot.

Was rifting triggered by doming above the Reunion hotspot? Some workers (White & McKenzie, 1989; Hooper, 1990) argued that the Reunion hotspot actually created the Carlsberg rift along which Deccan volcanism erupted. However, as discussed earlier, the Carlsberg rifting did not start before chron 29R, whereas Deccan volcanism started somewhat earlier around 30N. If the Sarnu-Dandali and Mundawara volcanics of Rajasthan are regarded as the earliest manifestation of the Deccan volcanism in Peninsular India and the initial location of the Deccan-Reunion hotspot (Basu et al., 1993), then the Deccan volcanism must have started 3.5 million years earlier than the timing of the Carlsberg Rift, making the causal link unlikely. Moreover, if the Carlsberg Rift was triggered by the Deccan-Reunion hotspot, its geographic location would be at the center of the Shiva Crater, offshore of the Bombay coast. However, the hotspot track

indicates that the Reunion hotspot always lay farther east within the Indian continent, probably near Igatpuri at the KT boundary (Fig. 9). If we consider the Rajasthan volcanics as the earliest and northernmost activity of the Reunion hotspot, it would be at least 500km northeast from the Carlsberg Rift at the time of eruption. Thus the timing of the eruption and the location of the Reunion hotspot do not suggest any close link between plume generation and rifting. On the other hand, at the KT boundary time, the impact had been coincidentally close enough to the Reunion hotspot to activate the major phase of the volcanic outbursts (Figs. 7A, 9). Reviewing all the evidence, the Deccan-Reunion hotspot remains the best model for the origin of Deccan volcanism.

How did the Deccan lava cover such an enormous area of India? The interconnected rift basins may be implicated in the distribution of Deccan lavas. Prior to the onset of Deccan volcanism the palaeodrainage of the Narmada and Godavari Rivers was directed toward the Bay of Bengal (Krishnan, 1982, p. 17). The Cambay Rift basin was tilted northward and westward at that time (Biswas, 1987). This centripetal pattern of drainage system was further accentuated by doming of the Western Ghats section around Igatpuri by the uprising plume (Fig. 9). Lava generated from the Deccan-Reunion hotspot flooded the Narmada, Cambay and Godavari rift basins. These lava rivers traveled many hundreds of kilometers in all directions with occasional flooding in the overbank areas. The main reason these flows could travel such great distances is their unusually large volume and rapid rate of eruption, coupled with their low viscosity. The
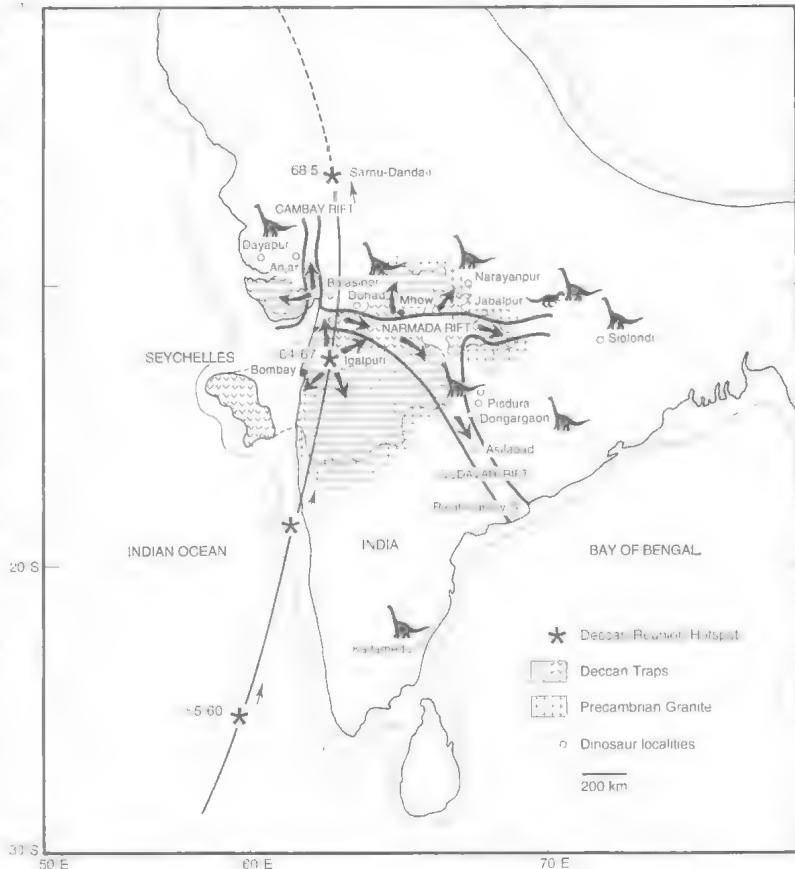

FIG. 9. Sketch map showing the localities of Maastrichtian dinosaurs around the Deccan volcanic province before the impact event; microcontinent Seychelles was adjacent to India; asterisks indicate the Deccan-Reunion hotspot track during the rapid northward drift of India. During Maastrichtian, the Deccan-Reunion hotspot was located near Igatpuri forming a domal structure with centripetal distribution of lavas; bold arrows indicate the possible directions of intercanyon flows of Deccan lavas along the drainage of the Narmada, Godavari and Cambay basins. Intercanyon flows may explain large areal distribution of Deccan Traps.

final distribution of the Deccan Traps may reflect the topography at the time of distribution and the palaeosplope of these interconnected rift basins (Fig. 10). Similar long-distance intercanyon flows are known from the Columbia Plateau basalt of western United States, where the Pomona Member of the Saddle Mountain Basalt flowed down the ancestral Columbia River from north-central Idaho to the Pacific Coast (Hooper, 1992).

MAASTRICHTIAN DINOSAURS OF INDIA

Although dinosaur (implying nonavian dinosaur throughout the text) extinction was a
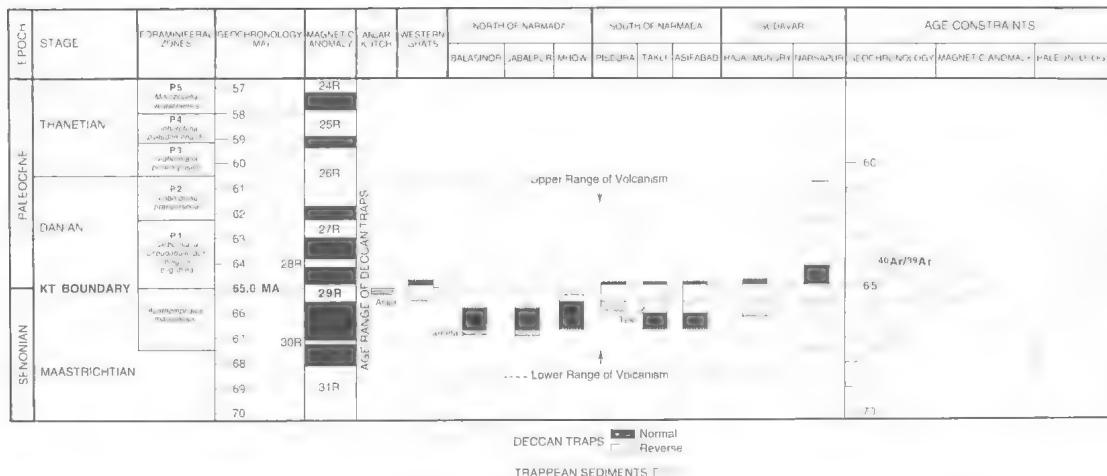
FIG. 10. Stratigraphic correlation of Deccan volcanic provinces in relation to KT boundary by geochronologic, palaeomagnetic and palaeontologic constraints. The minimum age span of Deccan volcanism may range from 67Ma to 64Ma; (data from Vandamme & Courtillot, 1992; Harland et al., 1989; Jaeger et al., 1989; Subbarao et al., 1988; Sahni & Bajpai, 1988; Chatterjee, 1992; and personal observations).

global phenomenon, there are very few places in the world where dinosaur-bearing sediments document the crucial KT boundary events; most of these exposures are known only from western North America (Wyoming, Montana, Alberta, Saskatchewan, Colorado, New Mexico and Texas), Mongolia and India. As a result, the tempo of dinosaur extinction, whether sudden or gradual, has been debated intensely (Clemens, 1982; Sloan et al., 1986; Sheehan et al., 1991). In this context, Indian biostratigraphic evidence may play a crucial role, since most of the dinosaur bones are known almost exclusively from the Deccan volcano sedimentary sequence such as Lameta Group which was deposited close to the KT boundary time. In the KT boundary section of Anjar, Gujrat, the last dinosaur bones occur precisely at the iridium layer. This is probaly a unique biostratigraphic evidence for a sharp truncation of dinosaurs supporting the sudden extinction event.

Maastrichtian dinosaurs from India are extremely rare. Some fragmentary remains of dinosaurs are also known from the Kallamedu Formation of Tamilnadu, South India (Fig. 9). Most of the Lameta dinosaurs came from a single quarry on the western slope of Bara Simla Hill of Jabalpur. This quarry in 1917-19 produced various dinosaurs including titanosaurids, coelurids, ornithomimids, allosaurids and ankylosaurids (Huene & Matley, 1933). Although the fauna from the Lameta Group indicates a moderate diversity of dinosaur community that

inhabited India as it collided with Asia near the very end of the Cretaceous, most of these bones are fragmentary limb, girdle and vertebral elements which have few diagnostic characteristics. Furthermore, all of the previous Lameta dinosaur collection, housed at the Geological Survey of India, Calcutta and the Natural History Museum, London, has been missing for the last 50 years. Thus the affinity of Indian Maastrichtian dinosaurs has never been thoroughly investigated in recent time because of lack of material. The only valuable specimen remaining from the early collection is a partial skull of a juvenile theropod *Indosuchus*, now at the American Museum of Natural History (AMNH 1955), collected by Barnum Brown in 1922 and subsequently described by Chatterjee (1978).

During the past thirty years, many attempts had been made to locate this important quarry at Bara Simla Hill without any success. The site was covered with thick vegetation, and no landmarks or quarry maps of the original excavation survive. In 1988, we found this classical site and began exploring. A preliminary excavation has uncovered the original bone beds with sauropod and theropod remains, but most of the new material is yet to be prepared. We collected a partial skeleton of a large titanosaurid associated with limbs, girdles, vertebrae and a beautiful braincase. The large size (femur more than a meter long), undivided cervical neural spine, and strongly procoelous caudal vertebrae establish its titanosaurid affinity. In addition, several cranial

fragments of *Indosuchus* were also recovered. In 1995, we discovered a rich graveyard of dinosaur bones in the mudstone facies of the Lameta Group near Raiholi village of Gujrat, western India. The most remarkable discovery from this quarry represents a nearly complete skeleton of a large theropod, about the size of *Allosaurus*. We have also collected various bones of titanosaurs and ankylosaurs from this quarry. Abundant sauropod eggs were also found from adjacent Dohad locality (Fig. 9). Finally, we have traced the missing dinosaur bones from Jabalpur described by Huene & Matley (1933) at the Indian Museum, Calcutta, last year. With this new information, we hope to get a first good look at the last dinosaurs in India. Here we provide a preliminary description of the new finds to evaluate the systematics of Indian Maastrichtian dinosaurs.

SAURISCHIAN DINOSAURS.

Sauropoda: Family Titanosauridae Lydekker, 1885. Titanosaurids were first recognized from the Late Cretaceous of India by Richard Lydekker in 1877 on the basis of their peculiar procoelous caudal vertebrae, and were later found in contemporaneous beds in South America, North America, Africa, Madagascar, Europe and Asia. They were among the largest dinosaurs that ever lived, but their origin and relationships are poorly understood, in part because no good skulls are known. They were the dominant herbivores of Gondwana during the Cretaceous, but radiated into Laurasian continents. The titanosaurids are characterized by vertebral attributes, especially by short cervicals, undivided neural spines in anterior dorsals, 6 sacrals and procoelous caudals (McIntosh, 1990). One of the most intriguing features of titanosaurids is the presence of body armor in the form of bony scutes and knobby dermal bones, known from *Saltasaurus* from Argentina (Bonaparte & Powell, 1980). There is no doubt that the dermal ossicle collected by Barnum Brown (AMNH 1359) from the Bara Simla locality, which was attributed to stegosaurs (Huene & Matley, 1933) and ankylosaurs (Coombs, 1978), actually belongs to titanosaurids.

Huene & Matley (1933) described two titanosaurid genera from the Lameta Group, based on size differences: the gracile-*Titanosaurus indicus*, Lydekker and a new robust species, *Antarctosaurus septentrionalis*. They figured a partial braincase of *Antarctosaurus* which compares well with *A. wichmannianus* of South America. However, the braincase of Indian *Titanosaurus* was unknown at that time. Later,

Berman and Jain (1982) described the braincase of a small titanosur from the Lameta Group at Dongargaon and concluded that new braincase is fundamentally different from *Antarctosaurus*. The associated postcranial material collected from the site, especially vertebrae, resembles that of *Titanosaurus indicus* (Jain, 1989). It is likely that the Dongargaon braincase belongs to *T. indicus* (Jain, pers. comm.). Thus, from the braincase morphology and postcranial characteristics, the coexistence of at least two titanosaur genera, *Antarctosaurus* and *Titanosaurus*, in the Lameta Group can be established. This conclusion is further strengthened with the discovery of two additional braincases, one belonging to *Titanosaurus*, the other to *Antarctosaurus*, which are described below. Braincases are conservative which makes them excellent tools for identifying taxa; they are less susceptible to convergences that characterise skeletal features associated with feeding and locomotion. Using braincase morphology as a guide, the distinction between *Titanosaurus* and *Antarctosaurus* appears very clear-cut. In *Titanosaurus* the basipterygoid processes are extremely short, reduced and lie almost at the level of basal tubera; moreover, the parocicipital processes are wide and moderately curved ventrally. In *Antarctosaurus*, the basipterygoid processes are very long, slender and directed considerably ventrally below the level of the basal tubera. The paroccipital processes in this genus are narrow and highly curved downward. In sauropods, the nature of the basipteryoid process is intimately linked to the attitude of the quadrate; the short basipterygoid process is associated with the vertical quadrate, whereas the long basipterygoid process indicates highly slanting quadrate.

Antarctosaurus septentrionalis Huene & Matley, 1933. The new braincase (ISI R 162) recovered from Bara Simla site is beautifully preserved and provides a wealth of anatomical information. All the bones are tightly sutured so demarcation of individual elements is difficult. Although the braincase described by Huene and Matley (1993, Fig. 5) as *Antarctosaurus septentrionalis* is fragmentary, the preserved part shows close resemblance to the new material, especially in the construction of basipterygoid process and paroccipital process. The new specimen probably belonged to a young individual, as it lacks the laterosphenoid, orbitosphenoid and skull roof. In this respect, this specimen is very similar to that of a French
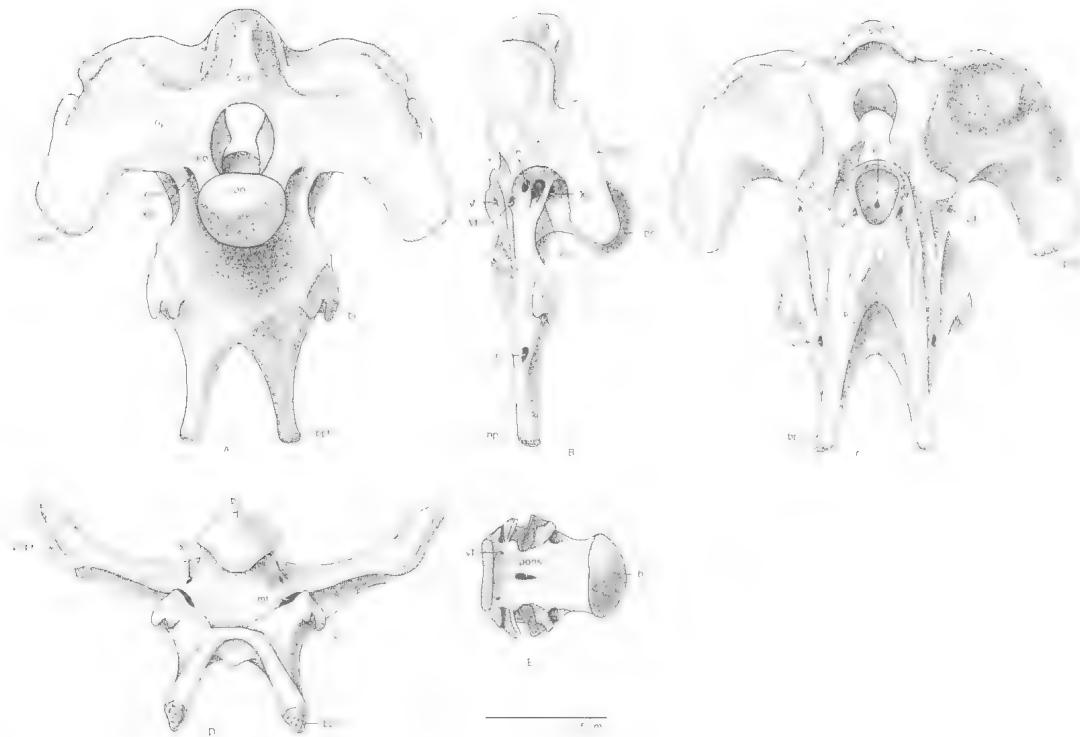
FIG. 11. Braincase of *Antarctosaurus septentrionalis*, a sauropod from the Lameta Group of Jabalpur, based on ISI R 162; A, caudal view; B, lateral view; C, rostral view; D, ventral view; E, dorsal view of basioccipital showing pons varioli. bo=basioccipital, bpt=basipterygoid process, bs=basisphenoid, bt=basal tubera, eo=exoccipital, fo=fenestra ovalis, ic=internal carotid artery, mf=metotic foramen, op=opisthotic, pif=pituitary fossa, popr=paroccipital process, pro=prootic, soc=supraoccipital; foramina for cranial nerves in Roman numerals.

titanosaurid (Loeuff et al., 1989), which also lacks the anterior and dorsal parts.

The braincase is short and extremely deep so that the basioccipital and the basisphenoid are telescoped (Fig. 11). The most outstanding feature is the highly enlarged basipterygoid processes, which are slender and directed downward as in several other titanosaurid genera such as *Amargosaurus*, *Nemegtosaurus* and *Saltasaurus*, (McIntosh, 1990). On the lateral wall of the basipterygoid process, at the level of the basal tubera, the openings for the canals of the internal carotid artery are visible. These tunnel through the bone and emerge at the base of the pituitary fossa through separate openings. The pituitary fossa is deep on the dorsal surface of the basisphenoid. The posterior wall of the fossa, the dorsum sellae, is pierced laterally by a pair of openings for the abducens (VI) nerves. On the lateral wall of the braincase, there are two prominent foramina at the middle ear region: the caudal one, the metotic foramen is very large and transmitted nerves IX-

XI and the caudal branch of the jugular vein; the rostral one, the fenestra ovalis, is relatively small to receive the stapes. Rostral to the fenestra ovalis is a small aperture indicating the outlet for the facialis (VII) nerve. Farther rostrally each prootic is notched by the trigeminal foramen (V) which would be enclosed by the laterosphenoid. Both laterosphenoid and orbitosphenoid bones are missing in our specimen. In the occiput, the strong nuchal crest on supraoccipital and obliteration of sutures between the exoccipitals, the supraoccipital and the basioccipital, can be seen. The paroccipital processes are narrow, wing-like structures extending outward and considerably downward. The occipital condyle is large and spherical. Each exoccipital bone near the lower rim of the foramen magnum is pierced by a foramen for the hypoglossal (XII). At the floor of the braincase, the basioccipital shows a median cavity for the pons variolii (Fig. 11).

Titanosaurus indicus Lydekker, 1877. Berman & Jain (1982) described a sauropod braincase (ISI
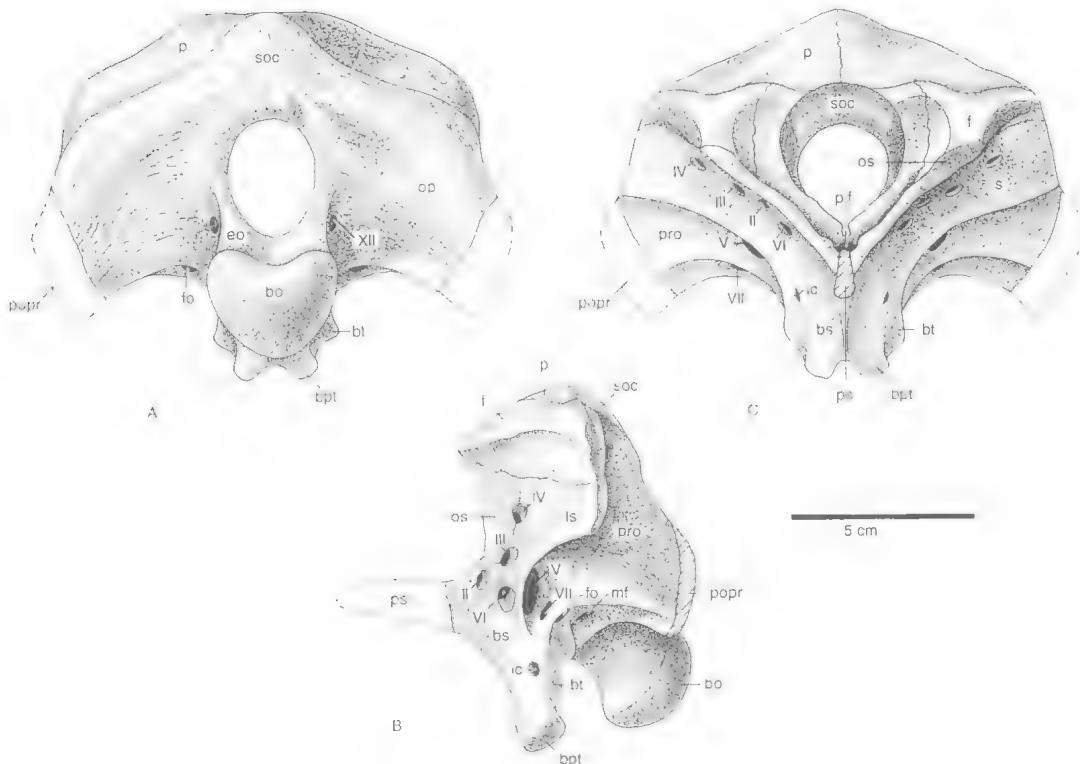
FIG. 12. Braincase of *Titanosaurus indicus*, a sauropod from the Lameta Group of Raiholi, based on ISI R 467. A, caudal view; B, lateral view; C, rostral view. Abbreviations as in Fig. 11; f=frontal, ls=laterosphenoid, os=orbitosphenoid, p=parietal, ps=parasphenoid rostrum.

R 199) from the Dongargon which was later assigned to *Titanosaurus indicus* (Jain, pers. comm.). The specimen is not well-preserved which makes the detailed interpretation somewhat difficult. This deficiency is remedied by the discovery of a better specimen from Raiholi site (ISI R 467). The new specimen is very similar to the Dongargaon specimen in size and morphology (Fig. 12), but fundamentally different from that of *Antarctosaurus*.

As in all sauropods, the braincase is completely ossified. The occipital condyle is hemispherical except for being somewhat concave dorsally to give a kidney-shaped appearance. Ventrally, the basal tubera are subdued and completely fused with the basipterygoid processes. The basipterygoid processes are very small and closely appressed. The foramen magnum is somewhat oval and smaller than the occipital condyle. At the base of the foramen magnum, each exoccipital is pierced by a single canal for cranial nerve XII. In Dongargaon specimen, there is a prominent

protuberance on the occipital bone representing the articular facet of proatlas. This feature is lacking in our specimen. The opisthotic is intimately fused with the exoccipital; it is directed laterally and somewhat ventraly as a robust wing of paroccipital process. The supraoccipital is fairly massive and forms the dorsal roof of the foramen magnum. Laterally it is overlapped by a ventral flange of the parietal.

In lateral aspect, the cranial foramina are beautifully preserved. In the middle ear region two foramina are visible; the rostral, smaller one is the fenestra ovalis; the caudal, large one is the metotic foramen for nerves IX-XI. Farther rostrally the large foramen, shared between the prootic and laterosphenoid, is the trigeminal opening for nerve V. Ventral to it, the entrance of the internal carotid artery to the pituitary fossa can be seen at the base of the basipterygoid process. Rostral to trigeminal foramen, three foramina are visible in a vertical row in the laterosphenoid-orbitosphenoid-basisphenoid complex.

The dorsal foramen indicates the exit for nerve IV, the middle one for nerve III and the ventral one for nerve VI. At the base of the parasphenoid rostrum a large opening within the orbitosphenoid indicates the lateral aperture for nerve II. In rostral aspect the fused orbitosphenoid-basisphenoid complex narrows considerably to form a median vertical ridge as seen in a Romanian titanosaurid specimen (Weishampel et al., Fig. 15). Dorsal to the parasphenoid rostrum, the large cavity indicates the pituitary fossa.

Theropoda. Huene & Matley (1933) described two large predatory dinosaurs from the Lameta Group of Jabalpur. *Indosuchus raptorius* and *Indosaurus matleyi* as late survivors of allosaurs. Both taxa are known from partial skull fragments as well as several postcranial elements. The distinction between *Indosuchus* and *Indosaurus* was based on the structure of the fronto-parietal region. In *Indosuchus*, the fronto-parietal region has a narrow crest as seen in tyrannosaurs. The skull roof is flat between the orbits and the postfrontal is smooth. In *Indosaurus*, on the other hand, the parietal is broad, the lower surface of the frontal is wide and the transverse crest lies above and below the orbit. The frontals are concave and decline in front. The supratemporal fossa is short and broad as in allosaurs. Huene & Matley also described a maxilla of *Indosuchus* which is identical to a similar element collected by Barnum Brown in 1922 from the Lameta Group (AMNH, 1955). Later, Chatterjee (1978) described partial jaws of AMNH specimens of *Indosuchus* as a juvenile tyrannosaurid, partly on the basis of narrow fronto-parietal crest, elongated supratemporal fossae, incisiform premaxillary teeth and similar dental formula. He accepted *Indosaurus* as an allosaurid.

The classification of *Indousuchus* and *Indosaurus* has been difficult in the past because of fragmentary material. Despite marked similarities to tyrannosaurs, *Indosuchus* is characterized by the absence of preantorbital fenestrae in the maxilla. Bonaparte & Novas (1985) described a large skull of a new theropod, *Abelisaurus comahuensis*, from the Maastrichtian Allen Formation of Rio Negro, Argentina. Later, Bonapart et al. (1990) described a virtually complete, articulated skeleton of another theropod, *Carnotaurus sastrei*, from the Middle Cretaceous Gorro Frigio Formation of Argentina. *Carnotaurus* shows unusual frontal horns. Its forlimbs are highly reduced, with extremely short radius and ulna. Bonaparte and associates placed

Abelisaurus, *Carnotaurus* and *Indosuchus* in the same family, Abelisauridae. This family is defined by large infratemporal fenestra, elongated quadrate, posteriorly directed squamosal with a ventral, rod-like process and a small maxillay fenestra near the preorbital opening. Comparison of *Abelisaurus* and *Indosuchus* clearly indicates close similarity between these two genera. *Indosuchus* is not a tyrannosaurid as was supposed earlier, but possibly an abelisaurid. Although abelisaurs were the dominant predators throughout Gondwana during the Cretaceous Period, our knowledge of these enigmatic theropods is still limited. The occurrence of a supposed abelisaur in the Late Cretaceous of France has been recognized recently (Buffetaut et al., 1988). Although abelisaurids superficially resemble large predatory dinosaurs such as allosaurs and tyrannosaurs, they are more primitive, probably a separate lineage evolving from ceratosaurs.

Various small coelurosaurs described from the Bara Simla quarry by Huene & Matley (1933), such as *Jubbulpuria tenuis* and *Laevisuchus indicus* are intriguing. We need additional material to assess their relationships.

Family Abelisauridae Bonaparte & Novas, 1985. Indosuchus raptorius Huene, 1933. The type specimen of *Indosuchus raptorius*, now housed at the Indian Museum, Calcutta is allocated to this species. Some of our recent finds may also belong to this species. For example, we have collected additional cranial bones of *Indosuchus*, such as the lacrimal, jugal and posterior part of the jaw (ISI R 163) from the Bara Simla Hill of Jabalpur. Furthermore, we have unearthed a nearly complete skeleton of *Indosuchus* from Raiholi site of Gujrat. The teeth are compressed laterally and serrated; the tooth crown is extremely low; the ratio of the crown height to rostro-caudal width is 1.5. The vertebrae are amphicoelous but lack pleurocoels. The scapulocoaracoid is narrow with a prominent acromion process. The forelimb is short relative to the hindlimb; the ratio to femoral to humeral length is about 2. Unlike *Carnotaurus* and *Tyrannosaurus*, the forelimbs of *Indosuchus* were as along as in allosaurs. Unfortunately, the postcranial elements of *Abelisaurus* are unknown. The iliac blade of *Indosuchus* has a deep preacetabular and long postacetabulr process; the pubis is expanded distally to form a foot. The hindlimb bones are hollow, thin-walled, stout and resemble the corresponding elements of *Carnotaurus*. The femur has a spherical, inturned
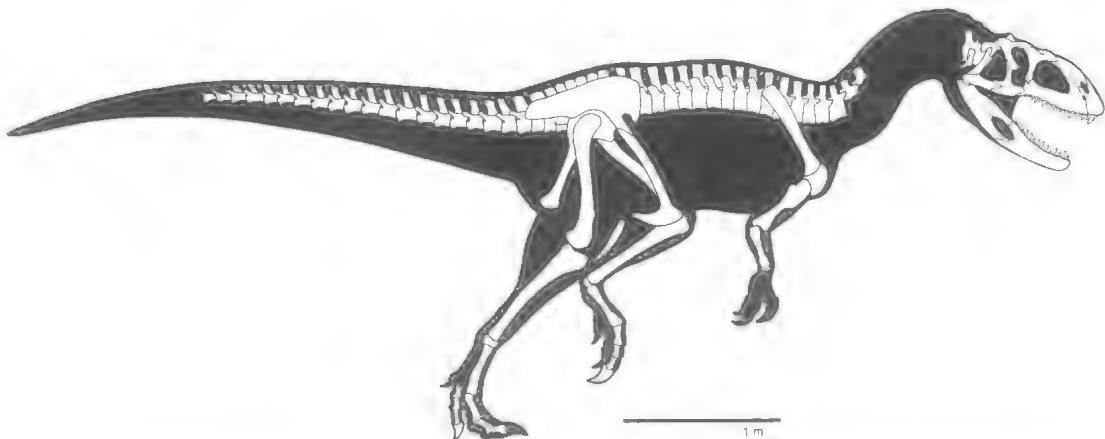
FIG. 13. Skeletal restoration of *Indosuchus raptorius*, a theropod from Raiholi site, showing preserved bones; skull modified from Chatterjee (1978). Restoration is based on disarticulated elements (ISI R 401 - 454).

head with a distinct neck. The lesser trochanter is fairly well-developed but lower than the greater trochanter. The tibia is robust with a distinct cnemial crest; distally it remains unfused with the astragalus. The astragalus is hemicylindrical in form, but its ascending process is relatively short. A preliminary skeletal reconstruction of *Indosuchus* is shown in Fig. 13 and restoration of the skull in Fig. 14.

Indosaurus matleyi Huene 1933. Another theropod partial skull from the Bara Simla quarry, *Indosuchus matleyi*, is generally allied to Allosauridae (Huene & Matley, 1933; Chatterjee, 1978), but Molnar (1990) pointed out some attributes in *Indosaurus* similar to those of *Carnotaurus* of Argentina and allocated it to Abelisauridae. Recently we have collected a *Carnotaurus*-like atlas-axis complex from the Lameta Group of Raiholi area, which strengthens Molnar's assessment.

ORNITHISCHIAN DINOSAURS. Various ornithischian fragments have occasionally been reported from the Late Cretaceous of India, but their identity is dubious except for the ankylosaurian *Lametasaurus*.

Ankylosauria. *Lametasaurus indicus* Matley 1923. *Lametasaurus* is known from the sacrum ilia, tibia, spine and armor (Matley, 1923; Huene & Matley 1933). It is a fossil chimera of mistaken association containing parts of two different dinosaurs: armour fragments often attributed to stegosaurs, nodosaurs (Huene & Matley, 1933), or ankylosaurs (Coombs & Maryanska, 1990), whereas sacrum, ilia and tibia probably belong to

theropods (Chakravarti, 1935), such as abelisaurids (Molnar, 1990). Yet Huene & Matley mentioned, but did not figure, two additional types of dermal scutes from the same bed that could be ankylosaurian (Galton, 1981). Recently we have recoverd definite remains of an ankylosaur from the Raiholi site. The new material represents isolated vertebrae, scapulocoracoid, humerus, femur and several pieces of armor such as hollow lateral spikes and solid dorsal scutes, typical of ankylosaurs, which will be described in a separate paper.

Stegosauria nomen dubium. *Dravidosaurus blanfordi* Yadagiri & Ayyasami (1979). A small, late surviving stegosaur was described from the marine Cretaceous *Kossmaticeras theobaldianum* Zone Trichinopoly Group by Yadagiri & Ayyasami (1979). In 1991, we visited the site and found only fragmentary remains of plesiosaurs. We also examined the holotype and could not see anything related to the stegosaurian plates and skull claimed by these authors. Instead, the bones are highly weathered limb and girdle elements and may belong to plesiosaurs.

DISTRIBUTION OF DINOSAURS. It appears from the above discussion that Indian Late Cretaceous dinosaurs remain rather poorly known. Fossil records indicate that they lived around the fringe of the Deccan volcanic province and adapted to the harsh environments (Fig. 9). Yet this distribution reflects an artifact of preservation because of unusual protection of intertrappean beds by the Deccan basalts. Most of the nonmarine Cretaceous deposits in penin-

sular India were removed by erosion except for the little patch in the Kallamedu area near Madras. As a result, the extent of dinosaur distribution, other than in the Deccan volcanic province, is unknown. Although Masstrichtian dinosaurs have been reported from all Gondwana continents including Antarctica, reasonably complete skeletons have been recovered only from South America. The disjunct distribution of the titanosaurid-abelisaurid assemblage in South America, India and Europe is interesting in the context of drifting continents in Late Cretaceous time. Palaeontologic evidence suggests that the India/Eurasia collision took place during this time, facilitating the migration of northern fauna to India (Chatterjee, 1992; Jaeger et al., 1989; Prasad et al., 1994). Isolation between the northern and southern continents produced dramatically different distributions among dinosaurs. In contrast to the nothern hemisphere, the dominant herbivores in the Late Cretacous of India and South America were titanosaurids rather than ornithischians, whereas the large predators were abelisaurids instead of tyrannosaurs (Fig. 15).

FIG. 14. Composite restoration of the skull of Indosuchus raptorius, an abelisaurid theropod from the Lameta Group; left lateral view; based on AMNH 1753, 1955, 1960 and ISI R 163. a=angular, ar=articular, d=dentary, j=jugal, l=lacrimal, m=maxilla, n=nasal, p=parietal, pm=premaxilla, po =postorbital, q=quadrate, qj=quadratojugal, sa=sarangular (modified from Chatterjee, 1978).

SAUROPOD NESTING SITES. Sauropod nesting sites from the Lameta Group underlying the Deccan volcanics represent one of the most extensive fossil hatcheries in the world (Mohavey & Mathur, 1989; Srivastava et al., 1986; Sahni et al., 1994). They can be traced almost continuously along the north of Narmada Rift from Anjar to Jabalpur for more than 1,000km, wherever the Lameta Group is exposed (Fig. 9). The eggs are particularly restricted to a thin (3-12m), sandy carbonate unit, interpreted as calcretized palaeosoil (Sahni & Khosla, 1994). Several hundred nests with 3-13 eggs and abundant fragmentary eggshells are found in this unit. Most of these eggs belong to titanosaurids. A partial skeleton of a baby titanosaur has been discovered among the nesting grounds in Gujrat (Mohabey, 1987), but Jain (1989) questioned its identity and

assigned it to a booid snake. We have collected excellent specimens of titanosaurid eggs from Jabalpur and Dohad areas. The eggs are spherical with an average diameter of 15cm and were laid in linear or circular fashion. Similar titanosaurid eggs are known from France and Spain.

BIOTIC EFFECTS OF THE KT BOUNDARY CATASTROPHIC EVENTS

The Cretaceous Period was rich in biodiversity. Yet by the end of the period, there was an unprecedented ecological crisis leading to extinctions of many groups of organisms, from the giant dinosaurs to microscopic plankton. The abruptness and importance of the KT boundary has been recognized from the birth of stratigraphy, as it was the basis for the demarcation of two geologic eras. Although both impacts and Deccan volcanism coincided with the KT boundary, their relative importance for global climatic instability and disruption of life is still hotly debated. There are three possible ways in which extinctions could have been brought about: 1, an abrupt cataclysm triggered by the impact; 2, a gradual extinction process induced by the prolonged Dec-
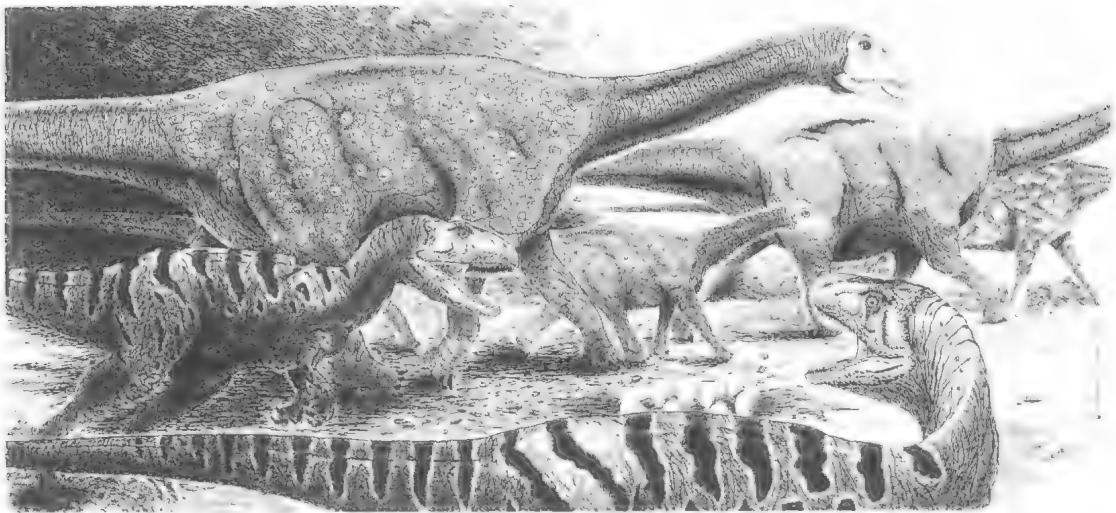
FIG. 15. Life restoration of the Masstrichtian Indian dinosaur community. In the foreground are two abelisaurid theropods, *Indosuchus raptorius* confronting a herd of titanosaurid sauropods, *Titanosaurus indicus*.

can volcanism that polluted the atmosphere and changed the world's climate; or 3, the combined effects of both impact and volcanism might have contributed to environmental crisis leading to mass extinction. The fossil record of victims and survivors across the KT boundary have been used by the proponents of both impact and volcanic models to champion their views.

BIOTIC EFFECTS IN INDIA. Since India was ground zero for both impact and Deccan volcanism, this would be an ideal place to search for the evidence of crisis on local biota. Unfortunately, the terrestrial sequence coinciding exactly with the KT boundary is limited in India as in other parts of the world. It is very unlikely that such a singular event would leave dense, multispecific dinosaur bone beds in the area of greatest mass mortality, unless the catastrophic bed is quickly buried and protected. Surprisingly, there is one dramatic event of mass mortality preserved in India which may be tied to the Shiva impact. In the Anjar KT boundary section of Kutch, the dinosaurs died out suddenly at the KT boundary which is defined on the basis of the iridium anomaly and isotopic dating (Bhandari et al., 1994). Here, the KT boundary section is a 1cm thick, pinkish clay layer above a cross-bedded limestone unit which contains associated titanosaurid bones. No dinosaur bones occur above the impact layer. We collected some KT boundary samples and dinosaur bones from this section and sent them to Dr Moses Attrep Jr, of Los Alamos National Laboratory for geochemical analysis. Dr Attrep found a signicant enrichment of iridium (348 parts per trillion) from the clay sample, but could not detect any anomaly in the dinosaur bone (82 ppt) or limestone unit. This is the first unequivocal evidence that the dinosaur extinction occurred precisely at the time of meteoritic impact.

The influence of Deccan volcanism on contemporary biotas can be inferred from the fossil record in the trappean beds. The most obvious local catastrophe posed by Deccan volcanism was the habitat destruction of $800,000km^2$ of tropical forest by extensive lava flows — an area of about the size of Texas (Fig. 9). The advancing flow and ash fallout must have destroyed the complex ecosystem for a large number of plant and animal species. The largest land vertebrates, the dinosaurs, were most affected by loss and fragmentation of habitats. The surviving populations of flora and fauna were forced to move out to the restricted space available in peninsular India, where they had to compete for food and resources. However, Deccan volcanism consisted largely of nonexplosive, tholeiitic eruptions similar to Kilauea and Reunion emissions, though on a grander scale. Recurrent eruptions do not disrupt much of the rich biota on the islands of Hawaii and Reunion. Although basaltic flows of relatively low viscosity commonly destroy plants, they move slowly enough that they seldom threaten the lives of the animals. Luxuriant vegetation thrived in the Deccan province as indicated by palaeobotanical evidence. Between the flows are the trappean beds that contain plant

remains of fungi, bryophytes, ferns, conifers and angiosperms. This flora, a very extensive one, is decidedly unusual in that it consists of seeds, fruits, leaves, trunks, branches and the like — thousands upon thousands of them. In 1988, we visited the little-known 'National Fossil Park' in Shahpura, about 80km from Jabalpur. This is probably one of the best petrified forests in the world, preserving this magnificient Deccan flora. We believe that these vast floral accumulations may signify recurrent deforestation events induced by Deccan ashfalls. In spite of floral deterioration, no major extinction event has been recorded among the Deccan flora (Lakhanpal, 1970). Within the intertrappeans beds, magnificent fossil accumulations indicate that life was resilient in this hostile environment. Deccan volcanism cannot be the proximate cause of the mass extinction.

The long-term hazard of Deccan volcanism would be several trillion tons of toxic gases pumped into the upper atmosphere, which would result in global climatic perturbations disrupting the ecosystem. Within the trappean beds, especially in the Lameta Group of rocks, the greenhouse effect can be identified, by the climate becoming more severe, with marked seasonal changes and aridity. There were large alkaline playa lakes around the periphery of the Deccan province where dinosaur bones and eggs were preserved in hot, arid conditions (Sahni et al., 1994). These lakes were subjected to alternate wet and dry seasons. Although pollution from the Deccan volcanism might have had some adverse effect on vertebrate populations, Prasad et al. (1994) could not detect any change in the composition or population of biota from infratraps to intertraps, during episodic volcanic activity. They concluded that the Deccan volcanism was not detrimental to life. There is another line of evidence which supports this theory. Midoceanic ridges spewing tholeiitic lava, toxic gases and sulfides, support a rich oasis of life, including tubeworms, polychaetes, crustaceans and mollusks. In fact, submarine vents provide a refuge for many relict forms that might have escaped the KT extinction (Tunnicliffe, 1991). Extrusion of the Deccan flows certainly affected the local flora and fauna by habitat destruction and pollution, but had little direct regarding the major extinctions.

Eggs are generally more sensitive indicators of environmental stress. As mentioned earlier, the world's largest fossil nesting sites have been discovered recently in the northern part of the Narmada lineament around the fringe of the Deccan province stretching for almost 1,000km. These eggs were apparently laid on wet, sandy-limey soils and were later subjected to prolonged intervals of aridity that resulted in considerable dehydration (Sahni et al., 1994). The abundant distribution of eggs suggests that sauropod population was thriving there when Deccan volcano was erupting. Sarkar et al. (1992) reconstructed the palaeoecology of the Lameta titanosaurids from stable isotope (^{18}O and ^{13}C) analysis of their eggs from the Kheda district of Gujrat. They found oxygen isotope data indicating that titanosaurids drank water from rivers and evaporative pools, whereas carbon isotope data suggesting they consumed C3-type plants (small palms, conifers, dicot shrubs, etc.) in a semiarid environment. It is well-known that pathological conditons in living reptiles and birds is caused by hormonal imbalance which can be induced by psychic stress due to overcrowding in a restricted space, or sudden a change in the environment (Erben et al., 1979). Surprisingly, in various nesting sites around the Deccan Province, embryos, hatchlings and juvenile skeletons are almost absent. Did these dinosaur eggs fail to hatch because of halogen poisoning from the Deccan flows? This seems unlikely because dinosaur eggs have been found at the KT boundary section in Anjar (Ghevaria & Srikarni, 1990). Unlike the condition in French and Spanish nesting sites (Erben et al., 1979), we could not detect any pathological abnormality in shell thickness and growth.

Was there any other mechanism of gradual reproductive failure among Indian dinosaurs? Heat from Deccan volcanism could have altered the sex ratio of the local dinosaur population. Paladino et al. (1989) proposed that sex in dinosaurs may be controlled by incubation temperature in the nests as seen among living reptiles such as turtles and crocodiles. They argued that during the Late Maastrichtian, climatic perturbations may have led to unisexual dinosaur populations and eventual extinction. This is an interesting concept but difficult to evaluate from the fossil record. Moreover, if dinosaur physiology was similar to that of birds (Bakker, 1975), temperature during incubation may not have had any role in sex determination. The occurrence of dinosaurs and eggs in the sediments intercalated with with Deccan lava flows indicates that volcanism had little direct effect on their demise. However, the pollution

from Deccan volcanism may have some global impact in conjunction with impact.

IMPACT-EXTINCTION MECHANISMS. One of the most important questions about the KT extinctions concerns its timing and duration. The extinction of six groups of marine microfossils — planktic and benthic forams, coccoliths, radiolarians, dinoflagellates and diatoms — took place precisely at the impact horizon and are compatible with this scenario (Smit, 1982; Thierstein, 1982; Alvarez et al., 1984). Brachiopods (Surlyk & Johnson, 1984) and ammonites (Ward et al., 1991) also show a similar abrupt pattern of extinction at the KT boundary. Similarly, pterosaurs, plesiosaurs and mosasaurs in the marine realm became extinct suddenly at the end of the Maastrichtian (Buffetaut, 1990). There is no question that the oceanic food chain collapsed by environmental changes around the KT boundary. In terrestrial communities, the sharp floral event exactly at this boundary strongly suggests a causal link with the impact scenario (Tschudy & Tschudy, 1986). Careful sampling indicates that dinosaurs in Montana died out suddenly at the KT boundary (Sheehan et al., 1991). We see the similar evidence of abrupt disappearance of dinosaurs precisely at the iridium KT boundary layer in Anjar section of Gujrat. Thus, the palaeontological record favors a sudden and simultaneous extinction pattern at the KT boundary among certain groups of organisms.

If, as seems likely, one or more meteorite impacts did play a role in the mass extinction event, what mechanism was involved? How devastating was the collision and how did it affect life? Various models have been proposed in recent times to explain the killing mechanism. A massive impact would generate earthquakes of high magnitude, inject a large volume of dust into the stratosphere, darken the skies, halt photosynthesis, ignite global fires, initiate tsunamis, produce acid rains, decrease ocean surface alkalinity and devastate the biosphere. Millions of organisms would die instantly from the direct effect of the impact — shock heating of the atmosphere by the expanding fireball (Alvarez 1986, 1987; Emiliani et al., 1981; 1987; Melosh et al, 1990). Comet Shoemaker-Levy 9 provided proof that the KT impact ignited global fires. As the ejecta fell back into the atmosphere after 20 minutes of each mpact, they reentered with a release of titanic energy; the heat from this reentry was so intense it was easily detected from

Earth (Weissman, 1995). Similarly, when the KT ejecta reentered into Earth's atmosphere, they ignited terrestrial forests and plant covers. The wildfires consumed oxygen and poisoned the atmosphere with CO. This massive impact would generate a 100-million megaton blast — 1000 times more powerful than the explosion of all nuclear arsenals of the world. The impact force would have vaporized not only the meteorite but also melted the target rock. This melt ejecta would spread in large waves, until it had formed a large crater. Huge tsunamis produced by the oceanic impact could destroy coastal habitats across the globe (Sharpton & Ward, 1990).

Available data suggest that the extinction of carbonate-secreting plankton was especially severe at the KT boundary (Smit, 1982; Keller, 1989). Acid trauma is likely a consequence of many biotic crisis in the oceans. Various impact mechanisms have been proposed to produce large volumes of HNO_3 and H_2SO_4 for acidification of surface marine waters. Shock heating of the atmosphere would cause nitrogen and oxygen to combine with steam to form nitric acid (Prinn & Fegley, 1987). The sheer size of the projectile cannot by itself account for the devastation. The unique composition of the crash sites provided additional arsenal. Because the target rock at the Yucatán Peninsula (and western coast of India) has a thick-cover of $CaSO_4$, an impact there could have released as much as a trillion tons of SO_2 (D'Hondt et al., 1994). Release of devolatilized SO_2 would form sulfuric acid aerosols which would contribute to a rapid decline in global surface temperature and halt photosynthesis. The subsequent showers of acid rain must have been agents for decreased ocean alkalinity and destruction of life. All of these events had cascading effects through the terrestrial and marine ecosystems to collapse the food chain.

All the extinction mechanisms cited above are based on a 10km-sized meteorite. If we consider the impact of a 40km meteorite, the devastation would be much more traumatic on the biosphere. One obvious consequence of a larger oceanic impact would be partial vaporization of the photic zone, raising the atmosphere's temperature to hundreds of degrees, and destoying all life in the ocean surface. Thus, a large body impact may explain the marine regression by vaporization of water which is generally associated with the KT event. The impact-induced thermal radiation would ignite global wildfires on land and destroy ecological niches (Melosh et al., 1990).

MECHANISM OF VOLCANIC-EXTINCTION. Many palaeontologists are skeptical about the scenario of impact holocaust. They argue that the KT extinction was neither global, nor instantaneous, but occurred over an extended period of time, because different organisms disappear at different levels at or near the KT boundary. They look for extinction agents that could explain a gradual extinction event and favor terrestrial causes, such as prolonged Deccan volcanism and regression of sea level, as main contributing factors for the biotic crisis (Clemens, 1982; Officer et al., 1987; Hallam, 1987; Stanley, 1987, p. 167; Keller, 1989; Zinsmeister et al., 1989; Courtillot, 1990).

However, the gradual extinction pattern seen among some organisms may be an artifact of preservation and declining sampling quality. Signor & Lipps (1982) showed theoretically how a sudden catastrophic extinction would appear to have been gradual in the fossil record, if the record was not dense. The Signor-Lipps effect weakens the case for a gradual extinction. Furthermore, the instantaneous extinction in both continental and marine organisms is not a necessary corollary of the impact theory (Alvarez et al., 1984). A large impact could trigger environmental crisis, and the latter could, in turn, cause extinctions spread over 10^4 to 10^5 years (Hsu et al., 1982). The most ecologically-sensitive organisms were probably the first victims, with progressively more tolerant groups succumbing in the later stages. The short term physical event may lead to long term biological events.

There are many examples of pre-boundary and post-boundary extinction events (Keller, 1979) which led many palaeontologists to advocate a close relationship between the biotic crisis and Deccan volcanism. There is no doubt that such a massive volcanic outburst over an extended period would have deleterious environmental consequences. Based on data known from the Laki eruption in 1783, the Deccan eruption must have pumped large volumes of SO_2, HCl and ash into the atmosphere to cause global cooling, immense amounts of acid rain, reduction in alkalinity and pH of the surface ocean and ozone layer depletion that might be harmful to both terrestrial and marine organisms (Hallam, 1987). Deccan volcanism must have produced large-scale aerosol clouds of sulphur and CO_2. The reduction in temperatures caused by sulphur aerosols in the stratosphere act in the opposite direction to the greenhouse gases such as carbon dioxide. Emissions of CO_2 from the Deccan volcanism would directly increase the atmospheric and oceanic CO_2, leading to sustained global warming.

SYNTHESIS. Some of the consequences of an asteroid impact and of massive volcanism would be quite similar, such as pollution of the atmosphere, darkness resulting from dust (either ejecta or ash), suppression of photosynthesis, acid rain, global cooling, carbonate crisis in the ocean waters, environmental stress, devastation of ecosystems and the collapse of the food chain. The scenario of extinction by food chain disruption is compatible with both impact and volcanic hypotheses. It is generally believed that the biotic crisis was most severe and sometimes limited to tropical-subtropical regions while high latitude faunas and floras were little affected (Keller, 1994). The geographic locations of two or three impact sites, Deccan volcanism and the distribution of impact deposits along the Alvarez Impact Belt may explain this geographic selection of KT extinction (Fig. 6B). The sudden cooling by H_2SO_4 aerosol and warming by CO_2 would result in chaotic climatic perturbations which would be especially traumatic for global organisms. However massive volcanism would lack some of the titanic lethal features that are generally associated with a large body impact, such as gigantic shock effects leading to vapor plume, global fire, thermal pulse, evaporation of the photic zone and concomitant sea regression, chondritic metal toxicity and volatilization of target rocks. Impacts probably made more dramatic changes to KT environments globally and a more traumatic crisis to the ecosystem than volcanic emissions. Impacts also perturbed the environment so suddenly and catastrophically that most organisms failed to adapt to these changes in such a short time and perished. In contrast, prolonged volcanism allowed enough time for some organisms to adapt, or for others to disappear gradually. Global fire must have decreased the amounts of atmospheric oxygen which would further exacerbate the hostile conditions already developing among terrestrial and marine life. Selectivity and a step-wise extinction pattern can be better explained by the volcanic model. It seems that impact was the proximate cause to the biotic crisis at the KT boundary, whereas long-term volcanism produced harmful changes that enhanced climatic stress and finished off the extinction process.

CONCLUSION

We have outlined two catastrophic events at the KT boundary in India: a giant meteorite impact at the India-Seychelles rift margin and the spectacular volcanic outbursts of Deccan volcanism. These two events were so closely intertwined in space and time that it is difficult to untangle them in proper chronologic order. The subsurface stratigraphy and geophysical data suggest that the Shiva Crater is a potential candidate for the long-sought KT impact scar. Biostratigraphic, geochronologic and palaeomagnetic evidence indicates a KT boundary age.

We speculate that an oblique impact by a 40km asteroid produced the oblong, complex, Shiva Crater on the continental shelf of western India, 600km across and more than 12km deep. Part of the crater rim survives in the Panvel Flexure and the Narmada Fault near western India and in the Amirante Arc south of the Seychelles. The central uplifts are represented by the elevated peaks of the Bombay High, Praslin and Mahe. Between the central peaks and the crater rim lay an annular trough, now preserved as the Surat Basin, the Dahanu-Panna Depression and the Amirante Basin, each containing thick Tertiary sediments (Fig. 5A). The impact melts were emplaced radially downrange of the trajectory and are clustered around the Shiva Crater in the form plugs of alkaline igneous complexes. Radiometric, palaeontologic and palaeomagnetic data suggest that the Shiva Crater was formed at the KT boundary.

We are aware that one serious shortcoming of the Shiva Impact hypothesis is the documentation of shock metamorphism in crater proximity. There are several possible reasons for this deficiency. First, we could not acquire any KT boundary core samples from Oil and Natural Gas Commission of India regarding Bomay High area. These samples are crucial to detect impact signatures such as iridium anomaly, shocked quartz, melt rocks, breccias, suevites and shatter cones. Second, the impact took place in a shallow-marine setting. The tsunami generated by this impact would have been efficient at removing ejecta material. Third, some of the shocked signatures may be preserved in the deeper part of the basin, yet to be penetrated by drilling. Fourth, contemporary Deccan volcanism and impact melt which had filled part of the crater and crater exterior must have consumed or erased other evidence of shocked features such as shatter cones, breccia and ejecta. The thick blanket of Deccan Traps on the western part of India must have concealed most of the crucial evidence of impact signatures. As in the case of Chicxulub, we need more subsurface data to confirm the impact origin of the Shiva structure. An international effort is needed to unravel the morphology of the Shiva Crater.

It is highly coincidental that critical evidence for both the Chicxulub and Shiva Craters came from petroleum prospecting, because the sediments overlying the central peak of a complex crater form a domal structural trap. The Shiva crater now preserves a complicated geological history, as well as valuable economic resources — the largest oil field in India. Thus the Shiva impact had created not only an immense crater and continental rifting, but also affected global climate, the chemistry of the world's ocean, a biotic crisis and perhaps even the production of oil traps.

The near-antipodal positions of the Chicxulub and Shiva structures suggest two possibilities: Either, two large meteorite fragments crashed on a rotating Earth at a short interval, creating two large scars along the Alvarez Impact Belt. Or, a large impact on one side of the Earth produced a similar signature on the far side. The first model finds support from the unusual concentration of impact deposits and biogeographic selectivity of extinction at low latitudes (Keller, 1994) along this Alvarez Impact Belt.

The impact-induced model of Deccan volcanism, though very appealing, is rejected because of conflict of timing. The revised calibration of Deccan volcanism indicates that the eruption began over 1Ma before the KT event and extended for 3Ma. If so, then the Shiva impact did not initiate the Deccan plume activity.

Although both impact and volcanism might have contributed to inhospitable environments and biotic crisis at the KT boundary, the impact must have played a major role in the killing mechanism. Both catastrophes contributed heavily to the breakdown of stable ecological communities and disrupted the biosphere. In the aftermath of the KT extinction, some forms of life, such as bird and mammals rebounded. They formerly played minor roles, but assumed prominence after the extinction. Today, they are abundant in both numbers of species and populations and can be found on every continent occupying virtually all available niches. The selectivity of KT extinction is still puzzling. For example, terrestrial dinosaurs became the victims, but their flying counterparts — birds —

survived the catastrophe. Birds rose like the Phoenix from the funeral pyre of terrestrial dinosaurs with renewed youth and beauty to carry their ancestral heritage into the Cenozoic cycle.

ACKNOWLEDGMENTS

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EARLY AVIAN EVOLUTION IN THE SOUTHERN HEMISPHERE: THE FOSSIL RECORD OF BIRDS IN THE MESOZOIC OF GONDWANA

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The record of Gondwanan Mesozoic birds, including osteological specimens, feathers and traces, is critically reviewed. Data regarding the paleoenvironment and associated biota of each record is provided. Several occurrences of controversial status in the Late Triassic-Early Jurassic of Africa and the Cretaceous of Australia and Africa, and misguided reports from the Cretaceous of South America are also discussed. The Mesozoic record of Gondwanan birds is limited, although it has provided relevant insights about the early evolution of birds. Undisputable records are known from the Cretaceous of South America, Australia, Africa and Antarctica. This material indicates that during the Cretaceous, Gondwanan birds were widely distributed, inhabiting a broad range of environments and developing various modes of life. ☐ *Birds, Mesozoic, Gondwana, evolution.*

Se revisa criticamente el registro Mesozoico de aves de Gondwana, incluyendo restos óseos, plumas y trazas. Para cada registro, se provee información con respecto al paleoambiente y la fauna asociada. Se discuten varios registros de status controvertido en el Triásico Tardío-Jurásico Temprano de Africa, y el Cretacico de Australia y Africa, como también reportes erroneos del Cretácico de América del Sur. El registro Mesozoico de aves de Gondwana es limitado, si bien ha provisto información relevante sobre la temprana evolución de las aves. Registros confiables son conocidos del Cretácico de América del Sur, Australia, Africa y Antártida. Este material indica que durante el Cretácico las aves de Gondwana estuvieron extensamente distribuidas, habitando un amplio espectro de ambientes y desarrollando diversos estilos de vida.

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The early evolutionary history of birds has been reconstructed mostly on the basis of fossil evidence provided by Mesozoic deposits of the northern hemisphere. It is not until recently that significant discoveries of Mesozoic birds from Gondwana have been made, and that this new evidence has strongly influenced our previous conceptions of avian evolution (Chiappe, 1995a).

The indisputable record of Mesozoic birds in Gondwana is restricted to the Cretaceous, although bird-like footprints have been found in pre-Cretaceous deposits. Among today's Gondwanan continental masses, South America, Antartica, Australia and Africa have provided Cretaceous evidence of birds. The South American (Chiappe, 1991) and Australian (Vickers-Rich, 1991) records have been previously discussed elsewhere, but additional new findings in these landmasses, along with the discovery of Cretaceous birds in Antarctica and Africa, and the recent interest in the pre-Cretaceous bird-like footprints from the latter continent, call for an update of the Gondwanan record. In this paper the Gondwanan record (Fig. 1, Table 1) is reviewed, including data on paleoenvironment and associated biota, and its contribution to the understanding of the early history of birds is emphasised.

MATERIALS AND METHODS

The taxonomical nomenclature employed here follows the traditional use of the taxon-name Aves. Hence, the term Aves names a clade, defined as the common ancestor of *Archaeopteryx lithographica* and Neornithes (modern birds) and all its descendants (Fig. 2). Gauthier (1986) and others (Perle et al., 1993, 1994; Norell et al., 1993) proposed restricting the taxon-name Aves to the crown-group of Theropoda, that is the common ancestor of all extant forms plus all its descendants. These authors (including myself in some cases) have used the term Avialae to name the clade traditionally regarded as Aves, while the latter term was used to replace the taxon-name Neornithes of the classical ornithological taxonomy. Perhaps the most attractive advantage of Gauthier's (1986) proposal is the idea of
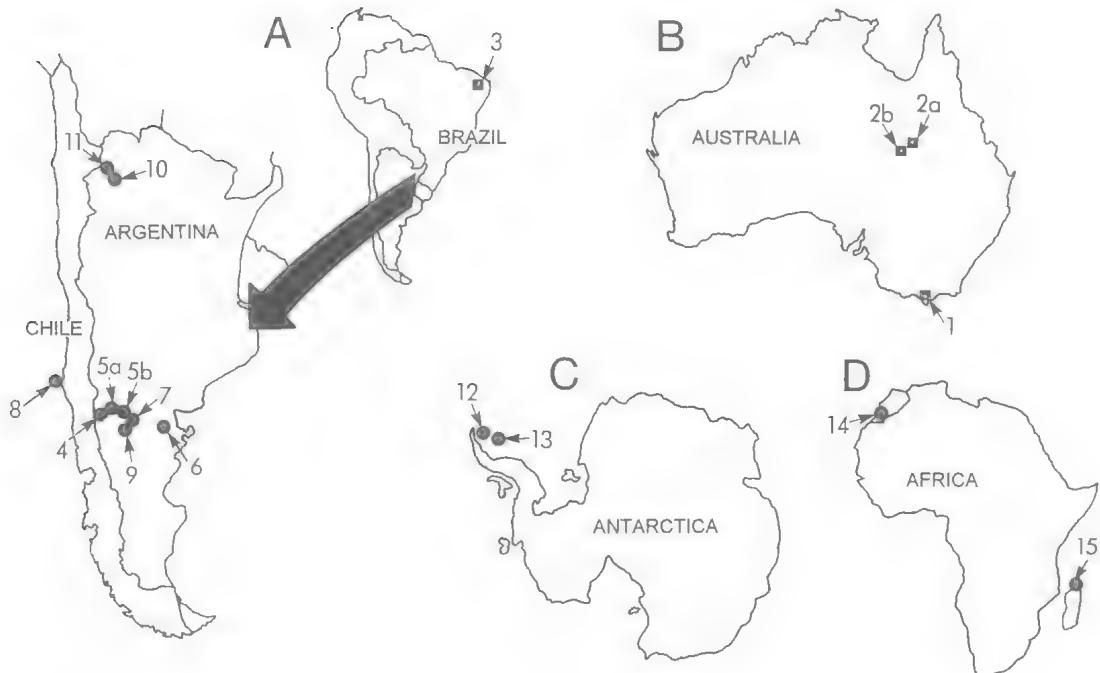
FIG. 1. Maps of A, South America and Argentina-Chile; B, Australia; C, Antarctica; and D, Africa, showing the occurrences of Mesozoic birds. ■ = Early Cretaceous occurrences. ● = Late Cretaceous occurrences. Numbers pointing each locality correspond to those used in Table 1. 1, Koonwarra, Victoria; 2a, 'Warra', Queensland; 2b, 'Canary', Queensland; 3, Santana do Cariri, Ceará; 4, area of Plaza Huincul, Neuquén; 5a, city of Neuquén, Neuquén; 5b, Puesto Tripailao, Río Negro; 6, Estancia Los Alamitos, Río Negro; 7, Salitral Moreno, Río Negro; 8, Bahía San Vicente, Concepción; 9, area of Ingeniero Jacobacci and 'Monton-I10', Río Negro; 10, El Brete, Salta; 11, Quebrada del Tapon, Salta; 12, Cape Lamb, Vega Island; 13, Marambio (Seymour) Island; 14, area of Agadir (Morocco); 15, Berivotra, Mahajanga (Madagascar).

having a widely used term, such as Aves, associated with a clade that can be diagnosed by numerous synapomorphies (many soft-tissue characters in addition to the osteological ones). It should be noted, however, that many of these characters (e.g., soft-tissue characters) have an ambiguous optimization when fossils are included in the analysis. The greatest argument against this proposal appears to be simply the universal way in which the name Aves has been associated to the clade composed of all birds (note that a phylogenetic definition is given above) during the last 130 years. Names are terms applied to a definition and ideally they should be conventional. For this reason I would keep using the term Aves in the way it is defined above. The casual terms 'birds' and 'modern birds' refer to Aves and Neornithes, respectively. The collective expression 'non-avian theropods' is used without any systematic meaning.

Several of the occurrences here regarded as Mesozoic birds are represented by footprints. It is well known that the identification of a footprint with a particular trackmaker always involves some degree of uncertainty. Several factors such as the stance, march, speed and the composition of the substrate may affect the morphology of the footprint and consequently its taxonomic interpretation (Padian & Olsen, 1984; Unwin, 1989). In this paper, the recognition of a footprint as avian is based primarily on the criteria summarised by Lockley et al. (1992). Most significant criteria used by Lockley et al (1992) are: 1) small size; 2) slender digit impressions with undifferentiated pad impressions; 3) wide divarication angle between digits II and IV; 4) plantarily directed hallux; 5) slender claws; and 6) distal curvature of lateral claws away from the axis of the pes.

The treatment of the avian occurrences of a particular continent are organised in the follow-

TABLE 1. Avian occurrences in the Mesozoic of Gondwana. Alb=Albian, Apt=Aptian, Bar=Barremian, Cam=Campanian, Con=Coniacian, Mae=Maastrichtian, Tur=Turonian, San=Santonian.

	TAXON	DISTRIBUTION	HORIZON/AGE	EVIDENCE	REFERENCE
			AUSTRALASIA		
1	Aves indet.	Koonwarra, Victoria	Strzelecki Group, Bar-Apt	feather	Talent et al., 1966; Rogers, 1987
2a,b	Enantiornithes: *Nanantlus eos*	Warra Station (2a), Canary (2b), Queensland	Toolebuc Fm., Alb	bone	Molnar 1986; Molnar pers. comm.
			SOUTH AMERICA		
3	Aves indet.	Santana de Cariri, Ceará, Brazil	Santana Fm., Apt-Alb	feather	Martins-Neto & Kellner, 1988; Kellner, 1990
4	Alvarezsauridae: *Patagonykus puertai*	Area of Plaza Huincul, Neuquén, Argentina	Río Neuquén Fm., Tur-Con	bone	Novas & Coria,1990; Novas, this volume
5a	Alvarezsauridae: *Alvarezsaurus calvoi*	City of Neuquén, Neuquén, Argentina	Río Colorado Fm., Con-San	bone	Bonaparte, 1991; Novas, this volume
5a	*Patagopteryx deferrariisi*	City of Neuquén, Neuquén, Argentina	Río Colorado Fm., Con-San	bone	Alvarenga & Bonaparte, 1992; Chiappe, 1992a
5a,b	Enantiornithes: *Neuquenornis volans*	City of Neuquén, Neuquén; Puesto Tripailao, Río Negro, Argentina	Río Colorado Fm., Con-San	bone	Chiappe, 1992a; Chiappe & Calvo, 1994
6	Ornithothoraces indet.	Estancia Los Alamitos, Río Negro, Argentina	Los Alamitos Fm. Cam-Mae	bone	Chiappe, 1992a
7	Ornithurae indet.	Salitral Moreno, Río Negro, Argentina	Allen Fm., Cam-Mae	bone	Powell, 1987; Chiappe, 1992a
8	Ornithurae: Gaviidae: *Neogaeornis wetzeli*	Bahía San Vicente Concepción, Chile	Quiriquina Fm., Cam-Mae	bone	Lambrecht, 1929; Olson, 1992
9	Aves indet.: "*Patagonichornis venetiorum*"	Area of Ingeniero Jacobacci, "Monton-110", Río Negro, Argentina	Unknown Fm., Mae	ichnite	Casamiquela, 1987; Leonardi, 1987; Chiappe, 1991
10	Enantiornithes indet.	El Brete, Salta, Argentina	Lecho Fm., Mae	bone	Walker, 1981; Chiappe, 1991
10	Enantiornithes: *Enantiornis leali*	El Brete, Salta, Argentina	Lecho Fm., Mae	bone	Walker, 1981; Chiappe, 1991
10	Enantiornithes: *Soroavisaurus australis*	El Brete, Salta, Argentina	Lecho Fm., Mae	bone	Walker, 1981; Chiappe, 1993
10	Enantiornithes: *Lectavis bretincola*	El Brete, Salta, Argentina	Lecho Fm., Mae	bone	Walker, 1981; Chiappe, 1993
10	Enantiornithes: *Yungavolucris brevipedalis*	El Brete, Salta, Argentina	Lecho Fm., Mae	bone	Walker, 1981; Chiappe, 1993
11	Aves indet.: *Yacoraitichnus avis*	Quebrada del Tapón, Salta, Argentina	Yacoraite Fm., Mae	ichnite	Alonso & Marquillas, 1986; Chiappe, 1991
			ANTARCTICA		
12	Ornithurae: Presbyornithidae indet.	Cape Lamb, Vega Island	López de Bertodano Fm., Cam-Mae	bone	Noriega & Tambussi, 1995
13	Ornithurae: Gaviidae indet.	Marambio (Seymour) Island	López de Bertodano Fm., Cam-Mae	bone	Chatterjee, 1989; Olson, 1992
			AFRICA		
14	Aves indet.	Area of Agadir, Morocco	Unknown Fm., Mae	ichnite	Ambroggi & Lapparent,1954; Lockley et al., 1992
15	Aves indet.	Berivotra, Mahajanga, Madagascar	Maevarano Fm., Cam	bone	Krause, pers. comm.

ing hierarchical arrangement: Aves, Metornithes, Ornithothoraces, Ornithurae, Neornithes. Indeterminate occurrences within a particular clade are listed first.

When anatomical nomenclature is applied, this follows Baumel & Witmer (1993), using the English equivalents of the Latin terminology.
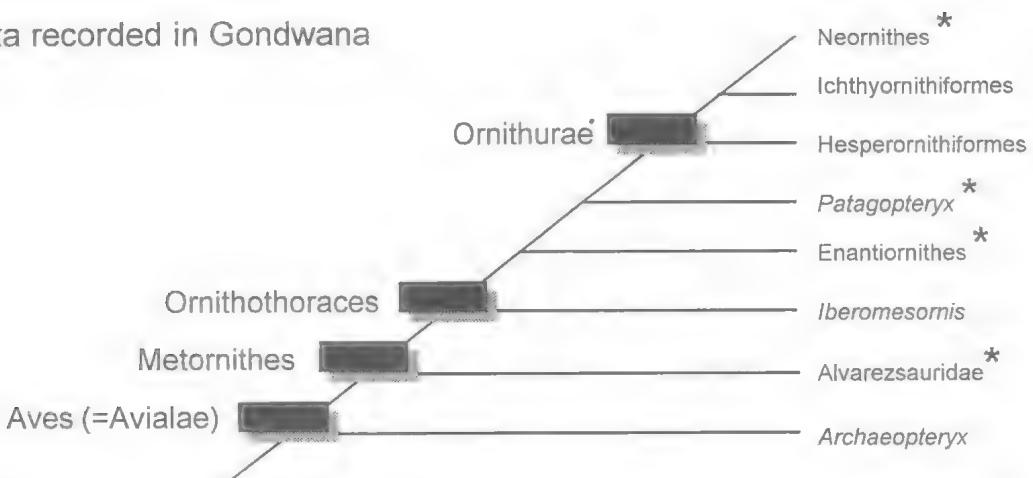
FIG. 2. Cladogram illustrating the relationships between Alvarezauridae, Enantiornithes, *Patagopteryx deferrariisi* and Neornithes (see Chiappe et al., this volume).

Institutional abbreviations. DNPM, Departamento Nacional da Produção Mineral (Rio de Janeiro, Brazil); GP, Instituto de Geociências, Universidade de São Paulo (São Paulo, Brazil); GPMK, Geologisch-Paläontologisches Institut und Museum, Kiel; LEIUG, Department of Geology, Leicester University (Leicester, United Kingdom); MACN, Museo Argentino de Ciencias Naturales (Buenos Aires, Argentina); MUCPv, Museo de Ciencias Naturales, Universidad Nacional del Comahue (Neuquén, Argentina); NMV, National Museum of Victoria (Melbourne, Australia); PVL, Fundación-Instituto Miguel Lillo, Universidad Nacional de Tucumán (San Miguel de Tuçumán, Argentina); PVPH, Museo Cármen Funes (Plaza Huincul, Argentina); QM, Queensland Museum (South Brisbane, Australia); SAMK, South African Museum (Cape Town, South Africa); SMNK, Staatliches Museum für Naturkunde Karlsruhe (Karlsruhe, Germany).

CONTROVERSIAL OCCURRENCES

Ellenberger (1972) described a series of bird-like footprints from the Lower Stormberg beds (Late Triassic) of South Africa, recognising several tridactyl and tetradactyl small ichnospecies (*Trisauropodiscus galliforrna, T. phasianiforma, T. levis, T. aviforma*) and other medium size tetradactyls (*T. popompoi, T. superaviforma*). Later, Ellenberger (1974) reported several other footprints from the upper Stormberg beds (Early Jurassic) recognising the ichnogroups carnavians (*Masitisisauropus*

palmipes, *M. angustus, M. exiguus, Masitisisauropezus minimus, M. minutus, M. perdiciforma*) and lacunavians (*Masitisisauropodiscus turdus, M. fringilla*). Interestingly, among the carnavians (*M. palmipes*), he claimed the presence of feather-like traces associated to impressions of the thoracic limb. Unfortunately, Ellenberger's descriptions appear to have been made directly in the field, and no holotype or referred specimen has ever been collected and deposited in an institution (Lockley, pers. comm.). This situation limits any comparison to the poorly figured illustrations of his papers (Ellenberger, 1972, 1974). In the case of the feather-like structures (*M. palmipes*), as pointed out by Molnar (1985), there is no compelling evidence to regard these traces as feathers and the footprints themselves are probably not of an avian theropod. The different footprints of *Trisauropodiscus*, however, have the small size and large divarication angle between digits II and IV characteristic of avian trackmakers (Lockley et al., 1992). Lockley et al. (1992) remarked upon the similarity of *Trisauropodiscus* with footprints reported by Ishigaki (1985, 1986) from the Early Jurassic of the Atlas Mountains in Morocco, pointing out that they would have been considered as being made by an avian trackmaker if they were of late Mesozoic age. However, the existence of pre-Late Jurassic birds has yet to be documented. The recent allocation of *Protoavis texensis* (Chatterjee, 1987, 1991) within Aves is not supported by the available evidence. Several authors have expressed their scepticism of Chatterjee's claims (see Ostrom, 1987, 1991; Anderson, 1991;

Monastersky, 1991), and after examination of the material, I also disagree with his hypothesis (Chiappe, 1995a). Therefore, given the fact that indisputable pre-Late Jurassic birds are yet to be documented in addition to the problems associated with the nature of footprints (see Materials and Methods), I prefer to leave these tracks out of the discussion of true birds.

Dettmann et al. (1992: note added in proof) mentioned the discovery of new avian fossils from the Early Cretaceous (Albian) Griman Creek Formation at Lightning Ridge (north-central New South Wales, Australia). Thanks to R.E. Molnar, I had the opportunity to examine casts of this material which comprise the distal ends of two small bones, possibly tibiotarsi. The specimens are fragmentary and I am not completely confident of their identification as tibiotarsi. However, if they are tibiotarsi, then the proximal tarsals are completely fused to the tibia and the fibula does not reaches the tarsus. These two characteristics are unique of avians among dinosaurs (Gauthier, 1986; Cracraft, 1986; Chiappe & Calvo, 1994; Chiappe, 1995b, 1996), and support Dettmann's et al. (1992) allocation. In light of the fragmentary condition of these specimens, however, I would wait for further evidence before regarding them as truly avian.

The occurrence of a putative bird bone was mentioned by Smith (1988) in his analysis of the paleoenvironment of a Late Cretaceous crater-lake in Stompoor, central South Africa. Unfortunately, this specimen (SAMK-6486) is a fragmentary left femur and is missing the distal end and most of the proximal one. Although hollow, small and bird-like in aspect, SAMK-6486 does not show any character that can be regarded as avian.

Mussi & Alonso (1989) reported an isolated bird footprint from the Late Cretaceous (Maastrichtian) deposits of the Yacoraite Formation at Dique Cabra Corral (Province of Salta, Argentina). In my opinion this 'footprint' is actually a peculiar disposition of small concretions embedded in the limestone slab and not a track made by a living organism.

Finally, in 1991 I commented on the occurrence of a fragmentary carpometacarpus from the Late Cretaceous (Maastrichtian) Bauru Formation of southern Brazil (Chiappe, 1991). Alvarenga (pers. comm.), however, has recently identified this bone as the extant Yellow-billed cuckoo (*Coccyzus americanus*), being the result of contamination of the Cretaceous material.

THE AVIAN RECORD

AUSTRALASIA

AVES Linnaeus, 1758

MATERIAL EXAMINED. At least five feathers (Fig. 3A), including covert and down ones (Talent et al., 1966; Waldman, 1970; Rogers, 1987; Vickers-Rich, 1991). Waldman (1970) and Rogers (1987) published on NMV P.26059A and P.26059B, slab and counter-slab, respectively.

LOCALITY AND HORIZON. Koonwarra, southeast Victoria, Australia. Strzelecki Group, Early Cretaceous (Aptian; Vickers-Rich, 1991; Dettmann et al., 1992).

REMARKS. These feathers (Fig. 3A) represent the oldest evidence of birds from this continent. Rogers (1987) studied NMV P.26059A and P.26059B in detail. This feather, regarded as either a primary covert or an alular, was found to be different from any modern feather (Rogers, 1987). This is interesting considering that the only avian material from the Cretaceous of Australia that allows a more precise taxonomic identification belongs to the Enantiornithes (see below), a group not closely related to modern birds (Fig. 2).

The lacustrine mudstones of Koonwarra have provided one of the best Mesozoic continental biota from Australia, including a diversified flora (e.g., bryophytes, ferns, conifers and angiosperms; see Douglas & Williams, 1982), and a large variety of insects, crustaceans, spiders, earthworms, bryozoans, bivalves and fishes (Dettmann et al., 1992). This biotic association becomes of particular interest considering that southeastern Victoria was situated in polar latitudes (~75°-85°S) during the early Cretaceous (Vickers-Rich & Rich, 1989). Douglas & Williams (1982) interpreted the paleoenvironment at Koonwarra as forested (primarily evergreen forests) in a warm to cool-temperate climate with moderate seasonality. However, Vickers-Rich & Rich (1989) emphasised the possibility of annual near-freezing conditions and a prolonged polar night.

METORNITHES Perle et al., 1993
ORNITHOTHORACES Chiappe, 1995
ENANTIORNITHES Walker, 1981

Nanantius eos Molnar, 1986

MATERIAL EXAMINED. HOLOTYPE: QMF12992 (Fig. 3C), complete left tibiotarsus (Molnar, 1986). REFERRED SPECIMENS: QMF31813, proximal end of a tibiotarsus (Molnar & Kurochkin, in press).
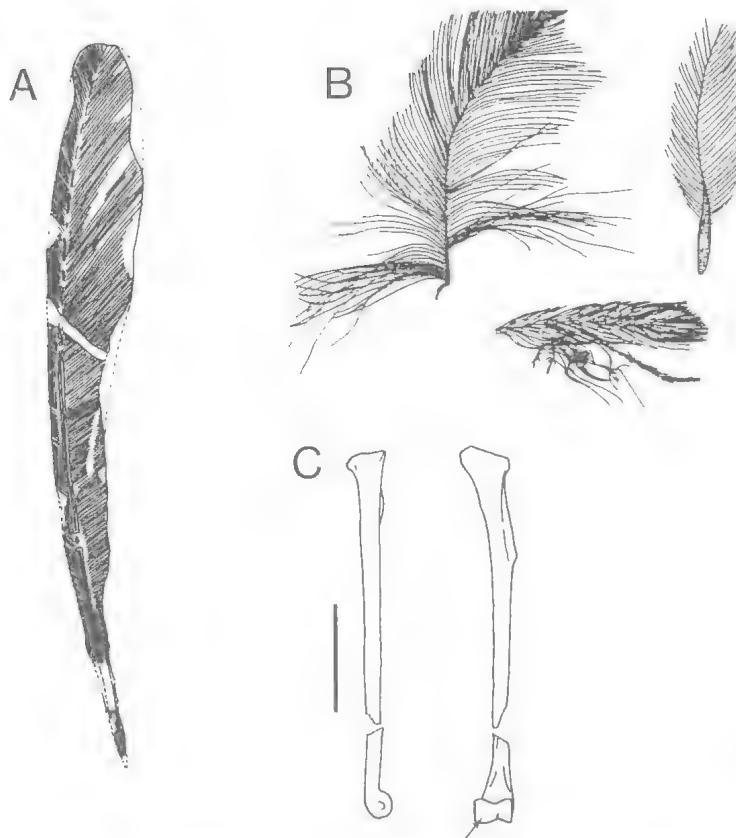
FIG. 3. Early Cretaceous birds from South America and Australasia. A, isolated feather (GP/2T-136) from the Late Aptian Crato Member of the Santana Formation near Santana do Cariri, northeastern Brazil (after Martins Neto & Kellner, 1987). B, Aptian feathers from the Strzelecki Group at Koonwarra, southeastern Victoria, Australia (after Vickers-Rich, 1976). C, medial (left) and cranial (right) views of the tibiotarsus (QMF12992) of *Nanantius eos* from the Albian Toolebuc Formation at Warra Station, western Queensland, Australia (after Molnar, 1986). Arrow points to the broad medial condyle characteristic of enantiornithine birds. In C scale = 1cm.

QMF12991, an anterior dorsal vertebra that may also be *Nanantius eos* (Molnar & Kurochkin, in press).

LOCALITY AND HORIZON. QMF12992 and QMF12991 were found at Warra Station, east side of Hamilton River near Boulia, west Queensland, Australia. QMF31813 is from Canary Station in west Queensland, Australia. Toolebuc Formation, Early Cretaceous (Albian; Molnar, 1986; Dettmann et al., 1992).

REMARKS. Molnar (1986) correctly placed *Nanantius eos* into the Enantiornithes. The tibiotarsus of *N. eos* shows a round proximal articular surface, a smooth craniolateral cnemial crest, and a wide and bulbous medial condyle (Fig. 3C), which are enantiornithine synapomor-

phies (Chiappe, 1992b, 1993). *N. eos* is a small enantiornithine, approximately the size of the American robin (*Turdus migratorius*) (Molnar, 1986). Nevertheless, the complete fusion of the proximal tarsals to the tibia in the holotype of *N. eos* suggests that this represents an adult individual. The size of *N. eos* is significantly smaller than any of the South American enantiornithines, and comparable to the size of the enantiornithines *Alexornis antecedens* (Brodkorb, 1976) and *Concornis lacustris* (Sanz et al., 1995) from the Cretaceous of Mexico and Spain, respectively.

Molnar & Kurochkin (in press) have identified QMF-31813 as *Nanantius* sp. remarking on a few subtle differences with respect to *Nanantius eos*. In my opinion, this specimen should be placed within *N. eos*. QMF12991, found at less than 5cm from the holotype of *N. eos*, may also belong to this species (Molnar & Kurochkin, in press), but these authors have pointed out that it belongs to an individual larger than the holotype of this species.

The Toolebuc Formation is composed of offshore marine limestones deposited during the middle-late Albian (Molnar & Thulborn, 1980; Dettmann et al., 1992). The holotype specimen was associated with fish remains, turtles, ichthyosaurs and pterosaurs (Molnar, 1986). The common occurrence of fossil logs within these deposits might indicate that the shoreline was forested near the type locality of *Nanantius eos* (Dettmann et al., 1992). *N. eos* is the only occurrence of a Gondwanan enantiornithine in marine deposits.

SOUTH AMERICA

AVES Linnaeus, 1758

MATERIAL EXAMINED. SEVERAL ISOLATED FEATHERS: GP/2T-136 (Fig. 3B), a flight feather (Martins-Neto & Kellner, 1988); DNPM MCT 1493-R,

a down feather (Kellner et al. 1994); LEIUG 114369, a semiplume (Martill & Filgueira, 1994); LEIUG 115562, SMNK 1247 PAL (counterpart), a contour, body feather (Martill & Frey, 1995).

LOCALITY AND HORIZON. All feathers are from the Araripe Basin in the State of Ceará, Brazil. GP/2T-136 and DNPM MCT 1493-R come from an indeterminate area around Nova Olinda (Kellner, pers. comm.); LEIUG 115562, SMNK 1247 PAL and LEIUG 114369 are from the Mina de Antone Phillipe, near Tatajuba. Santana Formation, Crato Member, Early Cretaceous (Late Aptian; Pons et al, 1990).

REMARKS. GP/2T-136 is a fairly small feather (approximately 64mm long), which might have belonged to a bird of the size of the neotropical brush finches (*Atlapetes*) (Kellner et al., 1991). It has a strong rachis and a very narrow outer vane (Kellner et al., 1991). The fact that this feather has asymmetric vanes (Fig. 3B) suggests it belonged to a flying bird (Feduccia & Tordoff, 1979), although no taxonomic assignment is possible with only this evidence. In LEIUG 115562 (and its counterpart, SMNK 1247 PAL), a small body feather, the color pattering is preserved. This consists of a series of transverse dark and light bands (Martill & Frey, 1995). Barbules have been preserved in both DNPM MCT 1493-R and LEIUG 114369 (Kellner et al., 1994; Martill & Filgueira, 1994). The presence of semiplumes, flight, body and down feathers in the Crato Member highlights the differentiation of feather types as early as the Early Cretaceous.

The paleoenvironment of the Crato Member has been generally regarded as a calm, fresh water lake existing under arid climatic conditions (Maisey, 1991), although restricted connections to marine waters may have existed (Martill & Filgueira, 1994; Martill & Frey, 1995). Sediments consist of laminated limestones with intervening beds of sands and shales (Maisey, 1991; Martill & Filgueira, 1994). The feathers were found in the laminated limestones, regarded as the marginal lake facies (Kellner et al., 1991; Martill & Filgueira, 1995). The fossil assemblage recorded from the Crato Member includes an abundant variety of insects (Grimaldi, 1990), along with scorpions, spiders, fishes, frogs and several floral elements (Maisey, 1991).

Yacoraitichnus avis Alonso & Marquillas, 1986

MATERIAL EXAMINED. Slab (without number when published) with several footprints (Fig. 4A) (Alonso & Marquillas, 1986; Alonso, 1989).

LOCALITY AND HORIZON. Quebrada del Tapón, Valle del Tonco, Department of San Carlos, Province of Salta, Argentina. Yacoraite Formation, Late Cretaceous (Maastrichtian; Alonso & Marquillas, 1986).

REMARKS. *Yacoraitichnus avis* consists of medium size footprints (approximately 80mm long), lacking the hallux impression (Alonso & Marquillas, 1986) (Fig. 4A). This ichno-species is one of the few avian tracks that shows digital pad impressions (Lockley et al., 1992). Alonso & Marquillas (1986) suggested that *Y. avis* could either belong to a galliform-like neognathine or to an enantiornithine bird, although they finally regarded it as indeterminate among avians. The hypothesis of a galliform affinity becomes unlikely considering that the earliest known galliform comes from the Early Eocene of North America. Likewise, despite the fact that diverse ensemble of enantiornithine birds is known from the Lecho Formation (see below) — a unit considered to be part of the same depositional event of the Yacoraite Formation (Gomez Omil et al., 1989) — no ichnites have been ever found associated with these and other enantiornithine remains making the latter hypothesis untestable (Chiappe, 1991).

The footprints of *Yacoraitichnus avis* occur in a narrow band of green claystone one meter above deposits with a variety of non-avian dinosaur footprints (Alonso & Marquillas, 1986; Alonso, 1989). Remains of fishes and crocodiles are also known to occur in the Yacoraite Formation at Quebrada del Tapón (Alonso & Marquillas, 1986). The footprints at Quebrada del Tapón occur in coastal plain beds deposited along the western margin of an extensive body of water (Alonso, 1989). This coastal plain was periodically submerged because of changes in the level of the water. Alonso (1989) concluded that the footprints of *Y. avis* were produced on an exposed layer of mud, left after a period of inundation.

'Patagonichnornis venetiorum' Casamiquela, 1987

MATERIAL EXAMINED. Footprints (no repository has been published; see Casamiquela, 1987).

LOCALITY AND HORIZON. Area of Ingeniero Jacobacci and 'Monton-110', Province of Rio Negro, Argentina. The footprints from around Ingeniero Jacobacci are referred to the Late Cretaceous without any further stratigraphical information (see Casami-

FIG. 4. Late Cretaceous footprints from South America and Africa. A, *Yacoraitichnus avis* from the Maastrichtian Yacoraite Formation at Quebrada del Tapón, Province of Salta, Argentina (after Alonso & Marquillas, 1986). B, C, D, bird tracks from Maastrichtian deposits near Agadir, southern Morocco (after Ambroggi & Lapparent, 1954).

quela, 1987); the ones from 'Monton-I10' are listed as Late Maastrichtian (see Leonardi, 1987: Plate XVIII).

REMARKS. Casamiquela (1987) reported the discovery of bird footprints associated with tracks of hadrosaurs and, although they were neither described nor illustrated, he named them '*Patagonichnornis venetiorum*'. On the other hand, a cast with several bird tracks from the Late Maastrichtian of the Argentine Río Negro Province ('Monton-I10') was illustrated by Leonardi (1987), although no further geographical reference was given. These latter tracks have long, slender digits and large divaricate angles between digits II and IV (Leonardi, 1987). Although not verified, it is likely that Leonardi (1987) was illustrating what Casamiquela (1987) named '*P. venetiorum*'.

Casamiquela (1987) allocated '*Patagonichnornis venetiorum*' in the extinct Cimolopterygidae within the Charadriiformes, the group that includes most extant shorebirds. As I have previously pointed out (Chiappe, 1991), there is no evidence to support such taxonomic allocation. The Cimolopterygidae are only known from elements of the forelimb and thoracic girdle (Brodkorb, 1963a; Olson & Parris, 1987; Tokaryk & James, 1989), and they are not the only Cretaceous charadriiforms (Olson, 1985; Olson & Parris, 1987). Furthermore, there are other shorebirds in the Cretaceous, such as *Gansus yumenensis* from the Early Cretaceous of China (Hou & Liu, 1984) and a new Presbyornithidae from the Late Cretaceous of Antarctica (Noriega & Tambussi, 1995; see below). Moreover, the morphology of the hind limb of the enantiornithine *Lectavis bretincola* from the Late Cretaceous Argentine Province of Salta (Chiappe, 1993; see below) suggest wading habits (Walker, 1981), making it equally likely that the footprints from Ingeniero Jacobacci belonged to an enantiornithine bird. Due to the lack of information, I

prefer to consider the identity of these footprints as indeterminate among avians.

METORNITHES Perle et al., 1993
ALVAREZSAURIDAE Bonaparte, 1991

Patagonykus puertai Novas, this volume

MATERIAL EXAMINED. HOLOTYPE: PVPH-37, isolated dorsal, synsacral and caudal vertebrae, along with portions of thoracic limb and coracoids, and pelvic girdle and limb (see Novas, this volume; in press).

LOCALITY AND HORIZON. Sierra del Portezuelo, Province of Neuquén, Argentina. Río Neuquén Formation, Late Cretaceous (Turonian-Coniacian; Legarreta & Gulisano, 1989).

REMARKS. *Patagonykus puertai* is unquestionably a new taxon, although the actual association of the different elements of PVPH-37 into a single individual or even a single species may be questionable (Chiappe et al., this volume). As emphasised by Novas (this volume; in press; see also Chiappe et al., this volume), several characters in the synsacrum, pelvic girdle and thoracic limb indicate a close relationship between *P. puertai*, the Patagonian *Alvarezsaurus calvoi* (Bonaparte, 1991; see below) and *Mononykus olecranus* from the Late Cretaceous of central Asia (Perle et al., 1993, 1994). *P. puertai* had the bizarre morphology of the thoracic limb of *M. olecranus* (Perle et al., 1993, 1994), but this bird was significantly larger than its closest relatives, being about the size of the non-avian theropod *Deinonychus antirrhopus* (Novas & Coria, 1990).

The Río Neuquén Formation is composed of fluvial deposits (Cazau & Uliana, 1973). In addition to *Patagonykus puertai*, this formation has provided remains of fishes, amphibians, turtles and titanosaurid dinosaurs (Novas & Coria, 1990; Bonaparte, 1992; Novas, pers. comm.).

Alvarezsaurus calvoi Bonaparte, 1991

MATERIAL EXAMINED. HOLOTYPE: MUCPv-54, articulated specimen including several cervical and dorsal vertebral remains, three synsacral and 13 caudal vertebrae, a scapula and part of a coracoid, portions of both ilia, femora, tibiae and proximal tarsals, and metatarsals and pedal phalanges (Bonaparte, 1991).

LOCALITY AND HORIZON. City of Neuquén, Province of Neuquén, Argentina. Río Colorado Formation, Bajo de la Carpa Member, Late Cretaceous (Coniacian-Santonian; Chiappe & Calvo, 1994).

REMARKS. Novas (this volume) included *Patagonykus puertai* and *Mononykus olecranus* along with *Alvarezaurus calvoi* in the Alvarezauridae, a taxon recognised by Bonaparte (1991) to include the latter species. Bonaparte (1991) remarked on the differences of alvarezsaurids to all theropods then known. In fact, this distinction was emphasised by his creation of the Alvarezsauria, a taxon that included both Alvarezsauridae and *A. calvoi*. Alvarezsauria, however, should be disregarded in that it only adds redundancy to the taxonomic system. Chiappe et al. (this volume) have presented evidence for the avian affinity of *A. calvoi*, which along with all alvarezsaurids are the sister-group of all birds other than *Archaeopteryx lithographica*.

The fluvial sandstones of the Bajo de la Carpa Member in the city of Neuquén have provided abundant remains of continental tetrapods such as the flightless bird *Patagopteryx deferrariisi* (Alvarenga & Bonaparte, 1992; see below), the enantiornithine bird *Neuquenomis volans* (Chiappe & Calvo, 1994; see below), notosuchian and baurusuchid crocodiles, dynilisid ophidians, small non-avian theropods, and titanosaurid sauropods (Bonaparte, 1991; Chiappe & Calvo, 1994). The beds of the Bajo de la Carpa Member have been regarded as high energy channels, deposited in a paleoenvironment of braided streams (Cazau & Uliana, 1973). In the area of the city of Neuquen, however, the characteristics of the fossil fauna and its preservation (i.e., small, articulated tetrapods, absent in other localities) suggest a lower energy depositional environment than the one envisioned previously (Chiappe & Calvo, 1994).

ORNITHOTHORACES Chiappe, 1995

MATERIAL EXAMINED. MACN-RN-976 (Fig. 5), an isolated cervical vertebra.

LOCALITY AND HORIZON. Estancia Los Alamitos, Cerro Cuadrado, Province of Río Negro, Argentina

(Bonaparte et al., 1984; Bonaparte, 1986. Los Alamitos Formation, Late Cretaceous (Campanian-Maastrichtian; Bonaparte, 1987).

REMARKS. This is the only avian specimen so far recorded from the rich fossil fauna of the Los Alamitos Formation (Bonaparte et al., 1984; Bonaparte, 1987, 1990). The presence of a well-developed ventral process (Figs 5F, G) indicates that MACN-RN-976 was a caudal element within the cervical series. MACN-RN-976 has a fully heterocoelic centrum (Figs 5F, G) and in this respect differs from both *Patagopteryx deferrariisi* and Enantiornithes in which the posterior cervicals have an incipient degree of heterocoely (Chiappe, 1992a, 1996). The presence of heterocoelic cervical vertebrae (including an incipient degree of development) diagnoses the clade formed by the common ancestor of Enantiornithes and modern birds plus all its descendants (unnamed node; see Chiappe, 1992a, 1995b, 1996; Chiappe & Calvo, 1994). The fragmentary nature of MACN-RN-976 makes it difficult to be more specific in its allocation.

The mudstone to sandstone deposits of Los Alamitos Formation at Cerro Cuadrado have yielded abundant remains of invertebrates, fishes, frogs, snakes, turtles, mammals and non-avian dinosaurs (Bonaparte et al., 1984; Bonaparte, 1987, 1990). Paleoenvironmentally, this formation has been interpreted as a shallow, permanent brackish body of water (Andreis, 1987; Bonaparte, 1990).

Patagopteryx deferrariisi
Alvarenga & Bonaparte, 1992

MATERIAL EXAMINED. HOLOTYPE: MACN-N-03, a partially complete specimen including several cervical, thoracic, synsacral and caudal vertebrae, portions of the wing and shoulder, part of the ilium and hind limb elements (Alvarenga & Bonaparte, 1992; Chiappe, 1992). REFERRED SPECIMENS: MACN-N-11 (Fig. 6), an almost complete skeleton; MUCPv-48 (Fig. 6), a complete hind limb associated with several fragmentary bones; MACN-N-10, MACN-N-14 and MUCP-207, fragmentary specimens (Chiappe, 1992a).

LOCALITY AND HORIZON. City of Neuquén, Province of Neuquén, Argentina. Río Colorado Formation, Bajo de la Carpa Member, Late Cretaceous (Coniacian-Santonian; Chiappe & Calvo, 1994).

REMARKS. *Patagopteryx deferrariisi* is a hen-sized, flightless bird known from the same deposits as *Alvarezsaurus calvoi* (see above). Alvarenga & Bonaparte (1992) and Alvarenga
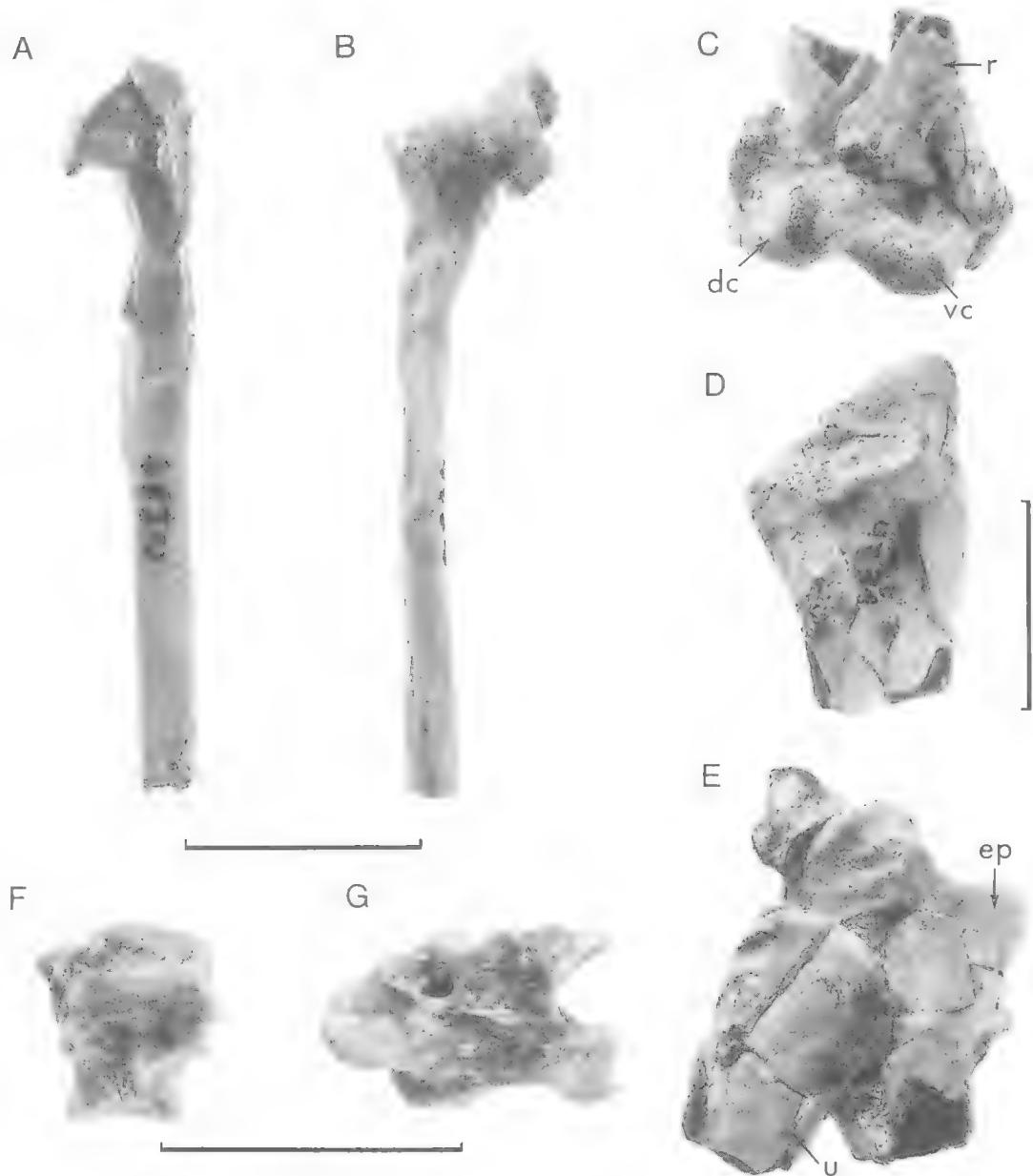
FIG. 5. Ornithurine specimens from the Maastrichtian Allen Formation at Salitral Moreno (A-E), and the Campanian-Maastrichtian Los Alamitos Formation at Estancia Los Alamitos (F, G), Province of Río Negro, Argentina. A, B, proximal half of left tibiotarsus (PVL-4730) in cranial (A) and lateral (B) views; C, distal end of the right humerus (PVL-4731) in cranial view (the radius is still articulated); D, proximal end of right ulna (PVL-4731) in ventral view; E, distal and proximal ends of right ulna and carpometacarpus (PVL-4731) in caudal and dorsal views, respectively. F, G, heterocoelic vertebra (MACN-RN-976) in cranial (F) and left lateral (G) views. dc, dorsal condyle of humerus; ep, extensor process of carpometacarpus; r, radius; u, ulna; vc, ventral condyle of humerus. Scales = 1cm.
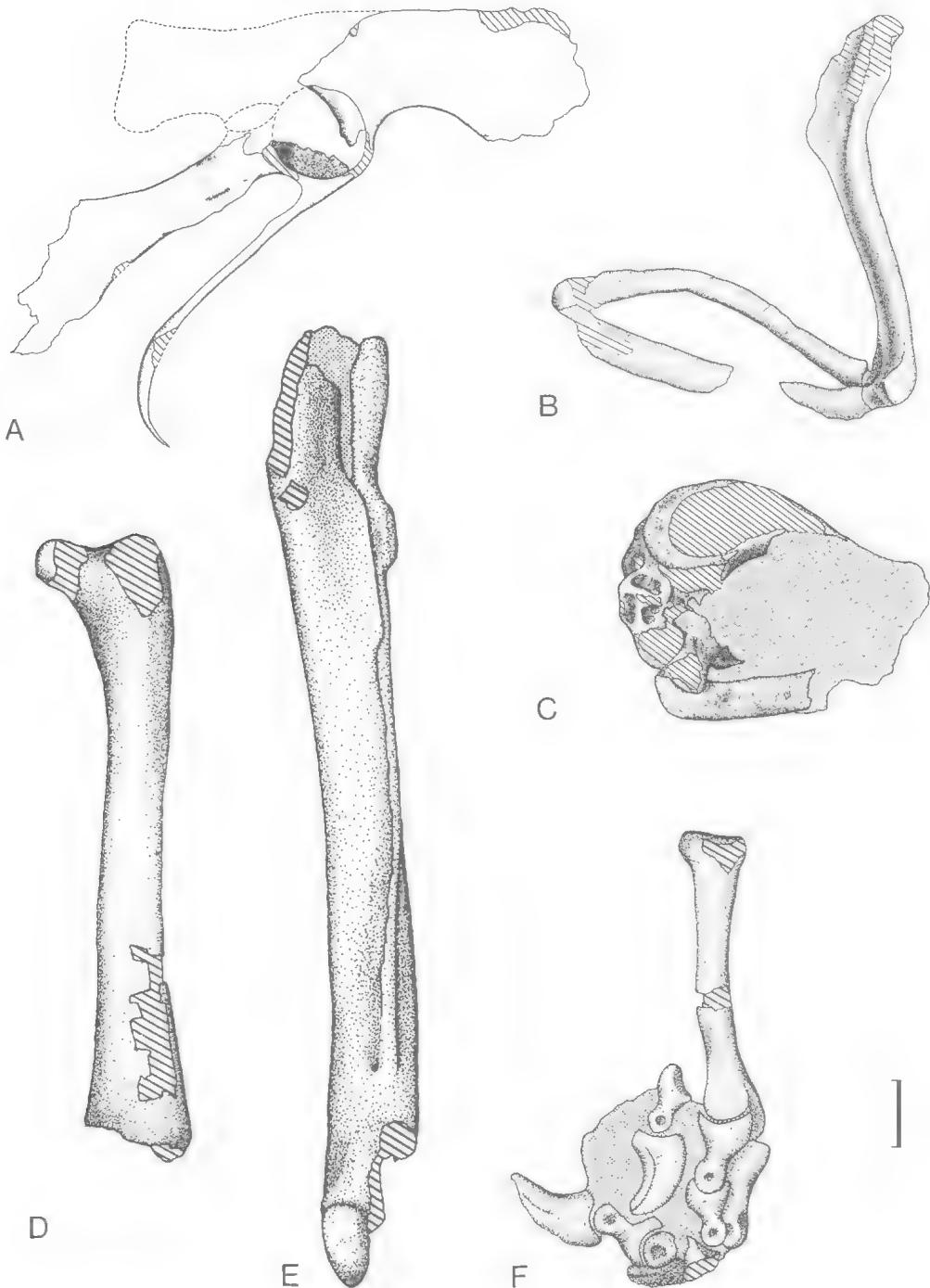
FIG. 6. *Patagopteryx deferrariisi* from the Coniacian-Santonian Río Colorado Formation at the city of Neuquén, Province of Neuquén, Argentina. A, right lateral view of the pelvis (MACN-N-11); B, ventral view of the right humerus, ulna and radius (MACN-N-11); C, right lateral view of the skull (MACN-N-11); D, cranial view of the left femur (MUCPv-48); E, cranial view of the left tibiotarsus and fibula (MUCPv-48); F, medial view of the left tarsometatarsus and phalanges MUCPv-48. Scale = 1cm.
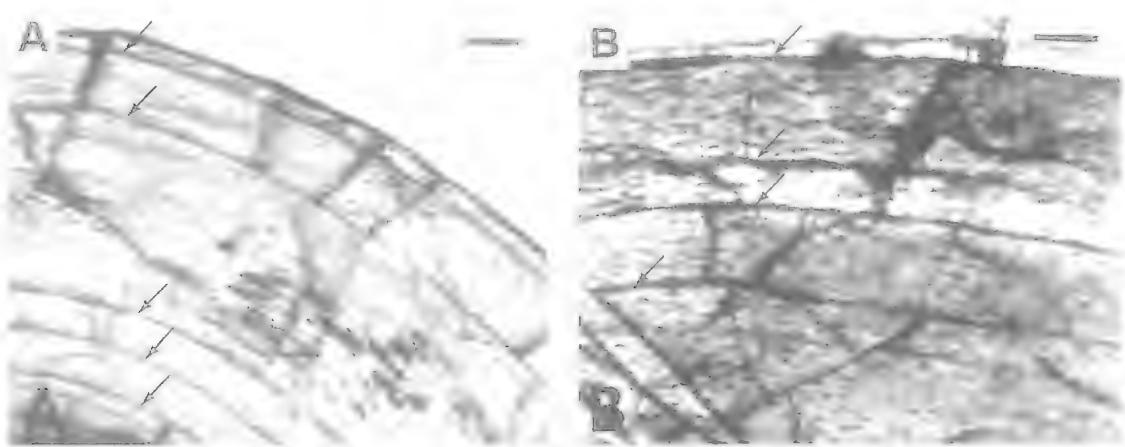
FIG. 7. Transverse sections of the enanthiornathine femora of PVL-4273 (A) and MACN-S-01 (B) from the Maastrichtian Lecho Formation at Estancia El Brete, Province of Salta, Argentina. Arrows show different lines of arrested growth (LAGs) in the compacta of these bones. Scales = 100μm.

(1993) related this species to the ratites (ostriches and its allies). A more parsimonious interpretation, however, supports the sister-group relationship between *P. deferrariisi* and Ornithurae (Chiappe, 1992a, 1995a, b; Chiappe & Calvo, 1994; Chiappe et al., this volume) (Fig. 2). Furthermore, the hypothesis of ratite affinities has been seriously challenged by recent histological studies documenting the presence of growth rings or lines of arrested growth (LAGs) in the compacta of the femora of both *P. deferrariisi* and the Enantiornithes (Chinsamy et al., 1994, 1995). This pattern of bone microstructure is absent in ornithurine birds, including ratites. The presence of cyclical pauses in bone deposition indicates that *P. deferrariisi*, and the Enantiornithes, had a rate of growth and associated physiology different from that of any modern bird (Chinsamy et al., 1994, 1995). In consequence, compelling osteological and histological evidence supports the hypothesis that *P. deferrariisi* acquired flightlessness independently from ratites and any other known flightless avian group (Chiappe, 1995a, b, 1996).

Curiously, Nessov (1993) recently related the Coniacian *Kuszholia mengi* (Nessov, 1992) from the Bissekty Formation at Dzhyrakuduk (Uzbekistan) to *Patagopteryx deferrariisi*. Nessov (1992) briefly described and illustrated two fragmentary synsacra, which appear to be all the available material, and concluded that *K. mengi* could have been either a bird or a non-avian theropod. Comparisons based on such limited evidence are very hard to make. The synsacrum of *K. mengi*, however, differs from that of *P. deferrariisi* in the presence of pleurocoels and a concave caudal articular surface.

ENANTIORNITHES Walker, 1981

MATERIAL EXAMINED. Large assortment of postcranial elements and a jaw housed at the Fundación-Instituto Miguel Lillo (Tucumán) and the Museo Argentino de Ciencias Naturales (Buenos Aires) (Walker, 1981; Chiappe, 1993, 1996).

LOCALITY AND HORIZON. Estancia El Brete, Department of Candelaria, Province of Salta, Argentina. Lecho Formation, Late Cretaceous (Maastrichtian; Bonaparte et al., 1977; Gómez Omil et al., 1989).

REMARKS. The Maastrichtian deposits of the Lecho Formation (Gómez Omil et al., 1989) have provided the most diverse and abundant collection of Gondwanan Cretaceous avians (Bonaparte et al., 1977; Bonaparte & Powell, 1980; Walker, 1981; Chiappe, 1991, 1993). Most of these avian remains were preliminarily studied by Walker (1981), who recognised them as part of a basal monophyletic group, the Enantiornithes. The phylogenetic relationships of the Enantiornithines have been a matter of debate (Chiappe, 1995a, b), although most authors regard them as basal birds. Recent cladistic analyses (Chiappe, 1995a, b, 1996; Chiappe & Calvo, 1994; Chiappe et al., this volume) support the hypothesis that the Enantiornithes is the sister-group of the clade formed by *Patagopteryx deferrariisi* and Ornithurae (Fig. 2). The number of species represented in the enantiornithine assemblage of El Brete is not yet known. It is likely,

however, that more than the four named species (see below) are present in this site. The fact that most bones are preserved disarticulated prevents a more precise evaluation of the actual specific diversity.

As mentioned in the discussion of *Patagopteryx deferrariisi*, recent histological studies of enantiornithine femora from this collection have documented the presence of LAGs in the compacta of these bones (Chinsamy et al., 1994, 1995) (Fig. 7). As pointed out by Chinsamy et al. (1994, 1995), cyclical bone deposition in Enantiornithes and other basal birds suggests important physiological differences with respect to their modern relatives.

The avian assemblage from El Brete (including the four species discussed below) is in association with remains of sauropod and non-avian theropod dinosaurs (Bonaparte et al., 1977; Bonaparte & Powell, 1980). The fine-grained sandstone entombing this assemblage has been regarded as deposited in a fluvial-lacustrine coastal plain, with abundant vegetation and ponds (Bonaparte et al., 1977).

Enantiornis leali Walker, 1981

MATERIAL EXAMINED. PVL-4035 (Fig. 8), a specimen including the proximal half of the humerus, the proximal portion of the scapula, and a coracoid (Walker, 1981). REFERRED SPECIMENS: PVL-4020, several thoracic limb and girdle elements; PVL-4039, PVL-4055, two isolated scapulae; PVL-4023, PVL-4181, two isolated ulnae.

LOCALITY AND HORIZON. Estancia El Brete, Department of Candelaria, Province of Salta, Argentina. Lecho Formation, Late Cretaceous (Maastrichtian; Bonaparte et al., 1977; Gómez Omil et al., 1989).

REMARKS. Unfortunately, Walker (1981) never described this species but just listed its name in the figure's caption. Below is a brief description of the holotype specimen. A more detailed description of all the available material would not
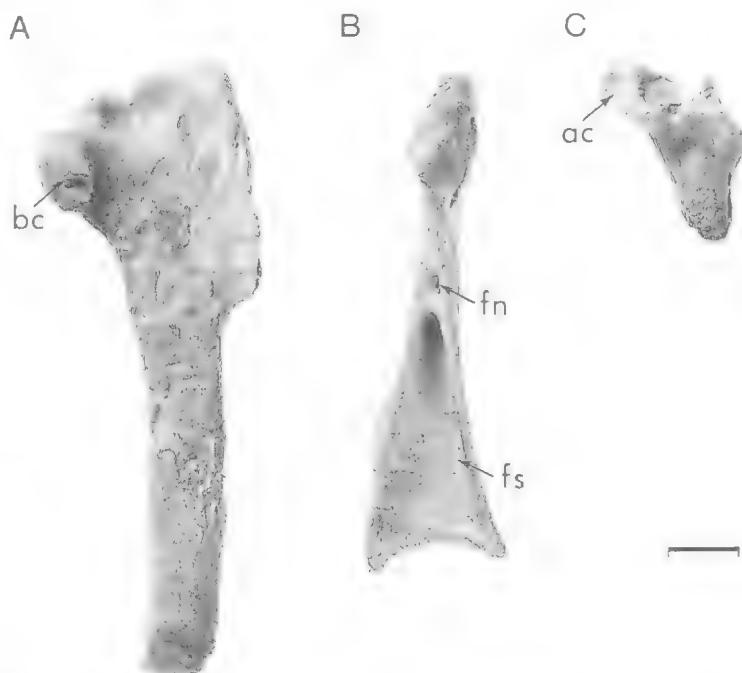
FIG. 8. *Enantiornis leali* (PVL-4035) from the Maastrichtian Lecho Formation at Estancia El Brete, Province of Salta, Argentina. A, proximal half of left humerus in cranial view; B, left coracoid in dorsal view; C, left scapula in medial view. ac=acromion, bc=bicipital crest, fn=foramen for supracoracoid nerve, fs=dorsal fossa of coracoid. Scale = 1cm.

be appropriate for this paper, but it will be provided elsewhere (Chiappe & Walker, in preparation).

The humerus of *Enantiornis leali* is very robust (Fig. 8A). The cranial side of the head is deeply concave. Distal to the head there is a deep, subcircular fossa. As in other enantiornithines, the bicipital crest is inflated and projected cranioventrally (Fig. 8A). The ventral tubercle is projected caudally and, most peculiarly, it is proximodistally perforated by a foramen. The pneumotricipital foramen is not developed. The coracoid is elongated (Fig. 8B). Its shoulder end is lateromedially compressed and it slopes dorsally. Medially, between the articular facet for the humerus and the acrocoracoid process, there is a subcircular tubercle. As typical of all enantiornithines, the dorsal surface of the coracoid is deeply excavated by a triangular fossa (Fig. 8B). Slightly above the vertex of this fossa is the dorsal opening of the foramen for the supracoracoid nerve. The position of this foramen differs from that in some other enantiornithines, where it opens inside the fossa. The scapula has a well-developed acromion (Fig. 8C). Its most charac-

teristic feature is the presence of a circular pit, medially situated between the acromion and the articular facet for the humerus.

Enantiornis leali was a fairly large bird, ranging between the size of a skua (*Catharacta skua*) and a turkey vulture (*Cathartes aura*). This species is represented by elements of the thoracic limb and girdle only, while all other named enantiornithine species from El Brete are known from elements of the pelvic limb (Chiappe, 1993). Thus, there is the possibility that *E. leali* might be a synonym of one of the three other enantiornithine species from El Brete.

Lectavis bretincola Chiappe, 1993

MATERIAL EXAMINED. HOLOTYPE: PVL-4021-1 (Fig. 9A, B), a tibiotarsus and tarsometatarsus missing the distal portion (Chiappe, 1993).

LOCALITY AND HORIZON. Estancia El Brete, Department of Candelaria, Province of Salta, Argentina. Lecho Formation, Late Cretaceous (Maastrichtian; Bonaparte et al., 1977; Gómez Omil et al., 1989).

REMARKS. The pedal morphology of *Lectavis bretincola* together with the inflation of the medial condyle of the tibiotarsus (Chiappe, 1993; Chiappe & Calvo, 1994) supports the allocation of this taxon in the Enantiornithes. The phylogenetic relationships of *L. bretincola* to other enantiornithines are not clearly understood, although a recent cladistic analysis indicates that this taxon lies outside the Avisauridae a group of small to medium size arboreal enantiornithines (Chiappe, 1993; see below). The very elongate tibiotarsus and tarsometatarsus of *L. bretincola* (Fig. 9A, B) suggest that it had wading habits (Walker, 1981).

Yungavolucris brevipedalis Chiappe, 1993

MATERIAL EXAMINED. HOLOTYPE: PVL-4053 (Fig. 9E, F), a nearly complete tarsometatarsus. REFERRED SPECIMENS: Several tarsometatarsi (PVL-4040, PVL-4052, PVL-4268, PVL-4692) (Chiappe, 1993).

LOCALITY AND HORIZON. Estancia El Brete, Department of Candelaria, Province of Salta, Argentina. Lecho Formation, Late Cretaceous (Maastrichtian; Bonaparte et al., 1977; Gómez Omil et al., 1989).

REMARKS. The presence of a metatarsal IV far smaller than metatarsals II and III, a tubercle on the dorsal face of metatarsal II, and a trochlea of metatarsal II broader than that of metatarsals II

and IV (Fig. 9E, F), identify this taxon as an enantiornithine (Chiappe, 1993). The phylogenetic relationships of *Yungavolucris brevipedalis* to other enantiornithines are not resolved, however. Like *Lectavis bretincola*, a cladistic analysis within the Enantiornithes indicates that it is not an avisaurid enantiornithine (Chiappe, 1993). The remarkable asymmetry of the tarsometatarsus of *Y. brevipedalis* (Fig. 9E, F) suggests that this species was probably aquatic (Walker, 1981).

AVISAURIDAE Brett-Surman & Paul, 1985

Soroavisaurus australis Chiappe, 1993

MATERIAL EXAMINED. HOLOTYPE: PVL-4690 (Fig. 9C, D), a tarsometatarsus (Chiappe, 1993). REFERRED SPECIMENS: PVL-4048, a tarsometatarsus articulated to several phalanges (Chiappe, 1993).

LOCALITY AND HORIZON. Estancia El Brete, Department of Candelaria, Province of Salta, Argentina. Lecho Formation, Late Cretaceous (Maastrichtian; Bonaparte et al., 1977; Gómez Omil et al., 1989).

REMARKS. *Soroavisaurus australis* can be regarded as an enantiornithine on the basis of the pedal characteristics mentioned for *Yungavolucris brevipedalis*, in addition to derived features shared with *Neuquenornis volans* (e.g., strong plantar projection of the medial rim of the trochlea of metatarsal III, transverse convexity of dorsal surface of the mid-shaft of metatarsal III; see Chiappe, 1993; Chiappe & Calvo, 1994). The avian affinity of *S. australis* was questioned by Brett-Surman & Paul (1985), who regarded it as non-avian dinosaur, together with *Avisaurus archibaldi* from the Late Cretaceous Hell Creek Formation of North America. The avian affinity of the Avisauridae, however, has been definitively established with the discovery of fairly complete specimens showing undisputable enantiornithine features (Chiappe, 1992b, 1993; Huchinson, 1993; Chiappe & Calvo, 1994).

A recent cladistic analysis (Chiappe, 1993; Varricchio & Chiappe, 1995) indicates that *Soroavisaurus australis* is the sister-group of the North American avisaurids (*Avisaurus archibaldi* and *A. gloriae*). This study demonstrates the non-monophyletic status of the El Brete enantiornithine assemblage, which is composed of taxa sharing a most recent common ancestor with North American taxa. The pedal morphology of
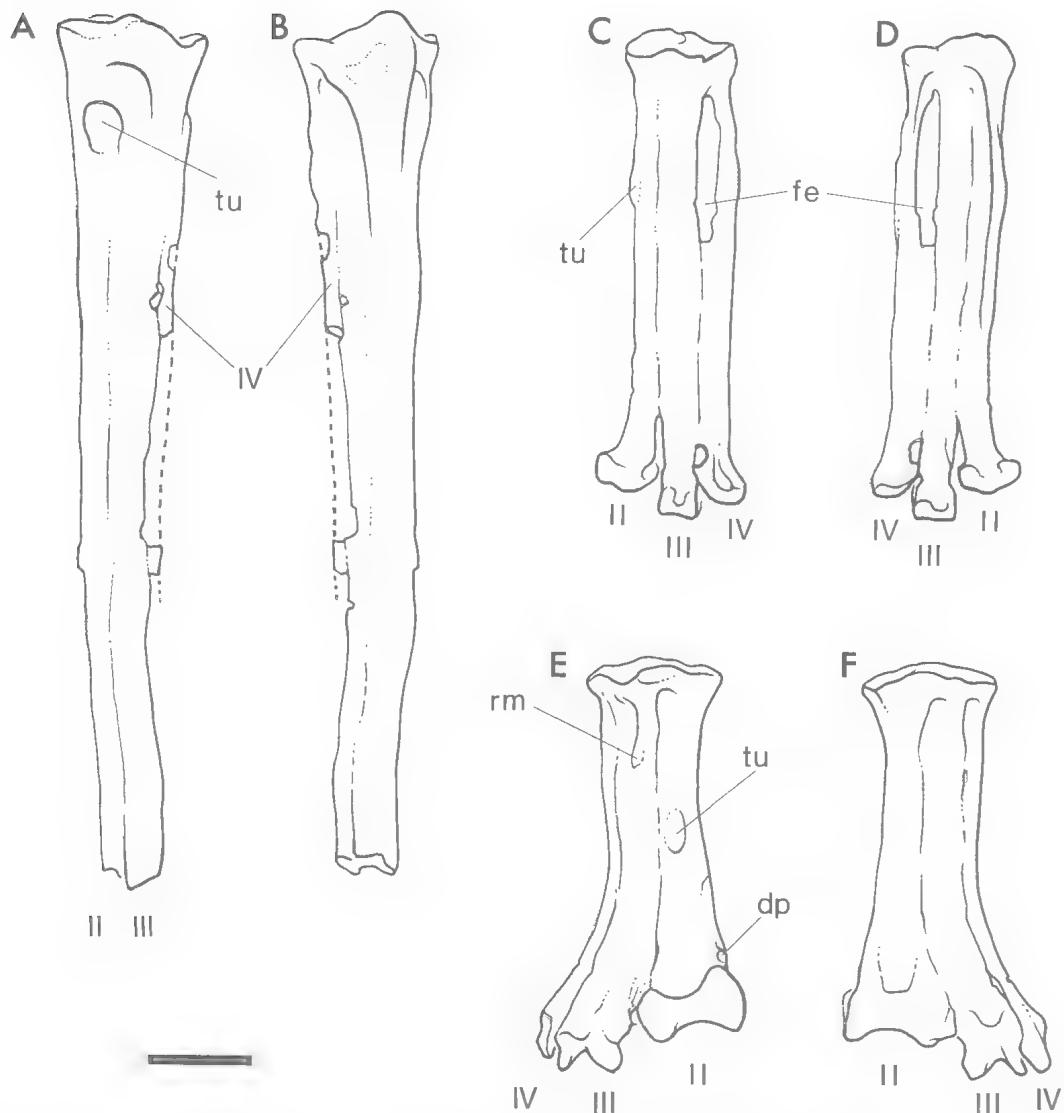
FIG. 9. Enantiornithine tarsometatarsi (dorsal and plantar views) from the Maastrichtian Lecho Formation at Estancia El Brete, Province of Salta, Argentina (after Chiappe, 1993). A, B, *Lectavis bretincola* (PVL-4021-1); C, D, *Soroavisaurus australis* (PVL-4690); E, F, *Yungavolucris brevipedalis* (PVL-4053). dp=dorsomedial projection of the distal end of metatarsal II, fe=fenestra between metatarsals III and IV, rm=elongate proximal ridge for muscle attachment, tu=tubercle for the attachment of the M. tibialis cranialis, II-IV, metatarsals II-IV. Scale = 1cm.

S. australis indicates that this species was capable of perching.

Neuquenornis volans
Chiappe & Calvo, 1994

MATERIAL EXAMINED. HOLOTYPE: MUCPv-142 (Fig. 10), fairly complete skeleton preserving the caudal portion of the skull, elements of the wing and shoulder, portions of the hind limb and a few thoracic vertebrae (Chiappe & Calvo, 1994). REFERRED SPECIMEN: MACN-RN-977, distal end of humerus.

LOCALITY AND HORIZON. MUCPv-142 comes from the city of Neuquén, Province of Neuquén. MACN-RN-977 was found at Puesto Tripailao, approximately 30km southwest of General Roca, Province of Río Negro, Argentina. Río Colorado Formation, Bajo de la
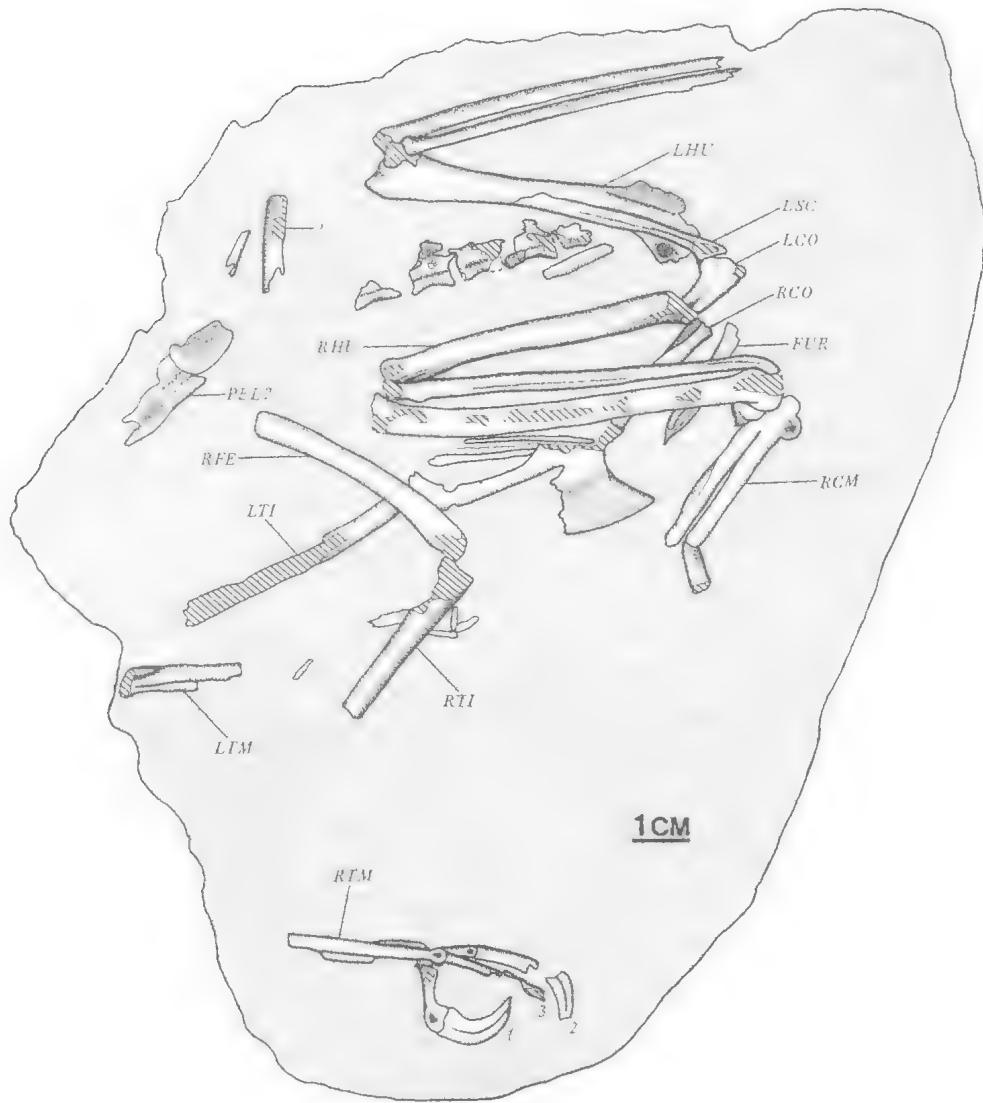
FIG. 10. *Neuquenornis volans* (MUCPv-142) from the Coniacian-Santonian Río Colorado Formation at the city of Neuquén, Province of Neuquén, Argentina (after Chiappe & Calvo, 1994). FUR=furcula, LCO=left coracoid, LHU=left humerus, LSC=left scapula, LTI=left tibiotarsus, LTM=left tarsometatarsus, PEL?=pelvis, RCM=right carpometacarpus, RCO=right coracoid, RFE=right femur, RHU=right humerus, RTI=right tibiotarsus, RTM=right tarsometatarsus.

Carpa Member, Late Cretaceous (Coniacian-Santonian; Chiappe & Calvo, 1994).

REMARKS. *Neuquenornis volans*, was a falcon-sized, active flyer whose enantiornithine affinity is supported by numerous synapomorphies in the thoracic limb (e.g., distal end of humerus craniocaudally compressed) and girdle (e.g., coracoid with a convex lateral margin and a wide triangular fossa on its dorsal surface), pelvic limb (e.g.,

well-developed posterior trochanter of femur) and vertebral column (e.g., lateral grooves on thoracic centra) [see Chiappe & Calvo (1994) for a complete list of characters] (Fig. 10). The pedal anatomy indicates that *N. volans* is a member of the Avisauridae (Chiappe, 1993) and like *Soroavisaurus australis*, was capable of perching (Chiappe & Calvo, 1994). Specimen MACN-RN-977, although fragmentary, is identical in

size and morphology to the holotype of *Neuquenornis volans*.

ORNITHURAE Haeckel, 1866

MATERIAL EXAMINED. PVL-4730, a proximal half of a tibiotarsus (Powell, 1987). PVL-4731, portions of humerus, ulna, radius, carpometacarpus, and the proximal phalanx of the major digit (Fig. 5).

LOCALITY AND HORIZON. Salitral Moreno, 20km south of General Roca, Province of Rio Negro, Argentina. Allen Formation, Late Cretaceous (Maastrichtian; Powell, 1987).

REMARKS. These two specimens were found in the same quarry (Powell, pers. comm.). PVL-4730 exhibits two well-developed cnemial crests, typical of ornithurine birds (Figs 5A, B). PVL-4731 is significantly larger than PVL-4730 and, although these specimens have not been studied in detail, it probably represents a different species (Fig. 5C-E). The presence of a well-projected, pointed metacarpal process of the carpometacarpus (Fig. 5E) and a cranio-caudally expanded proximal phalanx of the major digit both support the allocation of PVL-4731 to the Ornithurae.

The fossiliferous beds of the Allen Formation at Salitral Moreno have provided a variety of dinosaurian remains including hadrosaurids (Powell, 1987), titanosaurid sauropods (Salgado & Coria, 1993), non-avian theropods (Coria, pers. comm.) and turtles (Salgado & Coria, 1993).

NEORNITHES Gadow, 1893
GAVIIDAE Allen, 1897

Neogaeornis wetzeli Lambrecht, 1929

MATERIAL EXAMINED. HOLOTYPE: GPMK-123, a right tarsometatarsus (Lambrecht, 1929).

LOCALITY AND HORIZON. West end of Bahía San Vicente, Province of Concepción, Chile. Quiriquina Formation, Late Cretaceous (Campanian-Maastrichtian; Biró Bagóczky, 1982).

REMARKS. Lambrecht (1929) considered *Neogaeornis wetzeli* as a hesperornithiform, a group of Cretaceous marine foot-propelled divers mostly known from North American beds (Olson, 1985; Chiappe, 1995a). Brodkorb (1963b) remarked on the affinity of this species to the hesperornithiform *Baptornis advenus*, including both in the Baptornithidae, in which he was followed by Martin & Tate (1976). The hesperornithiform relationship of *N. wetzeli*, however, was recently challenged by Olson (1992). After

repreparing the specimen, Olson (1992) regarded it as a loon and placed it within the foot-propelled, modern Gaviidae.

The Quiriquina Formation has afforded a great variety of invertebrates, fishes and reptiles (Biró-Bagóczky, 1982). The depositional environment of the Quiriquina Formation appears to have been a tidal plain (Biró-Bagóczky, 1982).

ANTARCTICA

AVES Linnaeus, 1758
METORNITHES Perle et al., 1993
ORNITHOTHORACES Chiappe, 1995
ORNITHURAE Haeckel, 1866
NEORNITHES Gadow, 1893
GAVIIDAE Allen, 1897

MATERIAL EXAMINED. A single specimen preserving parts of the skull, limbs, and a few cervical vertebrae (Chatterjee, 1989).

LOCALITY AND HORIZON. Marambio (Seymour) Island, Antarctic Peninsula. López de Bertodano Formation, Late Cretaceous (Campanian-Maastrichtian; Medina et al., 1989).

REMARKS. The first report of an Antarctic Cretaceous bird was given by Chatterjee (1989), who reported a loon-like bird from the Campanian-Maastrichtian López de Bertodano Formation of Marambio (Seymour) Island. Chatterjee's (1989) allocation of this fossil within the modern gaviiforms was corroborated by Olson (1992). This specimen represents the most southern ocurrence of gaviiforms and along with *Neogaeomis wetzeli* (Lambrecht, 1929; see above) the oldest known loon.

The López de Bertodano Formation is primarily composed of marine medium-grained to silty sandstones (Zinsmeister, 1982; Medina et al., 1989), enclosing a diverse assemblage of microrganisms (Martinez Machiavello, 1987), plants (Askin, 1990) and invertebrates (Zinsmeister, 1982), along with fishes (Grande & Chatterjee, 1987), plesiosaurs (Gasparini et al., 1984) and mosasaurs (Gasparini & del Valle, 1984) among vertebrates. Medina et al. (1989) have summarised the paleoenvironment of this unit as ranging from an offshore marine shelf to near shore facies, including intertidal plains and deltaic environments.

PRESBYORNITHIDAE Wetmore, 1926

MATERIAL EXAMINED. MLP 93-1-3-1 and MLP 93-1-3-2, partial skeletons, apparently conspecific (Noriega & Tambussi, 1995).

LOCALITY AND HORIZON. Cape Lamb, Vega Island, Antarctic Peninsula. Cape Lamb strata, correlated to the López de Bertodano Formation (Unit B), Late Cretaceous (Campanian-Maastrichtian; Medina et al., 1989).

REMARKS. MLP 93-1-3-1 was briefly described by Noriega & Tambussi (1995). These authors regarded it as a member of the anseriforms Presbyornithidae (Ericson, 1992), an extinct group of Paleogene wading birds (Olson, 1985) previously represented in the southern continents by the Eocene *Telmabates* from Patagonia (Howard, 1955). If this interpretation is correct, these new findings expand the record of presbyornithids to the Cretaceous.

The marine deposits from where these fossils were recovered belong to the Maastrichtian section of the Late Cretaceous Cape Lamb strata (Zinsmeister, pers. comm.). These beds have been correlated to those of the López de Bertodano Formation at Marambio (Seymour) Island, although regarded as more marginal deposits within the same basin (Pirrie et al., 1991). The associated fauna primarily includes ammonites, gastropods, fishes and plesiosaurs (Zinsmeister, pers. comm.). The fact that these birds were found in marine deposits does not necessarily mean that they were oceanic birds, although it suggests that at least they inhabited marine littoral environments.

AFRICA

AVES Linnaeus, 1758

MATERIAL EXAMINED. Several footprints (Figs 4B, C, D) of unknown repository (Lockley et al., 1992).

LOCALITY AND HORIZON. 16km east of Agadir, Morocco (Ambroggi & Lapparent, 1954). Calcareous Maastrichtian beds (no formational name is given), Late Cretaceous.

REMARKS. Ambroggi & Lapparent (1954) regarded as avian a series of small tridactyl footprints (Figs 4B, C, D), about 3cm long, associated with other footprints of non-avian dinosaurs and lizards. The bird tracks were briefly described and poorly illustrated. One of them (Fig. 4D) was interpreted as having been made by a semi-palmate bird.

METORNITHES Perle et al., 1993

MATERIAL EXAMINED. Hind limb elements of two con-specific specimens (Krause, pers. comm.).

LOCALITY AND HORIZON. Near the village of Berivotra, Mahajanga Basin, northwestern Madagascar. Maevarano Formation, Late Cretaceous (Campanian; Krause et al., 1994).

REMARKS. The specimens belong to a new, undescribed taxon. Retention of several plesiomorphic characters (e.g., incompletely fused tibiotarsus and tarsometatarsus) suggest that this is a very primitive bird, although its phylogenetic placement remains to be analysed. This finding is extremely important because these specimens not only represent the first Mesozoic African bird known by skeletal evidence but also the first pre-Late Pleistocene avian from Madagascar.

The fossiliferous section of the Maevarano Formation consists of fluvial white sandstones. The poorly known Late Cretaceous fossil record of Madagascar has become substantially improved with the recent discovery of an ensemble of vertebrates from the Maevarano Formation that, in addition to the above mentioned birds, includes fishes, frogs, turtles, lizards, snakes, crocodiles, dinosaurs and mammals (Krause et al., 1994, in press).

DISCUSSION

In spite of a recent plethora of new findings, the Gondwanan record of Mesozoic birds is still very limited and restricted to the Cretaceous. This record is most diverse and extensive in South America, where birds are known from the Aptian to the Maastrichtian and from many localities. Within Australasia it is limited to the Early Cretaceous (Aptian-Albian) of Australia and in Antarctica it is restricted to the latest Cretaceous (Maastrichtian). Likewise, in Africa only a few footprints and a recently discovered new taxon from the Late Cretaceous of Morocco (Maastrichtian) and Madagascar (Campanian), respectively, stand as evidence of presence of Mesozoic birds in this continent.

Although the record is limited, the Mesozoic birds from Gondwana have contributed significantly to the growth of knowledge on early avian evolution. Taxa such as the Enantiornithes and *Patagopteryx deferrariisi* were among the first to provide evidence about the series of transformations which occurred between the primitive morphology of *Archaeopteryx lithographica* and that of more derived birds such as Hesperornithiformes and Ichthyornithiformes (Walker, 1981; Chiappe, 1992a, 1995a, b, 1996; Chiappe & Calvo, 1994). More recently, the histological

studies carried out on the bones of Enantiornithes and *P. deferrariisi* led to the first inferences on the rate of growth and related physiology of basal birds derived from reliable evidence (Chinsamy et al., 1994, 1995).

Using the Gondwanan record of Mesozoic birds for large scale paleobiogeographic analysis (e.g., Bonaparte, 1986, 1991; Chiappe, 1991; Noriega & Tambussi, 1995) is considered unreliable on the basis of the still insufficient evidence. For example, a Gondwanan origin of the Enantiornithes was claimed by Bonaparte (1986, 1991) on the basis of assumptions such as their 'oldest' record and their 'high' taxonomic diversity in South America [see Humphries & Parenti (1986) for a discussion of these theoretical issues]. This idea, however, has been shown to be an erroneous generalization based on an inadequate record. At present an abundant diversity of enantiornithine birds is known worldwide during the Cretaceous, and their oldest record to date is not in Gondwanan continents but in Europe and Asia (Chiappe & Calvo, 1994; Chiappe, 1995a; Sanz et al. 1995).

A general look at the Mesozoic record of birds from Gondwana reflects a broad, although punctuated, spectrum of geographic distributions, habitats and modes of life. During the Cretaceous, Gondwanan birds occupied a large latitudinal range, from near the equator to close to the Southern pole. These fossils have been recovered primarily from inland environments, although birds probably inhabited marine realms and seashores as well. The paleoenvironmental conditions of the localities in which Mesozoic Gondwanan birds were found range from warm and arid to near-freezing, at least during winter. A variety of modes of life have been inferred from their anatomy, such as flightless cursorials to foot-propelled divers, waders and perching active fliers.

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PHYLOGENETIC POSITION OF *MONONYKUS* (AVES: ALVAREZSAURIDAE) FROM THE LATE CRETACEOUS OF THE GOBI DESERT

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In order to assess the phylogenetic relationships of *Mononykus*, a cladistic analysis was performed. Using velociraptorine theropods as outgroups, the analysis resulted in a single most parsimonious cladogram. In this cladogram the monophyletic Alvarezsauridae (including *Mononykus* and the Argentine *Alvarezsaurus* and *Patagonykus*) is the sistergroup of all other birds except *Archaeopteryx*. The monophyly of Aves (= Avialae sensu Gauthier) is supported by seven unambiguous synapomorphies, four of which are present in *Mononykus*. These characters include fewer than 26 caudal vertebrae, caudal vertebrae with short distal prezygapophyses, teeth with unserrated crowns and a caudal tympanic recess opening only inside the tympanic cavity. The monophyly of Metornithes (Aves exclusive of *Archaeopteryx*) is supported by six unambiguous synapomorphies all of which occur in *Mononykus*. Among these characters are the presence of prominent ventral processes on the cervicodorsal vertebrae, a carpometacarpus, a prominent antitrochanter in the pelvis and a rectangular, carinate sternum. Furthermore, six synapomorphies (all present in *Mononykus*) ambiguously diagnose both Aves and Metornithes. The distribution among avian and nonavian taxa of all these characters is discussed. Several authors have criticised the hypothesis of avian relationships for *Mononykus*. In this paper we address those criticisms. We also discuss the rationale of testing phylogenetic hypotheses within a cladistic framework and establish that our critics have not furnished much beyond a priori speculation. □ *Birds, Cretaceous, phylogeny, homology.*

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One of the central problems in palaeontology is the origin of the major groups of terrestrial amniotes. One of these, birds, has received intense scrutiny ever since, and even before, the first specimens of *Archaeopteryx lithographica* were collected. Since the publication of the London specimen in 1861 (Meyer, 1861), this and subsequent specimens of *Archaeopteryx* have been key elements in discussions of bird origins.

Surprisingly, except for specimens of *Hesperornis* and *Ichthyornis*, it took over a hundred years for significant new specimens of basal birds to be recognised (Chiappe, 1995a, b). The last 15 years, however, has seen surprising progress on this front and many important new specimens of basal birds have been described (e.g., Walker, 1981; Kurochkin, 1985; Sanz et al., 1988, 1995; Chiappe, 1991, 1993, 1995a, b; Alvarenga & Bonaparte, 1992; Sanz & Buscalioni, 1992; Sereno & Rao, 1992; Wellnhofer, 1992, 1993; Zhou et al., 1992; Chiappe & Calvo, 1994; Hou et al., 1995).

Mononykus olecranus (Perle et al., 1993) from the Late Cretaceous of Mongolia, is one of the most unusual of these (Fig. 1). *Mononykus* is larger than most basal birds and instead of well developed wings it possessed stout arms that are ridiculously short, terminating in a robust hand with a hypertrophied digit (Perle et al., 1993, 1994; Norell et al., 1993a). Many other aspects of its morphology are a peculiar melange of primitive, derived and just plain weird (Perle et el., 1994). Apparently, *Mononykus* was a common element of the Late Cretaceous fauna of Central Asia (Norell et al., 1993a). In the last few years many specimens have been collected at several Mongolian localities by the Mongolian American Museum Paleontological Project (Novacek et al., 1994; Dashzeveg et al. 1995). Furthermore, specimens collected during the 1920s from the Djadokhta Formation at Bayn Dzak (Norell et al., 1993a) and the Iren Dabasu Formation in northern China have been recently found in the collections of the AMNH. In earlier papers, we predicted that such a highly recognisable mor-

phology may foster discovery of members of this clade in other faunas, where material is usually more poorly preserved. Recently, close relatives of *Mononykus* have been identified in the Late Cretaceous of Argentine Patagonia (Novas, this volume). Because of this discovery a discussion of the phylogenetic relationships of *Mononykus* fits the scope of a symposium on Gondwanan dinosaurs.

In our 1993 paper we proposed a hypothesis based on shared derived characters placing *Mononykus* in a sister-group relationship to all birds except *Archaeopteryx* (Perle et al., 1993, 1994). The discovery of *Patagonykus* and the reinterpretation of *Alvarezsaurus* as another relative of *Mononykus* (see Novas, this volume) documented that the Alvarezsauridae (e.g., *Alvarezsaurus*, *Mononykus*, and *Patagonykus*) comprise a diverse, but monophyletic group of primitive birds not only present in the Late Cretaceous of central Asia but also in southern South America and probably in western North America (Holtz, 1994a). In this paper, we summarise the evidence supporting the sistergroup relationship of Alvarezsauridae to all other birds except *Archaeopteryx*, making emphasis on *Mononykus* [see Novas (this volume) for information on *Alvarezsaurus* and *Patagonykus*]. Phylogenetic relationships among Alvarezsauridae are discussed elsewhere (see Novas, this volume).

FIG. 1. Skeletal reconstruction of *Mononykus* (modified from Perle et al., 1994).

MATERIALS AND METHODS

ANATOMICAL NOMENCLATURE. Anatomical terms mostly follow Baumel & Witmer (1993), using the English equivalents of the Latin terminology. The extrapolation of modern avian nomenclature to successive sister groups and even non-avian theropods is based on acceptance of the theropodan hypothesis of avian origins (Ostrom, 1976a; Gauthier, 1986). For most features of modern birds it is possible to trace homologous structures in more basal birds and non-avian theropods.

TAXONOMIC NOMENCLATURE. In recent years there has been disagreement as to what taxa comprise Aves. Traditionally it is used to name a group including all species descended from the last common ancestor of *Archaeopteryx*

lithographica and modern birds (Neornithes), although Hennig's (1969, 1981) concepts of total group (e.g., Ax, 1987; Patterson, 1993) and crown group (e.g., Gauthier, 1986; Norell et al., 1993b; Perle et al., 1993, 1994) have been also applied to this clade. Using the latter concept, Gauthier (1986) recognised the term Avialae to name the clade traditionally named with the term Aves (see also Rowe & Gauthier, 1992; De Queiroz & Gauthier, 1992). In doing this, Gauthier (1986) replaced the term Neornithes — traditionally used to name this group — by redefining the term Aves. In this paper — based on the preferences of the senior author — we follow the traditional nomenclature and therefore we use the term Aves to name a clade composed of the common ancestor of *Archaeopteryx lithographica* and modern birds (Neornithes) plus all its descendants. Note that this definition uses a node-based phylogenetic definition (see De Queiroz & Gauthier, 1992) and not a character-based — usually feathers — definition of the taxon Aves. Therefore, the inclusion of a particular taxon within Aves is only based on its genealogical history. The collective terms 'modern birds' and 'birds' refer to all members of the monophyletic taxa Neornithes and Aves, respectively, while 'nonavian theropods' refer to all theropod outgroups of birds, used without any implication of monophyly.

PHYLOGENETIC ANALYSIS. The character analysis includes 99 characters (Appendix 1). Ten of these are multistate characters. All characters were treated as additive (any two states are

separated by a number of steps that equals their absolute arithmetic difference) except for four multistate characters (34, 40, 64 & 92) that were treated as non-additive (any two states are separated by a single step). The data set was processed using the computer program 'Hennig 86' (Farris, 1988). Using the implicit enumeration (ie) command — which generates trees that are certain to be of minimal length — a single most parsimonious tree was obtained (Fig. 2). In order to address the character optimisation in alternative topologies, the resultant tree was re-rooted by using the dos equis (xx) command of 'Hennig 86' (see Discussion).

Because our objective is to assess relationships rather than diagnose all groups, only characters in which the derived state (or at least one of the derived states of a multistate character) is present in two or more different terminal taxa were analyzed. In order to avoid influence on the consistency index, derived characters exclusive to a single terminal taxon were not included (Carpenter, 1988; Wiley et al., 1991). As the result of the phylogenetic analysis, however, some characters are autapomorphies of different taxa (e.g., characters 64a, 98; Fig. 2).

Polarisation of character states used in the character analysis was established by using velociraptorine theropods as the outgroup. We are aware that the use of a different outgroup (e.g., Troodontidae, Oviraptoridae) might result in a different tree topology. This decision, however, was based on a combination of previous phylogenetic research with the anatomical information currently at hand: Several recent phylogenetic hypotheses on maniraptoran dinosaurs have considered velociraptorine theropods (e.g., *Deinonychus, Velociraptor, Adasaurus*) as closely related to birds (Gauthier, 1986; Novas, 1992; Holtz, 1994b) and the available information on other nonavian maniraptoran dinosaurs (e.g., troodontids, oviraptorids, segnosaurids) is still limited.

The analysed ingroup included taxa hypothesised to be closely related to *Mononykus* such as the Argentine *Alvarezsaurus* (Bonaparte, 1991) and *Patagonykus* (Novas, this volume), along with the best represented avian taxa: *Archaeopteryx*, *Iberomesornis*, Enantiornithes, *Patagopteryx*, Hesperornithiformes, Ichthyornithiformes and Neornithes.

MATERIAL EXAMINED. The anatomical information on Velociraptorinae was based mostly on the AMNH and YPM's specimens of *Deinonychus antirrhopus* (Ostrom, 1969) and the holotype, and several new unpublished specimens (see Norell et al., 1992) of *Velociraptor mongoliensis* (Osborn, 1924). Additional information was taken from Ostrom (1969, 1974, 1976b, 1990) and Barsbold (1983).

Five specimens of *Mononykus olecranus* were used in this study: the holotype (MGI 107/6) and specimens MGI N100/99, MGI 100/975, MGI 100/977 and IGM 100/1001. The holotype specimens of *Alvarezsaurus calvoi* (Bonaparte, 1991) and *Patagonykus puertai* (Novas, this volume) from the Late Cretaceous of Patagonia (Argentina) were also studied.

The osteological data on *Archaeopteryx lithographica* was taken from De Beer (1954), Wellnhofer (1974, 1992, 1993), Ostrom (1976a), Martin (1983), Whetstone (1983), Walker (1985), Bühler (1985), Witmer (1990) and Elzanowski & Wellnhofer (1995) as well as examination of the Eichstätt, Solnhofen and London specimens, and a cast of the Berlin specimen. The holotype specimen of *Iberomesornis romerali* (Sanz et al., 1988; Sanz & Bonaparte, 1992) was also studied. Almost all the available material of Enantiornithes was examined, including undescribed specimens from the Late Cretaceous of Argentina (El Brete; see Chiappe, 1993, 1996) and specimens of *Enantiornis leali* (Walker, 1981; Chiappe, this volume), *Lectavis bretincola* (Chiappe, 1993), *Yungavolucris brevipedalis* (Chiappe, 1993), *Soroavisaurus australis* (Chiappe, 1993), *Neuquenornis volans* (Chiappe & Calvo, 1994), *Concornis lacustris* (Sanz & Buscalioni, 1992; Sanz et al., 1995) and *Cathayornis yandica* (Zhou et al., 1992). Casts of the enantiomithines *Sinornis santensis* [Sereno & Rao, 1992; arguments supporting its inclusion within Enantiornithes are presented elsewhere (Chiappe, 1995b)], *Avisaurus gloriae* (Varricchio & Chiappe, 1995), *Avisaurus archibaldi* (Brett-Surman & Paul, 1985; Chiappe, 1992b, 1993) and *Nanantius eos* (Molnar, 1986) were also studied. All the available material of *Patagopteryx deferrariisi* (Alvarenga & Bonaparte, 1992; Chiappe, 1992a, 1996) was also examined. The anatomical data on the Hesperornithiformes mostly derives from the seminal monograph of Marsh (1880), and papers of Martin & Tate (1976), Martin (1980, 1983, 1984), Bühler et al. (1988), Witmer (1990) and Elzanowski (1991). Specimens at the AMNH, FMNH, UK and YPM were also examined. Information on Ichthyornithiformes was derived mainly from Marsh's (1880) description of *Ichthyornis dispar* and *Ichthyornis victor* and the study of specimens labeled as *Ichthyornis* sp. at the YPM. The skeletal material of different representatives of several groups of modern paleognathes and neognathes (Aves) was surveyed. This information was supplemented by such general osteological papers such as Jollie (1957), Webb (1957), Bellairs & Jenkin (1960), King & McLelland (1984) and Baumel & Witmer (1993).

Institutional Abbreviations. AMNH, American Museum of Natural History (New York); FMNH, Field Museum of Natural History (Chicago); MGI, Mongolian Geological Institute (Ulan
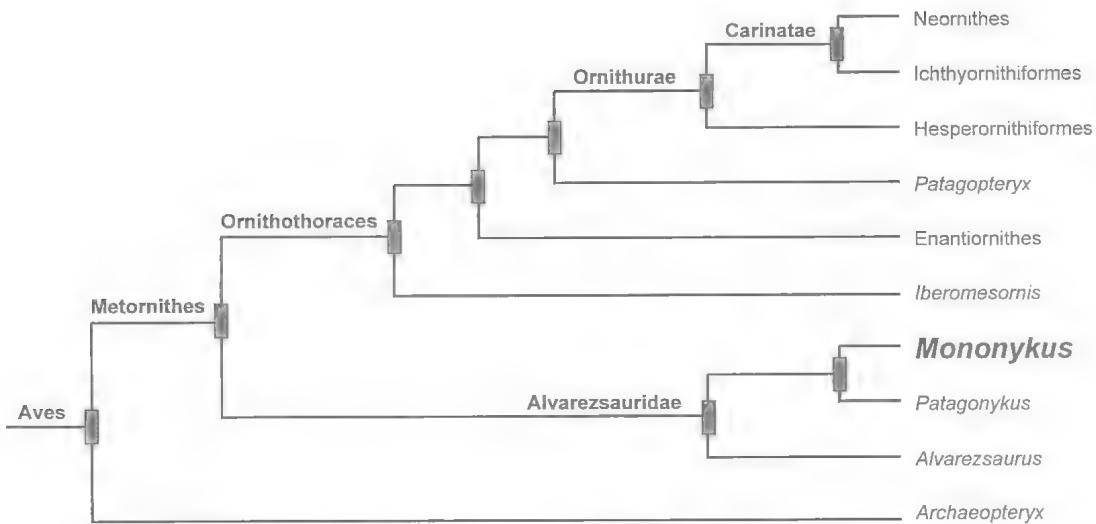
FIG. 2. Analysis cladogram. Coding: asterisked characters (*) have equivocal optimization; the symbol (-) indicates a character reversal; 'a' and 'b' refer to states 1 and 2, respectively, of a multistate character (see Appendix 1). NODE 1 (Aves = Avialae sensu Gauthier, 1986): 11*, 15*, 19a, 23a, 46*, 59a*, 68*, 71, 72*, 74*, 81, 83*, 84*, 85a, 86*, 87, 88, 90*, 95*, 96*. NODE 2 (Metornithes): 6*, 8*, 11*, 13, 14a*, 15*, 29, 30, 31*, 34a*, 34b*, 36*, 39, 41*, 44, 45*, 46*, 47*, 51*, 55*, 59a*, 68*, 69, 72*, 74*, 83*, 84*, 86*, 90*, 92a*, 95*, 96*. NODE 3 (Ornithothoraces): 1*, 3*, 5*, 6*, 7*, 8*, 10*, 11*, 14a*, 18, 21*, 23b, 24*, 25, 26*, 27, 31*, 32*, 34a*, 34b*, 36*, 37*, 38, 40a*, 40b*, 41*, 45*, 47*, 50*, 51*, 53*, 54a*, 55*, 60*, 63*, 67*, 70*, 72*, 83*, 84*, 86*, 90*, 92a*, 93*, 96*, 97*. NODE 4: 1*, 3*, 5*, 6*, 7*, 10*, 11*, 16, 17, 19b*, 21*, 24*, 26*, 31*, 32*, 34b*, 35, 36*, 37*, 40a*, 40b*, 45*, 47*, 50*, 51*, 53*, 54a*, 55*, 56, 60*, 62, 63*, 67*, 70*, 72*, 73, 76*, 83*, 84*, 86*, 90*, 92a*, 93*, 96*, 97*. NODE 5: 2*, 4*, 6*, 7*, 10*, 11*, 19b*, 28, 31*, 32*, 40a*, 40b*, 45*, 47*, 49, 54b, 55*, 61, 66, 67*, 70*, 72*, 76*, 82, 85b, 87*, 90*, 92a*, 93*, 94*, 97*. NODE 6 (Ornithurae): 2*, 4*, 6*, 7*, 9, 11*, 12, 14b, 19b*, 20, 22, 32*, 40a*, 40b*, 42, 43, 48, 52, 57, 58, 59b, 64b, 65, 67*, 70*, 72*, 87*, 91*, 92a*, 93*, 94*, 97*, 99*. NODE 7 (Carinatae): 11*, 32?, 33, 40b*, 70*, 87*, 91*, 92a*, 92b*, 99*. NODE 8 (Alvarezsauridae, see Novas, this volume): 6*, 8*, 11*, 14a*, 23*, 31*, 34a*, 34b*, 36*, 41*, 45*, 47*, 48*, 51*, 55*, 75*, 78*, 79*, 80*, 83*, 84*, 89, 90*, 92a*, 96*. NODE 9: 6*, 8*, 11*, 14a*, 23*, 31*, 34a*, 36*, 41*, 47*, 48*, 51*, 75*, 76, 77, 78*, 79*, 80*, 83*, 84*, 90*, 92a*, 96*. Resultant apomorphies: *Mononykus* (64a), Enantiornithes (98), Neornithes (98). In nodes 4 and 5, if character 76 is synapomorphic, it becomes a reversal in node 6 (Ornithurae).

Bator); UK, Museum of Natural History, University of Kansas (Lawrence); YPM, Yale Peabody Museum (New Haven).

CHARACTER ANALYSIS

This analysis resulted in a single most parsimonious cladogram with low homoplasy (length, 143; rescaled consistency index, 0.76; retention index, 0.81). In this cladogram (Fig. 2) the monophyly of Alvarezsauridae (*Mononykus*, *Patagonykus* and *Alvarezsaurus*; see Novas, this volume) is supported, and this group is the sistergroup of all birds other than *Archaeopteryx*. In an earlier paper we coined the term 'Metornithes' to name this monophyletic group (Perle et al., 1993).

Below we describe those characters synapomorphic of both Aves and Metornithes and which are known to be present in *Mononykus*. Reference is made to the condition in the ingroup and outgroup taxa, along with that found in other nonavian theropods. Missing entries are in most cases not mentioned (see data matrix in Appendix 1 for character scoring).

CHARACTERS SUPPORTING THE MONO-PHYLY OF AVES. The monophyly of Aves (= Avialae sensu Gauthier, 1986) is supported by seven unambiguous synapomorphies (Fig. 2). Four of these (character states 19a, 71, 81 & 85a) are present in *Mononykus*. The available material of *Mononykus* and the remaining Alvarezsauridae does not allow determination of the condition in two of these characters (87 & 88), while *Mononykus* shows the primitive condition for the remaining character (23a). The four avian synapomorphies present in *Mononykus* are:
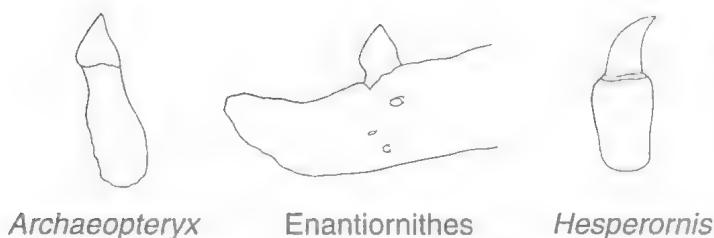
FIG. 3. Avian dental morphology of *Archaeopteryx*, the enantiornithine *Cathayornis* and *Hesperornis*. Drawings not to scale.

1) Caudal vertebral count smaller than 25-26 elements (character 19). In modern birds, the tail is composed of a series of free caudal vertebrae and the pygostyle. The free vertebral count of modern birds ranges between four and eight, being typically between five and seven (Verheyen, 1960). The pygostyle is usually composed of five or six vertebrae (Baumel & Witmer, 1993). Hence, the total caudal count of modern birds (free caudals + pygostyle) includes fewer than 15 elements. Among hesperornithiforms, Marsh (1880) estimated 12 elements in the tail of *Hesperornis* and Martin & Tate (1976) illustrated 14 caudal vertebrae in *Baptornis*. *Iberomesornis* has eight free caudals and a large pygostyle. Some of the elements forming the pygostyle of *Iberomesornis* are clearly distinguishable. Sanz & Bonaparte (1992) correctly estimated that 10 to 15 elements form the pygostyle. Therefore, *Iberomesornis* has a caudal count of no more than 23 vertebrae. In *Archaeopteryx*, the number of caudal elements ranges from 20 to 23 in the different specimens (Ostrom, 1976a).

Velociraptorines and other nonavian theropods, on the contrary, have much longer tails with at least 36 vertebrae (Osborn, 1916; Lambe, 1917; Osmolska et al., 1972; Madsen, 1976). There are approximately 36 to 40 caudal vertebrae in *Deinonychus* (Ostrom, 1969). Curiously, the troodontid *Sinornithoides* (Russell & Dong, 1993a) has 27 preserved caudals and, as estimated by these authors, a total caudal count of no more than 30 elements.

The number of caudal vertebrae in *Mononykus* is significantly lower than in the outgroup and similar to the number found in *Archaeopteryx*. In specimens MGI N100/99 and MGI 100/975, 19 caudal elements are preserved. Some distal elements are missing but based on the size and morphology of the last preserved elements we are

confident in our estimate that the number of caudal elements of *Mononykus* was not larger than 25-26.

2) Teeth with unserrated crowns (character 71). Neornithine birds lack teeth, but a variety of basal birds bear both cranial and mandibular dentition. In the teeth of Hesperornithiformes, Ichthyornithiformes and *Archaeopteryx* the enamel of the crowns is smooth, lacking serrations (Martin et al., 1980; Martin, 1985) (Fig. 3). The same condition is present in the Early Cretaceous enantiornithine *Cathayornis* (Zhou et al., 1992).

In contrast, adult velociraptorine theropods have serrated crowns (Osborn, 1924; Ostrom, 1969; Currie et al., 1990) (Fig. 4). This is the case for most other non-avian theropods in which the enamel is serrated in at least some areas of the crown tooth (Currie et al., 1990; Fiorillo & Currie, 1994; see Ostrom, 1991 for a few exceptions). In the description of *Archaeornithoides*, Elzanowski & Wellnhofer (1992) considered the absence of dental serrations as a synapomorphy of the clade formed by the latter taxon and birds. The only, and very fragmentary, specimen of *Archaeornithoides* is clearly a juvenile and therefore not an adequate specimen for phylogenetic inferences. As we have recently shown, dromaeosaurid neonates lack serrations as well (Norell et al., 1994), suggesting that in dromaeosaurids, teeth became serrated during postnatal ontogeny. A similar ontogenetic modification is known to occur in extant non-avian archosaurs (i.e., crocodiles). The absence of dental serrations in the juveniles of theropods closely related to birds might indicate that the avian tooth morphology arose through heterochrony (Norell et al., 1994).

In our preliminary description of *Mononykus* (Perle et al., 1993) and in a later paper (Perle et al., 1994), we described a tooth that was found isolated inside the fragmentary skull. The crown of this tooth possesses rostral and caudal carinae and lacks serrations (Fig. 5). Confirmation of this dental morphology has come from a recently discovered articulated specimen (MGI 100/977), including the skull, from the Djadokhta-like red beds of Ukhaa Tolgod (Dashzeveg et al., 1995), in the southwestern Mongol Gobi. In specimen MGI 100/977 both cranial and mandibular teeth

FIG. 4. Teeth of *Velociraptor* (AMNH6518). Note the serrated margins.

FIG. 5. Electron micrograph of a tooth of *Mononykus* (MGI 107/6). Note the complete absence of serra-

are preserved in their natural position, and they lack serrations.

3) Caudal tympanic recess opens inside the collumelar recess and not in the paroccipital process (character 81). The caudal tympanic recess of modern neornithine birds, the recess formed by the caudal evagination of the tympanic air sac (Witmer, 1990), consistently opens inside the collumelar recess (Witmer, 1990; Baumel & Witmer, 1993). A similar configuration of the tympanic region occurs in Hesperornithiformes and *Archaeopteryx* (Witmer, 1990) (Fig. 6).

The caudal tympanic recess is well-preserved in a recently discovered braincase of *Velociraptor* (Norell et al., 1992). CAT scan imaging has shown that, as in modern birds, it extends inside the paroccipital process. An important difference with birds (Witmer, pers. comm.), however, is that the caudal tympanic recess opens on the rostral surface of the paroccipital process, outside the collumelar recess. This braincase configuration is known to occur in several non-avian theropods such as *Dromaeosaurus* and *Itemirus* (Currie, 1995), *Struthiomimus* and a new maniraptoran from the St Mary River Formation (Witmer & Weishampel, 1993; Witmer, pers. comm.) and *Protoavis* (Chatterjee, 1991), which we do not regard as a bird (see Chiappe, 1995b). Interestingly, Currie & Zhao (1993b) have mentioned that this external paroccipital opening is absent in troodontids.

The tympanic region of *Mononykus* resembles that of *Archaeopteryx*, *Hesperornis* and neor-

FIG. 6. Braincase morphology of *Archaeopteryx* (redrawn from Walker, 1985) and *Mononykus* (MGI 107/6). Note that the caudal tympanic recess does not open into the paroccipital process. AFQ=articular facet for the quadrate, AOF=antorbital fossa, MX=maxilla, POP=paroccipital process, Q=quadrate, RTR=rostral tympanic recess. Drawings not to scale.

Deinonychus

PRZ

Gallimimus

PRZ

Archaeopteryx

PRZ
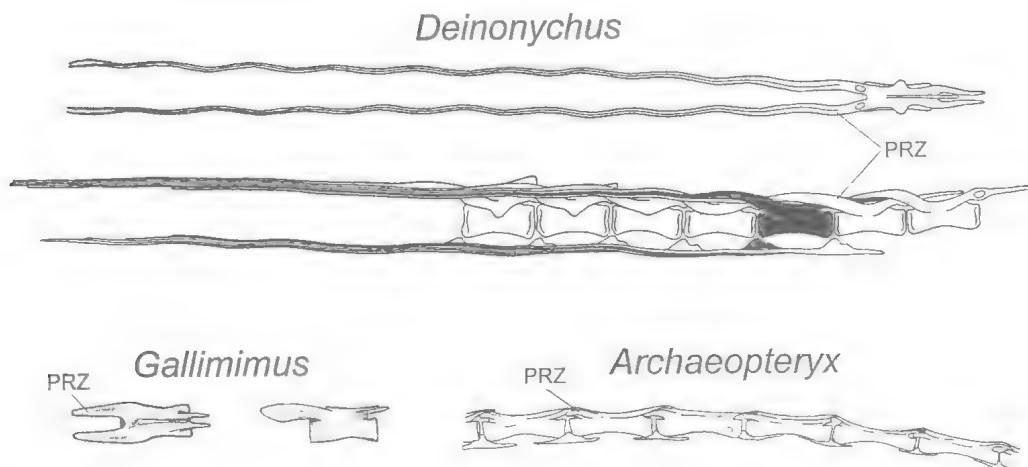
FIG. 7. Caudal vertebrae of *Deinonychus* (after Ostrom, 1969) and *Gallimimus* (twenty second caudal; after Barsbold & Osmólska, 1990) in dorsal and lateral views. Caudal vertebrae of *Archaeopteryx* (tenth to fifteenth vertebrae; after Wellnhofer, 1974). PRZ=prezygapophysis. Drawings not to scale.

nithine birds. In the braincase preserved in the holotype specimen (Perle et al., 1994), the paroccipital process is not perforated by any foramen (Fig. 6) and the caudal tympanic recess opens in the collumelar recess (as in *Archaeopteryx*; contra Currie, 1995).

4) Short or reduced prezygapophyses in distal caudal vertebrae (character 85). The caudal vertebrae of modern birds typically have small, or even absent, prezygapophyses. Caudal prezygapophyses are absent in Hesperomithiformes (Marsh, 1880; Martin & Tate, 1976) and *Patagopteryx* (Chiappe, 1992a). In Ichthyornithiformes (Marsh, 1880), distinct but short prezygapophyses are present in the proximal caudals. Within the Enantiornithes, this character is not determinable in the caudal vertebrae of either *Concornis* (Sanz et al., 1995) or *Cathayornis* (Zhou et al., 1992). Nevertheless, a caudal vertebra preserved in an as yet undescribed enantiornithine specimen from Alabama (Lamb et al., 1993) has short prezygapophyses. The free caudal vertebrae of *Iberomesornis* (Sanz & Bonaparte, 1992) also bear short or reduced prezygapophyses as well. In *Archaeopteryx*, the caudal prezygapophyses appear to be fairly short, extending only slightly over the preceding vertebra (Fig. 7). This is the condition present in the Eichstätt specimen (Wellnhofer, 1974). In the London specimen, the prezygapophyses seem to be longer, however it is hard to provide an accurate estimate of their cranial projection because the articulations between the centra are not ex-

posed. In any case, it is clear that the prezygapophyses of the London specimen are far shorter than those of several non-avian theropods (see below), projecting less than 25% the length of the preceding vertebra.

The presence of remarkably long, rod-like prezygapophyses in the caudal series of velociraptorine theropods is well known (Ostrom, 1969, 1990) (Fig. 7). In *Deinonychus*, the elongate prezygapophyses are present in all caudals distal to the eighth or ninth element (Ostrom, 1969). Elongated prezygapophyses — yet not to extent of the extremely apomorphic condition seen in velociraptorines — are known to occur in the distal caudals of several non-avian theropods, in particular in the middle and distal portions of the tail (see Lambe, 1917; Ostrom, 1969; Barsbold, 1974). The ornithomimid *Gallimimus*, for example (Fig. 7), has distal caudal prezygapophyses extending up to two-thirds the length of the preceding vertebra (Barsbold & Osmólska, 1990) and in *Allosaurus* they extend for at least half the length of the preceding element (Madsen, 1976).

In *Mononykus*, the caudal prezygapophyses, and in particular those of the distal portion of the tail, are short and do not extend to the preceding vertebra. Interestingly, in contrast to those non-avian theropods with long caudal prezygapophyses, the proximal caudal vertebrae of *Mononykus* have prezygapophyses that are longer — though still relatively short — than those of the distal vertebrae (Fig. 8).
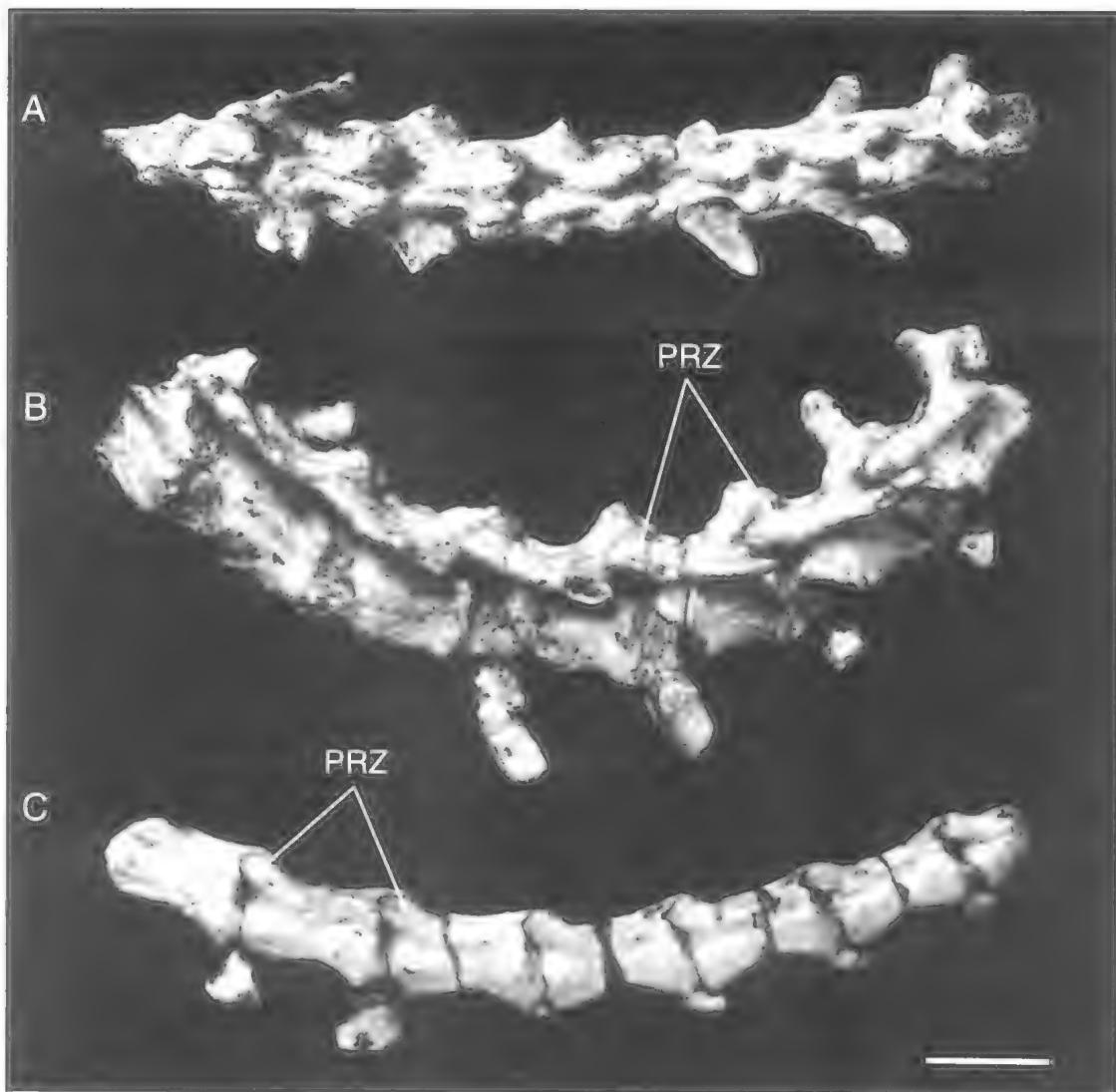
FIG. 8. Caudal vertebrae of *Mononykus* (MGI 100/975). A, B, first? to seventh? vertebrae in dorsal and lateral view. C, 13th? to 19th? vertebrae in lateral view. Note the short prezygapophyses (PRZ). Scale = 1cm.

CHARACTERS SUPPORTING THE MONO-PHYLY OF METORNITHES. The monophyly of Metornithes (Perle et al., 1993), the clade composed of the closest common ancestor of *Mononykus* and Neornithes plus all its descendants, is supported by six unambiguous synapomorphies. All these synapomorphies are present in *Mononykus*. These synapomorphies are:

1) Prominent ventral processes on cervicodorsal vertebrae (character 13,). The cervicodorsal vertebrae of ornithurine birds (Neornithes,

Hesperornithiformes and Ichthyornithiformes) bear prominent ventral processes for the origin of M. longus colli ventralis (Chiappe, 1992a, 1996), a primary depressor of the neck (Zusi, 1962) (Fig. 9). These processes are also well developed in the cervicodorsal vertebrae of *Iberomesornis*, Enantiornithes and *Patagopteryx deferrariisi*, but they appear to be absent in *Archaeopteryx* (Chiappe, 1996).

In contrast, ventral processes are only slightly developed in velociraptorine theropods (Ostrom, 1969; Gauthier, 1986) (Fig. 9) and are usually

Deinonychus   *Sinraptor*
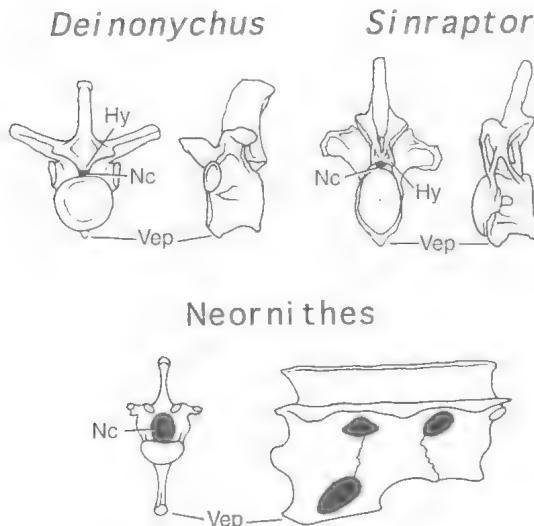
Neornithes

FIG. 9. Dorsal vertebrae of *Deinonychus* (fourth? dorsal; after Ostrom, 1969) and *Sinraptor* (first dorsal; after Currie & Zhao, 1993a) in caudal and lateral views. Dorsal vertebrae of a neornithine bird in cranial and lateral views. Note the large neural canal and the absence of hypantrum in neornithine birds. Hy=hyposphene, Nc=neural canal, Vep=ventral process. Drawings not to scale.

absent (Osborn, 1916; Lambe, 1917; Madsen, 1976; Ostrom, 1978; Bonaparte et al., 1990) or barely developed (Russell & Dong, 1993a; Currie & Zhao, 1993a) in other non-avian theropods (Fig. 9).

In *Mononykus* ventral processes are present in the cervicodorsal region (Fig. 10). In the holotype specimen (Perle et al., 1994), the last two transitional vertebrae between cervicals and dorsals have small ventral processes but the first preserved dorsal bears a much more prominent, well-developed process (Fig. 10). The development of the ventral process of the first(?) dorsal of *Mononykus* resembles that of more advanced birds and not the blunt process of velociraptorine theropods.

2) Sternum of longitudinal rectangular shape (character 29). In the Ornithurae the sternum is typically large and rectangular, with its craniocaudal axis longer than the transverse axis. In these birds, the ratio between maximum length and maximum width (including lateral trabeculae) (ML/MW) is usually larger than 1.4 (Chiappe, 1996). (In some birds with broad sterna, such as Cuculidae, Caprimulgidae, Picidae and Trogonidae, this ratio is slightly smaller). This derived condition is also present in the Enan-

tiornithes. The sterna of the enantiornithines *Neuquenornis* (Chiappe & Calvo, 1994) and *Concornis* (Sanz et al., 1995) are large and rectangular, with a ML/MW ratio of at least 1.66 in the former taxon. In *Archaeopteryx*, in contrast, the sternum is transversely broader than long as has been recently described by Wellnhofer (1993) in the 'Solenhofer Aktien-Verein' specimen (Fig. 11).

In velociraptorines and other non-avian theropods in which sternal ossifications are known, these are formed by two quadrangular plates, which sometimes fuse to each other (Lambe, 1917; Barsbold, 1983; Bonaparte et al., 1990; Currie & Zhao, 1993a). Currie & Zhao (1993a) considered the absence of fusion between sternal plates as related to immaturity. In *Velociraptor* (Fig. 11), the ML/MW ratio is about 1.04 (Barsbold, 1983) and approximately 0.95 and 0.77 in the oviraptorids *Oviraptor* and *Ingenia*, respectively (Barsbold, 1983).

Mononykus has a longitudinally rectangular sternum (Perle et al., 1993, 1994), as it has been described in the holotype specimen and corroborated by specimen MGI 100/977 in which the sternum is preserved in natural position. The ML/MW ratio of the sternum of the holotype specimen of *Mononykus* is at least 1.93 (Fig. 12).

3) Ossified sternal keel (character 30). In neornithine birds generally (except in ratites and some other flightless birds), the sternum has a large ventral keel from which the main flight muscles arise. A sternal carina is also present in ichthyornithiforms (Marsh, 1880), in the enantiornithines *Neuquenornis* (Chiappe & Calvo, 1994), *Concornis* (Sanz et al., 1995), and *Cathayornis* (Zhou et al., 1992), but it is absent in hesperornithiforms (Marsh, 1880) and *Archaeopteryx* (Wellnhofer, 1993) (Fig. 11).

In velociraptorines (Fig. 11) and most non-avian theropods in which sternal ossifications are known, the carina is completely absent (Lambe, 1917; Barsbold, 1983; Bonaparte et al., 1990). An exception has been recently reported by Currie & Zhao (1993a) who described a low, blunt ventral keel in the sternum of *Sinraptor*, a taxon related to *Allosaurus*.

In *Mononykus* the sternum has a well-developed ventral keel (Fig. 12). Although carinate, this sternum differs from all other carinate sterna in that it is subtriangular in cross-section and not T-shaped. This latter condition has been considered an apomorphy of *Mononykus* (Perle et al., 1994).

4) Distal carpals fused to metacarpals forming a carpometacarpus (character 39). Neornithine
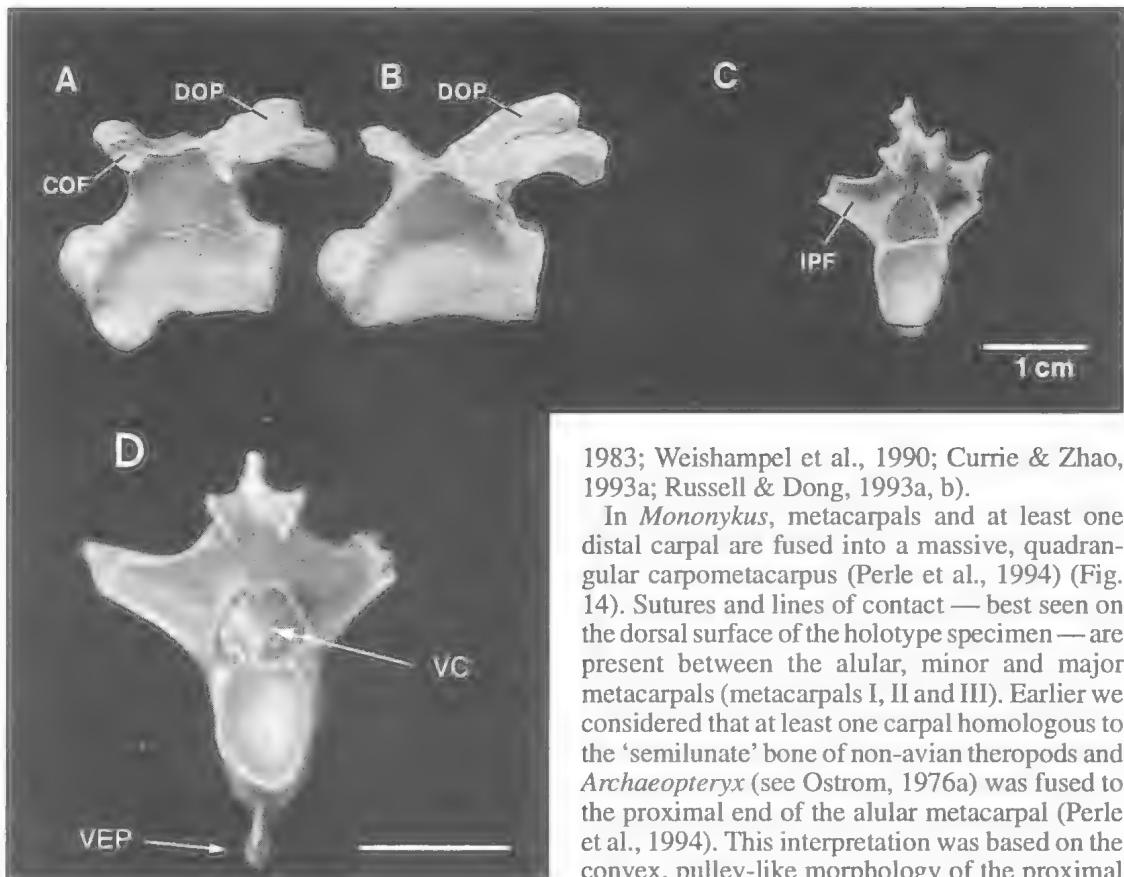
FIG. 10. Dorsal vertebrae of *Mononykus* (MGI 107/6).
A, D, anterior first preserved vertebra in lateral and
caudal view; B, C, anterior second preserved vertebra
in lateral and caudal view. COF=costal fovea
(parapophysis), DOP=dorsal process, IPF=in-
frapostzygapophysial fossa, VC=vertebral canal,
VEP=ventral process. Scale = 1cm.

birds have a carpometacarpus formed by the
fusion of several central and distal carpals with
the metacarpals of the alular, major and minor
digits (digits I, II, III) (Fig. 13). Fusion of carpal
and metacarpal bones to form a carpometacarpus
also occurs in ichthyornithiforms, enantior-
nithines and *Patagopteryx* (Chiappe, 1996). In
contrast a carpometacarpus does not occur in
Archaeopteryx (Fig. 13), in which the metacar-
pals fuse neither with each other nor with the
distal carpals (Ostrom, 1976a).

The carpals and metacarpals of velociraptorine
theropods are not fused to each other (Ostrom,
1969, 1990) (Fig. 13), a condition common to all
non-avian theropods (Madsen, 1976; Barsbold,

1983; Weishampel et al., 1990; Currie & Zhao,
1993a; Russell & Dong, 1993a, b).

In *Mononykus*, metacarpals and at least one
distal carpal are fused into a massive, quadran-
gular carpometacarpus (Perle et al., 1994) (Fig.
14). Sutures and lines of contact — best seen on
the dorsal surface of the holotype specimen — are
present between the alular, minor and major
metacarpals (metacarpals I, II and III). Earlier we
considered that at least one carpal homologous to
the 'semilunate' bone of non-avian theropods and
Archaeopteryx (see Ostrom, 1976a) was fused to
the proximal end of the alular metacarpal (Perle
et al., 1994). This interpretation was based on the
convex, pulley-like morphology of the proximal
end of the carpometacarpus (Fig. 14) which
resembles the condition in *Archaeopteryx* and
non-avian maniraptoran dinosaurs. Were the
'semilunate' carpal not fused to the alular
metacarpal, the proximal end of the latter would
be nearly flat to slightly concave, as in non-avian
theropods.
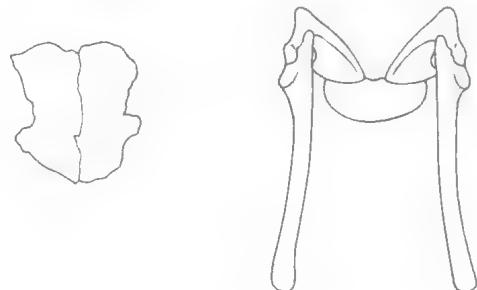
FIG. 11. Sterna of *Velociraptor* (after Barsbold, 1983)
and *Archaeopteryx* (after Wellnhofer, 1993) in
ventral view. Drawings not to scale.
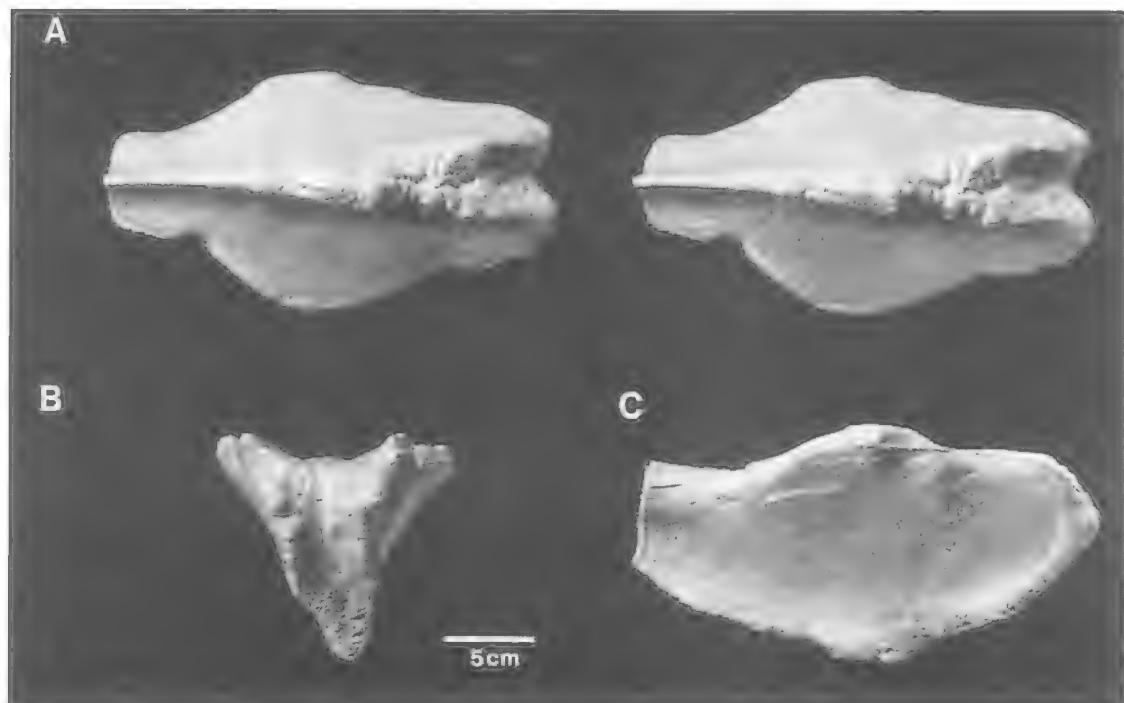
FIG. 12. Sternum of *Mononykus* (MGI 107/6). A, stereopair in ventral view; B, cranial view; C, lateral view.

5) Pelvis with prominent antitrochanter (character 44, Appendix 1). In the caudodorsal angle of the acetabulum of ornithurine birds there is a prominent articular facet, the antitrochanter, typically formed by contributions of the ischium and ilium (Fig. 15). A prominent antitrochanter is found in both Enantiornithes and *Patagopteryx* but it is absent in *Archaeopteryx* (Chiappe, 1996) (Fig. 15).

In contrast, a prominent antitrochanter is not developed in velociraptorine theropods (Ostrom, 1969, 1976b) (Fig. 15) nor in any other non-avian theropod (see Osborn, 1916; Osmólska et al., 1972; Madsen, 1976; Weishampel et al., 1990; Currie & Zhao, 1993a; Zhao & Currie, 1993). Russell & Dong (1993a) reported the presence of an antitrochanter in the troodontid *Sinornithoides*, but the absence of detailed illustrations along with the fact that we have not seen the specimen prevents comparisons with those of birds.

In *Mononykus*, the pelvis has a very robust and well-developed antitrochanter (Perle et al., 1994) (Fig. 16). The degree in which both ischium and ilium contribute to the formation of the antitrochanter of *Mononykus* is obscured by the fact that in adult specimens such as the holotype, the ischium and ilium are fused. The fact that the robust antitrochanter of *Patagonykus* (Novas, this volume) is formed by equal contributions of both ilium and ischium suggests that this was probably the case for *Mononykus*. In contrast to most ornithurine and enantiornithine birds the antitrochanter is developed below the dorsal margin of the acetabulum, and its main axis is not oriented dorsocaudally but caudoventrally (Figs 15, 16). A similar position and orientation of the antitrochanter, however, is present in *Patagopteryx* (Chiappe, 1992a, 1996).

6) Ischium more than two-thirds of pubic length (character 69). In neornithine birds the pubis is longer than the ischium but this difference is typically much less than one-third the length of the ischium (Fig. 15). The pubis is only slightly longer than the ischium in hesperornithiforms, *Patagopteryx* (Fig. 15) and the enantiornithines *Concornis* (Sanz et al., 1995) and *Sinornis* (Sereno & Rao, 1992). In contrast, in *Archaeopteryx* the length of the ischium is between 44 to 48% that of the pubis (Wellnhofer, 1985, 1992) (Fig. 15). Interestingly, the ischium appears to be proportionally shorter in the 'Solenhofer Aktien-Verein' specimen, recognised as a different species — *Archaeopteryx bavarica* instead of *Archaeopteryx lithographica* — by Wellnhofer (1993).
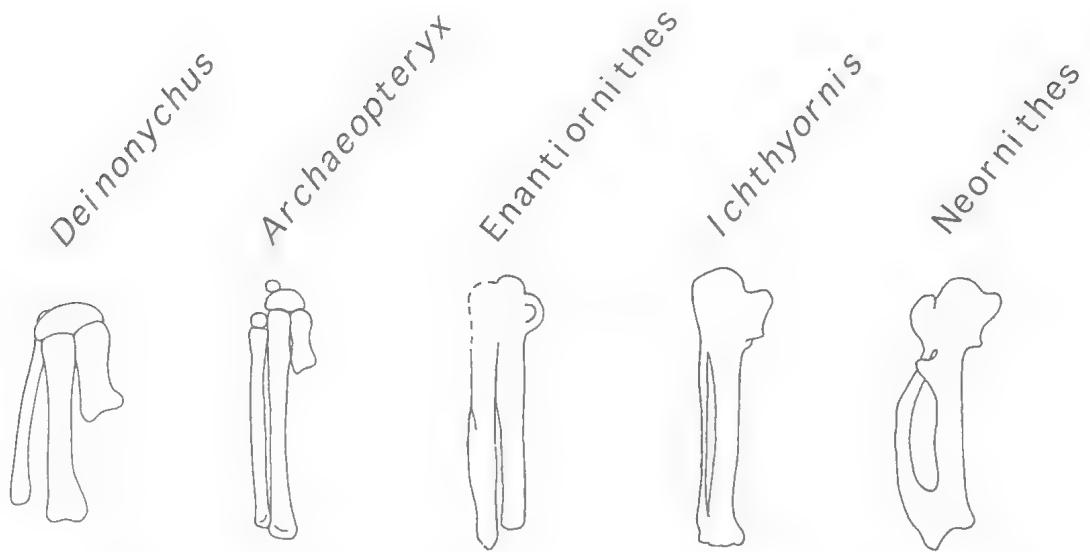
FIG. 13. Distal carpals and metacarpals of *Deinonychus*, *Archaeopteryx*, Enantiornithes, *Ichthyornis* and Neornithes. Note the fusion of these elements in the three latter taxa.
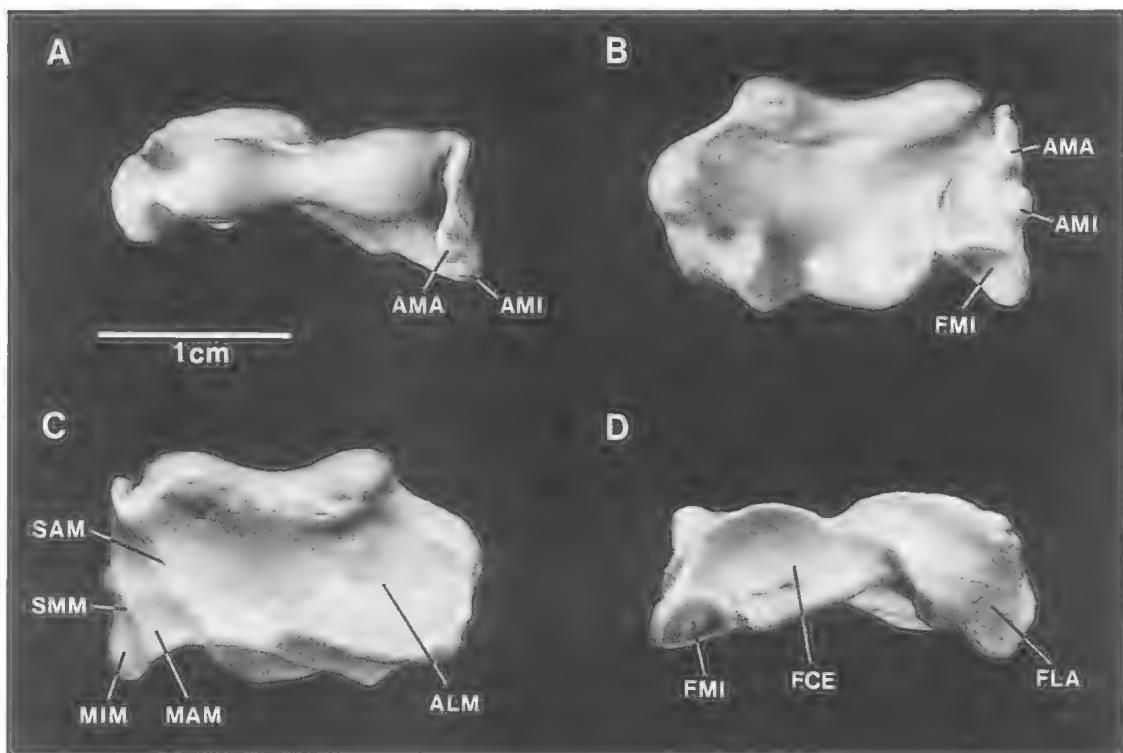

FIG. 14. Carpometacarpus of *Mononykus* (MGI 106/7). A, distal view; B, ventral view; C, dorsal view; D, proximal view. ALM=alular metacarpal, AMA=articular facet of major metacarpal, AMI=articular facet of minor metacarpal, FCE=central proximal articular facet, FLA=lateral proximal articular facet, FMI=proximal articular facet of minor metacarpal, MAM=major metacarpal, MIM=minor metacarpal,SAM=suture between alular and major metacarpals, SMM=suture between major and minor metacarpals.
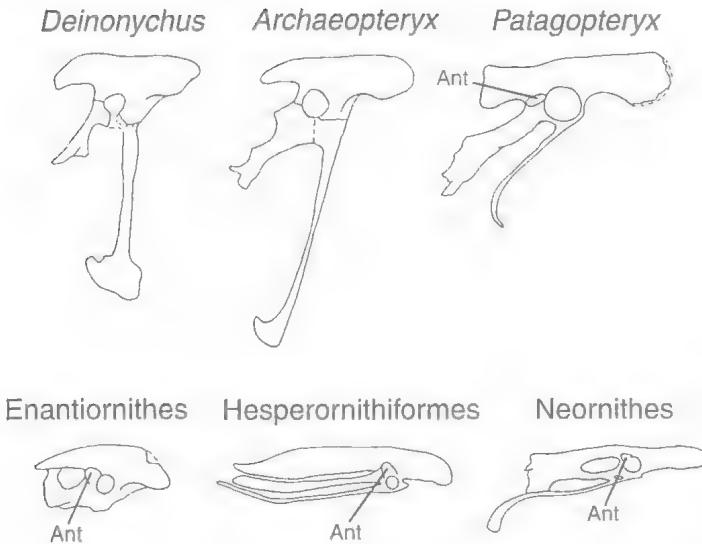
FIG. 15. Lateral view of the pelvis of *Deinonychus*, *Archaeopteryx*, *Patagopteryx*, Enantiornithes, Hesperornithiformes and Neornithes. Ant=antitrochanter. Drawings not to scale.

Velociraptorine theropods, as in other non-avian maniraptoran theropods (e.g., Russell & Dong, 1993a), have ischia that are two-thirds or less the length of the pubis (Gauthier, 1986). In *Deinonychus* (Ostrom, 1976b) and *Adasaurus* (Barsbold, 1983), the ischium is nearly 50% the size of the pubis (Fig. 15). In contrast, in *Mononykus*, both pubis and ischium — oriented some 45° caudoventrally — have delicate, rod-like shafts of subequal length (Fig. 17).

Gauthier (1986) has hypothesised that the more similar length of the pubis and ischium in or-nithurine birds was acquired through reduction of the former bone. Nevertheless, the fact that the obturator process of the ischium of these birds is located proximally and not mediodistally as in velociraptorines or *Archaeopteryx* suggests the opposite. It is probably the elongation of the ischiadic blade that accounts for the proportion seen in ornithurine birds.

AMBIGUOUS SYNAPOMORPHIES EXCLUSIVE OF BOTH AVES AND METORNITHES.

Additional support for the avian affinity of *Mononykus* and the Alvarezsauridae comes from six other characters in which optimisation is ambiguous or equivocal for the present character distribution. A closer examination of the data indicates that the ambiguity for this optimisation is mostly derived from the fact that these character states are uncertain in *Archaeopteryx*. It is

important to note that given a known morphology for *Archaeopteryx*, these characters would be unambiguously synapomorphic of either Aves or Metornithes. The fact that these character states are clearly not present in the outgroup, and that they represent symplesiomorphies for clades more derived than Alvarez-sauridae, provides further support for our hypothesis. These synapomorphies are:

1) Wide vertebral foramen in dorsal vertebrae, vertebral foramen/cranial articular facet ratio greater than 0.40 (character 15). The dorsal vertebrae of modern, neornithine birds possess a large vertebral foramen (Chiappe, 1996) (Fig. 9). Despite wide variation, in the sample of neornithine birds taken for this study, the ratio between the vertical diameters of the vertebral foramen and the cranial articular surface ranges approximately from 0.55-2.75. Typically, the anterior dorsals give larger ratios than the posterior ones. In hesperornithiforms and ichthyornithiforms this value is at least 0.70 (Marsh, 1880). In Enantiornithes and *Patagopteryx*, although the size of the vertebral foramen falls among the lower values observed in neornithine birds, the ratio is clearly greater than 0.40.

A quite contrasting condition occurs in velociraptorines and other non-avian theropods in which the vertebral foramen of the dorsal vertebrae is very small (Fig. 9), with the above ratio being much lower than 0.40 (see for example Ostrom, 1969; Madsen, 1976; Currie & Zhao, 1993a). In the holotype specimen of *Mononykus*, however, the ratio between the vertebral foramen/articular cranial facet is approximately 0.75 in the anterior-most dorsals (Fig. 10) and about 0.58 in the more posterior biconvex vertebra. This ratio is approximately 0.45 in the only dorsal vertebra of *Patagonykus* that preserves the cranial portion (Novas, this volume, in press).

2) Lack of contact between ischial terminal processes (lack of ischial symphysis) (character 46). In all ornithurine birds, excepting only the Rheidae (i.e., rheas), the terminal processes of the ischia do not contact with each other. The is-chiadic terminal processes do not contact each other in Enantiornithes (based on *Concornis*; see
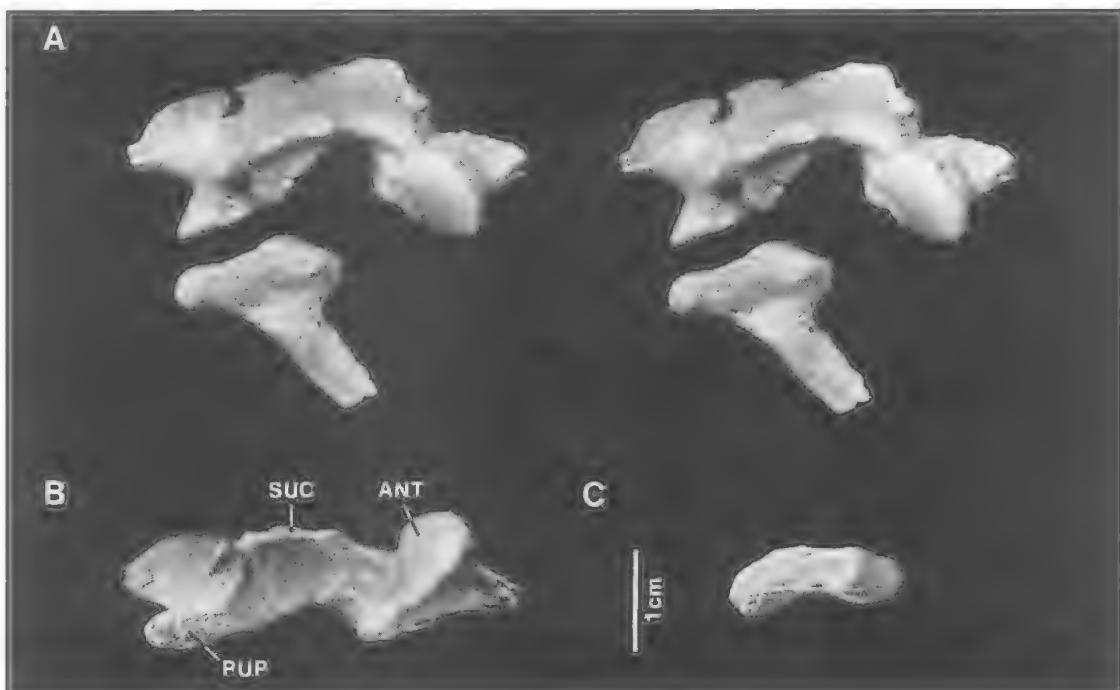
FIG. 16. Pelvis of *Mononykus* (MGI 106/7). A, stereopair of lateral view of the ilium and pubis; B, ventral view of the ilium; C, proximal view of the pubis. ANT=antitrochanter, PUP=pubic peduncle, SUC=supraacetabular crest.

Sanz et al., 1995) and *Patagopteryx* (Chiappe, 1992a, 1996).

In velociraptorines and the remaining non-avian theropods (Romer, 1956; Osmólska et al., 1972; Madsen, 1976; Currie & Zhao, 1993a) the ischia form a terminal symphysis. In contrast, in *Mononykus* the distal ends of the ischia do not contact each other (Perle et al., 1993, 1994), as is clearly visible in specimens MGI N 100/99 and MGI 100/975 in which the pelvic elements are in articulation.

3) Fibular tubercle for M. iliofibularis laterally projecting (character 59, Appendix 1). In the fibula of ornithurine birds, just proximal to the spine, there is a caudolaterally, or caudally, projecting tubercle for the insertion of M. iliofibularis, an important flexor of the tibiotarsus. The fibula is not well known for most non-ornithurine birds. In *Patagopteryx*, however, it is well-preserved and exhibits a robust tubercle for the M. iliofibularis, which projects directly laterally instead of caudolaterally or caudally (Chiappe, 1992a).

In velociraptorine theropods and other non-avian theropods, this tubercle (also known as the anterolateral process) typically projects craniolaterally (Osborn, 1916; Lambe, 1917;

Ostrom, 1969; Osmólska et al., 1972; Welles, 1984; Currie & Zhao, 1993a).

Mononykus shares the condition of *Patagopteryx*, with a robust and laterally oriented M. iliofibularis tubercle (Fig. 18). Assuming that the anterolateral process of non-avian theropods and the tubercle for M. iliofibularis of ornithurines are homologous, this tubercle must have migrated caudally during the early evolution of birds. The lateral position of this tubercle in both *Mononykus* and *Patagopteryx* represents an 'intermediate' stage in this transformation.

4) Quadratojugal not contacting the squamosal (character 68). Neornithine birds are characteristic among theropods (and most archosaurs) in that the quadratojugal is a rod-like bone lacking a dorsal process for its articulation with the squamosal, which forms a free, ventrally projected zygomatic process. This derived condition is clearly present in Hesperornithiformes (Marsh, 1880; Bühler et al., 1988; Elzanowski, 1991). In *Patagopteryx* and Ichthyornithiformes the quadratojugal is not known (at least for the published specimens), but the presence of a zygomatic process indicates that the squamosal and the quadratojugal do not contact each other.
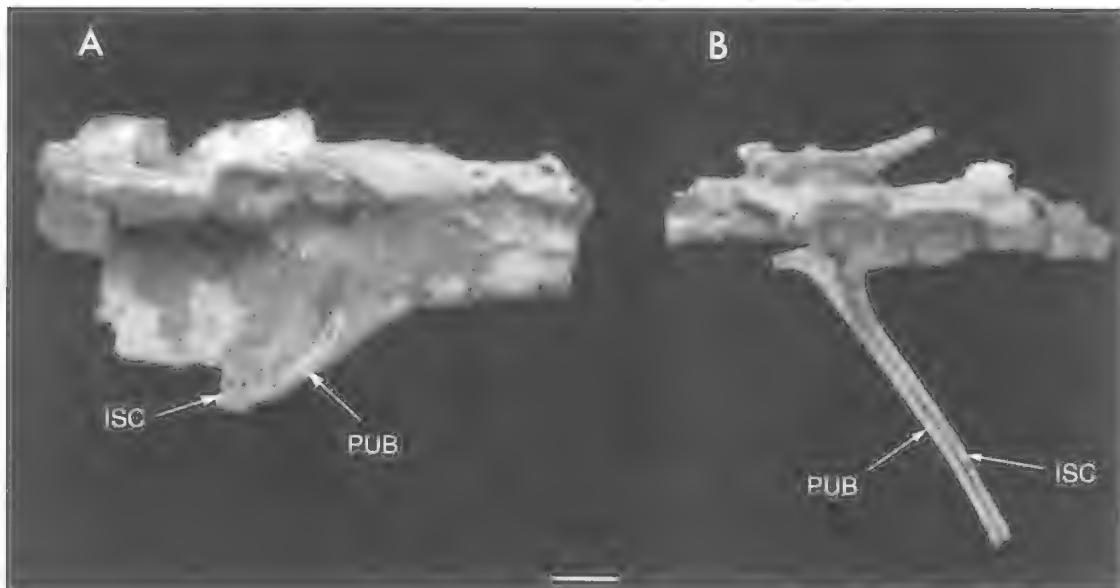
FIG. 17. Pelvis of *Mononykus* (MGI 100/975, left; MGI N 100/99, right) in lateral view. Note the subequal length of the pubis (PUB) and ischium (ISC). Scale = 1cm.

In *Archaeopteryx*, the quadratojugal has a dorsal process comparable to that of non-avian theropods, as it can be seen in the counter-slab of the recently found 'Solenhofer Aktien-Verein' specimen (Wellnhofer, 1993). The morphology of the squamosal of *Archaeopteryx* has been a matter of strong debate (cf. Wellnhofer, 1974; Whetstone, 1983; Bühler, 1985; Walker, 1985; Martin, 1991). In the 'Solenhofer Aktien-Verein' specimen, however, the squamosal appears to be well preserved and it shows a prominent ventral process (Elzanowski & Wellnhofer, 1995). Regardless the presence of these processes, it is not clear whether the quadratojugal and squamosal contacted each other, hence this character has been scored as uncertain for the Solnhofen bird.

In contrast to the condition present in neornithines, the squamosal of velociraptorines and all other non-avian theropods has an extensive contact with the quadratojugal (see Osborn, 1912; Colbert & Russell, 1969; Osmólska et al., 1972; Madsen, 1976; Weishampel et al., 1990; Currie & Zhao, 1993a; Clark et al., 1994). This relationship of the squamosal to the quadratojugal is in fact the primitive amniote condition (Romer, 1956).

In *Mononykus*, the quadratojugal forms a rod-like ossification, identical to the condition in neornithine birds, as it seen in the recently collected IGM 100/1001 from Ukhaa Tolgod (Dashzeveg et al., 1995). Furthermore, the squamosal

lacks any ventral projection. Clearly, these two bones do not contact each other.

5) Absence of medial fossa on the proximal end of the fibula (character 75). The medial surface of the fibula of neornithine birds is generally flat. This is the case in Hesperornithiformes and *Patagopteryx* (Chiappe, 1992a). As remarked above, the fibula is missing or poorly preserved in most non-ornithurine birds, and the present character is uncertain for Enantiornithes, *Iberomesornis* and *Archaeopteryx*.

In contrast, in *Deinonychus* the medial face of the proximal end of the fibula is excavated by a shallow fossa. This medial fossa is much more prominent in other non-avian theropods such as ornithomimids, tyrannosaurids (Lambe, 1917), *Sinraptor* (Currie & Zhao, 1993a) and *Allosaurus* (Madsen, 1976).

The proximal end of the fibula of *Mononykus* is flat in its medial surface, with no excavation (Fig. 18). A fragment of the fibula of *Patagonykus* shows that this derived morphology was also present in the Argentine taxon (Novas, this volume).

6) Absence of postorbital-jugal contact (character 95). The bird skull is characterised by having the orbit confluent with the archosaurian infratemporal fenestra (Zusi, 1993), a derived feature achieved by the reduction of the postorbital-jugal bar. This derived morphology is known to occur in Neornithes [although secondarily modified in some lineages (e.g., Psittaciformes,

Galliformes)], Ichthyornithiformes (Marsh, 1880) and Hesperornithiformes (Witmer & Martin, 1987; Bühler et al., 1988) in which the postorbital bone is absent. As with other cranial features, the presence or absence of a postorbital bone in *Archaeopteryx* is controversial. Wellnhofer (1974) regarded as a postorbital bone an impression on the counter-slab of the Eichstätt specimen, an identification followed by Walker (1985) who considered several fragments between the quadrate and the fronto-parietal suture as portions of the postorbital. Both Wellnhofer (1974) and Walker (1985) regarded the postorbital bone to contact the dorsocaudally projected caudal portion of the jugal, a feature well-preserved in the 'Solenhofer Aktien-Verein' specimen (Wellnhofer, 1993). Whetstone (1983), Bühler (1985) and Martin (1991), however, considered that a postorbital bone was absent in *Archaeopteryx*, and that this bone had no contact with the jugal bar caudally confining the orbit.


FIG. 18. Fibula of *Mononykus* (A, B, MGI N 100/99; C, D, AMNH-6570). A, D, lateral view; B, caudal view; C, medial view. IFT=tubercle for the M. iliofibularis. A, B, scale = 0.5cm; C, D, scale = 1.0cm.

In velociraptorine theropods, as in all other nonavian theropods (Osborn, 1912; Colbert & Russell, 1969; Osmólska et al., 1972; Madsen, 1976; Weishampel et al., 1990), the jugal has a robust dorsal process that contacts a ventral process of the postorbital closing the orbit caudally.

Mononykus presents an intermediate condition between the morphology of non-avian theropods and that of more advanced birds such as Hesperornithiformes or Neornithes. In *Mononykus* (MGI 100/977) the postorbital has a long, slender ventral process, but this process does not reach the jugal. In fact, opposite the postorbital's ventral process, the jugal has a smooth, convex surface and no trace of a dorsal process is present. The orbit of *Mononykus* was clearly not closed caudally but conected with the infratemporal fenestra.

DISCUSSION

This cladistic analysis supports the allocation of *Mononykus*, along with *Patagonykus* and *Alvarezsaurus*, within Aves (i.e., Avialae sensu Gauthier, 1986). This hypothesis is supported by four unequivocal synapomorphies of Aves

present in *Mononykus* (character states 19a, 71, 81 & 85a) and six unequivocal synapomorphies (character states 13, 29, 30, 39, 44 & 69) supporting the monophyly of Metornithes (Perle et al., 1993), the clade composed of the common ancestor of *Mononykus* and Neornithes, plus all its descendants. The allocation of *Mononykus* within Aves is further supported by its possession of several other derived characters which diagnose, although equivocally, both Aves and Metornithes (character states 15, 46, 59a, 68, 74 & 95). The equivocal status of these synapomorphies means that pending determination of the condition in *Archaeopteryx*, these characters might become synapomorphies of either Aves or Metornithes. Although the precise status of these characters is yet unclear, they are both absent in the outgroup and symplesiomorphic of less inclusive clades (e.g., Ornithothoraces, Ornithurae), and examination of the data indicates that there is no optimisation dependance for these characters.

Our initial description of *Mononykus* (Perle et al., 1993), although brief, identified many of the characters diagnosing Metornithes presented in this paper. The avian affinity of *Mononykus* has been corroborated by Novas (this volume) on the basis of a cladistic analysis of a different data set, but criticised by others (Patterson, 1993; Feduc-

cia, 1994; Martin & Rinaldi, 1994; Ostrom, 1994; Wellnhofer, 1994).

As with any hypothesis, our hypothesis of relationship can be, and should be, tested by others. The rationale for cladistic analysis (described in detail by Farris, 1983 and Schoch, 1986) dictates that phylogenetic hypotheses are tested by the distribution of characters among taxa. Thus, to falsify our hypothesis: 1, characters supporting an alternative relationship for *Mononykus* must be identified; and 2, the weight of the evidence must support this alternative. Because the published criticisms do not furnish such evidence, our disagreements with these critics primarily concerns methodological issues and our criterion for evidence and testability in phylogenetic reconstruction.

Patterson's (1993) criticism was not focused on the phylogenetic position of *Mononykus*. Instead it reflects nomenclatural issues, which Norell et al. (1993b) subsequently addressed. Others centered their criticisms on the peculiar forelimb specialisations of *Mononykus*. For example, Wellnhofer (1994: 306) states that *'it would be very difficult to imagine how a primitive bird wing, such as that of* Archaeopteryx, *could have evolved into a forelimb like that of* Mononykus'. Such an assumption lacks rigor (Chiappe et al., 1995). If one agrees with Wellnhofer's argument it would be 'very difficult to imagine' how the flippers of a seal evolved from the forelimb of an ancestral carnivore. Likewise, Ostrom (1994) uses the flightless condition of *Mononykus* to claim that its keeled sternum must have evolved convergently, as a burrowing adaptation. Indeed, Ostrom misleadingly cites the keeled sternum as the only evidence we provide in support of our hypothesis, a claim belied by the figure from our original paper reproduced in his article, with five characters highlighted. The logic behind this argument seems to be that structures never change function, so that if similar structures have different functions they cannot be homologous. Thus, the explanation of this structure as an adaptation for burrowing takes precedence over the explanation of this structure as evidence for a close relationship between *Mononykus* and birds. The fallacy of such arguments has been pointed out many times (e.g., Gould & .Vrba, 1982; Lauder, 1994, 1995). Function and structure are not always phylogenetically correlated (Lauder, 1995) and one wonders whether Ostrom would consider the forelimb of *Deinonychus* to be non-homologous with that of *Archaeopteryx* because they have different functions.

In their zeal to refute our phylogenetic hypothesis, some critics claim that the similarities we pointed out do not exist. For example, Feduccia (1994: 32) states *'the keeled breastbone doesn't resemble that of birds, but it is very much like that of a mole'*. While we do not deny that the sternum of *Mononykus* is similar to that of some moles, this similarity is irrelevant to comparisons between *Mononykus* and other maniraptoran archosaurs unless a close relationship between these archosaurs and this group of placental mammals is being seriously entertained. More to the point, the undeniable resemblance between the sternum of *Mononykus* and that of other birds cannot be ignored simply because it is at odds with a favorite scenario of bird evolution. Feduccia's other arguments against the avian affinities of *Mononykus* are mistaken or misleading. Within the context of his argument that birds are unrelated to dinosaurs, he claims that *Mononykus 'has many typical theropod dinosaur features, including a large 'dinosaur' tail, a small head, and no collarbones'* (Feduccia, 1994: 32). The presence of many 'dinosaur' features in birds has been broadly documented (e.g., Ostrom, 1976a; Gauthier, 1986; Weishampel et al., 1990). Incidentally, none of these features are those pointed out by Feduccia. The presence of a *'large 'dinosaur' tail'* in *Mononykus* is erroneous, whereas the significance of the size of the head and the absence of clavicles (if not due to lack of preservation) is unclear. As noted above (character 19; see Characters Supporting the Monophyly of Aves, Character Analysis), the tail of *Mononykus* is like that of *Archaeopteryx* in being shorter than that of non-avian theropod dinosaurs. As for the lack of furcula, the presence of either unfused clavicles or furculae in several groups of theropod dinosaurs (see Barsbold, 1983; Bryant & Russell, 1993; Russell & Dong, 1993a) indicates that if they are indeed absent in *Mononykus* then this absence is a derived feature of this taxon. With regard to the skull, at the time our earlier paper was published the only evidence from the skull was a portion of a braincase and a bone tentatively identified as part of the maxilla. For these reasons our reconstruction of the skull was clearly indicated as such. We now know, from the recently discovered skull of specimen MGI 100/977, that the skull of *Mononykus* is actually larger than what we thought (Fig. 1). However, the suggestion that non-avian theropod dinosaurs have smaller skulls than birds is incorrect.

Martin & Rinaldi (1994) claimed that *Mononykus* is not avian but related to or-

nithomimid theropods (see also Martin, 1995). Unlike most of our critics, they at least proposed a specific hypothesis of relationships for *Mononykus*. Our differences with Martin & Rinaldi are both methodological and empirical. These authors both misunderstand and misrepresent cladistic techniques. In their view '*clearly almost any outcome is possible in that sort of an analysis [cladistic analysis]*'. Martin & Rinaldi (1994) prefer to enumerate a series of characters that supposedly differentiates *Mononykus* from *Ichthyornis*, and which are alleged to be similarities between *Mononykus* and ornithomimids. Methodological differences aside, the problem with their procedure is that the majority of the characters listed for *Mononykus* are problematic or absent in this taxon. For example, Martin & Rinaldi claimed that *Mononykus* '*lacks or has few teeth*', '*has a small head*', '*no furcula*', '*no free carpals*', '*unusually short ribs*', '*a long tail*', '*astragalus enlarged to the point that the calcaneum is reduced to a nub or lost*', and '*no antitrochanter on the pelvis*'. As mentioned earlier, *Mononykus* has numerous tiny teeth and a skull which is larger than that illustrated in our original reconstruction, a tail shorter than any non-avian theropod, and a well-developed antitrochanter. The furcula (see above) and free carpals are not necessarily absent but not preserved in the known specimens. In fact, facets on the proximal articular surface of the carpometacarpus indicate that free carpals are missing (Perle et al., 1994).

Likewise, the astragalus and calcanum of *Mononykus* are completely fused (Perle et al., 1994), preventing estimation of their relative sizes. The new specimen MGI 100/977 shows that the ribs are not particularly short. Obviously Martin & Rinaldi have based their comments on our original reconstruction (Perle et al., 1993: Fig. 2) despite the fact that the ribs were indicated (along with most of the skull) as unpreserved elements. The remaining characters used by Martin & Rinaldi (1994) are either primitive (e.g., elongated haemal arches, preacetabular ilium short), autapomorphic (e.g., ischium slender, reduced forelimbs, enlarged metacarpal 1), or so highly variable as to be of uncertain generality (e.g., postacetabular ilium elongate, long neck). Of all the characters listed by Martin & Rinaldi, only the '*enlarged metacarpal I*' (alular metacarpal in this paper) is derived and shared by ornithomimids. Nevertheless, the morphology of this metacarpal in *Mononykus* is distinctly different than that of ornithomimids. In or-

nithomimids, metacarpal I is more than half the length of metacarpals II and III (Barsbold & Osmólska, 1990); in advanced ornithomimids all the metacarpals are nearly equivalent in length (e.g., *Gallimimus*, *Ornithomimus*). Aside from length, however, all known ornithomimids have metacarpals that are proportionally similar. This is not true in *Mononykus* where the alular metacarpal (equivalent to metacarpal I) is significantly larger than the major and minor metacarpals (metacarpals II and III, respectively) (Fig. 14). This condition (an alular metacarpal that is larger than the remaining metacarpals) is synapomorphic of a group containing *Mononykus* and *Patagonykus*, and it is unrelated to the condition seen in ornithomimids. By rejecting our phylogenetic hypothesis, our critics have implicitly indicated that the evidence used to include *Mononykus* within Aves (in addition to the evidence presented here) is nonhomologous (i.e., homoplastic). These authors, however, have failed in providing logical support for such a claim. As extensively discussed elsewhere (e.g., Patterson, 1982; Rieppel, 1992, 1994; Pinna, 1991; Hall, 1994), homology is a two-statement concept ultimately based on the congruence of characters. Primary homology refers to statements about the similarity of characters prior to phylogenetic constructions, while secondary homology refers to interpretations of common origins through character congruence on a particular tree (Pinna, 1991); the largest number of characters which congruently support a specific hypothesis of relationships are considered as homologies. Therefore, a statement of nonhomology — as used by our critics — cannot be derived from a 'priori' observation, but it should be ultimately revealed by the mismatch between primary and secondary homology. In order to say, for example, that the carinate sternum or the absence of a jugal-postorbital contact shared by *Mononykus* and more advanced birds is not homologous, it is necessary to have an alternative hypothesis in which the 'congruence' between the distribution of characters supporting that hypothesis is maximised.

In using a cladogram to determine evolutionary relationships, one need only assume that the hierarchical distribution of characters reflects the evolutionary relationships of taxa. The possible function of a particular structure, or a scenario about how a particular structure or function arose are not relevant. Instead, the relationships identified by cladistic analysis are the ones that provide the framework for testing functional or

adaptational hypotheses (Coddington, 1988; Gatesy, 1995; Witmer, 1995) and to use these scenarios as evidence for or against a phylogenetic hypothesis confuses the phenomenon to be explained with the explanation for the phenomenon (Brady, 1985).

The avian affinity of *Mononykus* is supported by the present study and corroborated independently (Novas, this volume). Re-rooting this cladogram so that Alvarezsauridae falls outside Aves requires a number of additional steps. Four and six additional steps are required for the placing Alvarezsauridae either as the sister-group of Aves or the clade formed by Aves plus Velociraptorinae, respectively. As for any phylogenetic hypothesis, the addition of characters, taxa, or both to the data set may change the topology of the resultant cladogram. It is hoped that the discovery of more fossil taxa and better specimens (in particular representatives of the lineage leading to *Mononykus*, *Patagonykus* and *Alvarezsaurus*) will provided additional character information to further test this cladogram. Furthermore, an alternative outgroup hypothesis may modify our result. Several derived characters shared by *Mononykus* and other birds appear in some troodontid taxa but are absent in velociraptorines (e.g., characters 44 & 81). These similarities may suggest that troodontids are closer to birds than velociraptorines are; however this needs to be evaluated in light of a larger, more inclusive analysis. Our choice for velociraptorines instead of troodontids is based on the fact that the latter are poorly known and their selection as an outgroup would have added numerous missing entries to the data set.

CONCLUSIONS

The cladistic analysis presented here supports the inclusion of *Mononykus* and the Alvarezsauridae, within Aves. The Alvarezauridae is the sister-group of Ornithothoraces and is closer to Neornithes than is *Archaeopteryx*.

The alternative, that *Mononykus* is not a member of Aves, is based on misleading evolutionary assumptions and 'a priori' speculation. Falsification of our hypothesis requires that a new hypothesis better summarising the pattern of similarities shared by *Mononykus* and birds be proposed. Or, with the addition of new characters or taxa, our evidence for relationship (synapomorphy) is contradicted. What this means is that it is insufficient to authoritatively proclaim that *Mononykus* is not avian (or not a bird), without

proposing an alternative hypothesis of what it is related to (supported by character evidence).

Several years ago evolutionary biologists arrived at a consensus that hypotheses of phylogenetic relationships should be based on the simplest explanation for the distribution of characters shared among organisms. It is unfortunate that our critics support their claims with arguments that lie outside the lines of modern systematics and comparative biology.

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APPENDIX 1

Skeletal characters and data-matrix used in the cladistic analysis. Multistate characters have been considered as additive except for characters 34, 40, 64, and 92 in which any two distinct states are separated by a single step. In the text and Fig. 2, 'a' and 'b' refer to states 1 and 2, respectively, of a multistate character. Scoring: 0 = primitive; $1,2$ = derived; $?$ = missing or uncertain.

1. Premaxillae in adults. *0*. unfused. *1*. fused.

2. Maxillary process of premaxillary. *0*. restricted to the rostral portion. *1*. forming most of the facial margin.

3. Frontal process of premaxilla. *0*. short. *1*. long, extending caudally to the level of lacrimals.

4. Premaxillary teeth. *0*. present. *1*. absent.

5. Osseous external naris. *0*. smaller, or *1*. considerably larger than antorbital fenestra.

6. Maxillary fenestrae. *0*. present. *1*. absent.

7. Rostral jugal border. *0*. away. *1*. very close to the caudal margin of the osseous external naris.

8. Ectopterygoid. *0*. present. *1*. absent.

9. Quadrate orbital process (pterygoid ramus). *0*. broad. *1*. sharp and point-shaped.

10. Quadratojugal. *0*. sutured to the quadrate. *1*. articulating in a cotyle in the lateral face of the quadrate mandibular process.

11. Quadrate pneumaticity. *0*. absent. *1*. present.

12. Articular pneumaticity. *0*. absent. *1*. present.

13. Prominent ventral processes on cervico-dorsal vertebrae. *0*. absent. *1*. present.

14. Dorsal vertebral count. *0*. 13-14. *1*. fewer than 13. *2*. fewer than 11.

15. Wide vertebral foramen in thoracic vertebrae, vertebral foramen/cranial articular facet ratio (vertical diameter) larger than 0.40. *0*. absent. *1*. present.

16. Synsacrum formed by *0*. less. *1*. more than 8 vertebrae.

17. Heterocoelous cervical vertebrae. *0*. absent *1*. present.

18. Pygostyle. *0*. absent *1*. present.

19. Caudal vertebral count. *0*. more than 35. *1*. fewer than 25-26. *2*. fewer than 15.

20. Ossified uncinate processes. *0*. absent *1*. present.

21. Scapula and coracoid articulation. *0*. through a wide, sutured articulation. *1*. through more localised facets.

22. Procoracoid process. *0*. absent. *1*. present.

23. Coracoid shape. *0*. short. *1*. elongated with subrectangular profile. *2*. strut-like.

24. Scapulocoracoid articulation. *0*. at the shoulder (proximal) end of coracoid. *1*. well below to it.

25. Supracoracoid nerve foramen. *0*. centrally located. *1*. situated (often as an incision) in the medial margin of coracoid.

26. Coracoid and scapula. *0*. placed in the same plane. *1*. forming a sharp angle at the level of the glenoid cavity.

27. Scapular caudal end. *0*. blunt. *1*. sharp.

28. Scapular shaft. *0*. straight. *1*. sagittally curved.

29. Sternum. *0*. subquadrangular to transversally rectangular. *1*. longitudinally rectangular.

30. Ossified sternal keel. *0*. absent. *1*. present.

31. Proximal and distal humeral ends. *0*. twisted *1*. expanded nearly in the same plane.

32. Ulna. *0*. shorter, *1*. longer or nearly equivalent to humerus.

33. Humeral head. *0*. concave cranially and convex caudally. *1*. globe shaped, craniocaudally convex.

34. Ventral tubercle of humerus. *0*. projected ventrally. *1*. proximally *2*. or caudally, separated from the humeral head by a deep capital incision.

35. Humerus with well developed transverse ligamental groove. *0*. absent. *1*. present.

36. Humeral distal condyle location. *0*. mainly on distal aspect. *1*. cranial aspect.

37. Semilunate ridge on ulnar dorsal condyle. *0*. absent. *1*. present.

38. Ulnar shaft considerably thicker than radial shaft; radial shaft/ulnar shaft ratio. *0*. larger *1*. smaller than 0.70.

39. Distal carpals and metacarpals. *0*. unfused. *1*. fused forming a carpometacarpus.

40. Extensor process on carpometacarpus. *0*. absent. *1*. round shaped. *2*. with a sharp point.

41. Pelvic elements. *0*. unfused. *1*. fused or partially fused.

42. Small acetabulum; acetabulum/ilium ratio equal or smaller than 0.11. *0*. absent. *1*. present.

43. Pubis more or less parallel to ilium and ischium. *0*. absent. *1*. present.

44. Prominent antitrochanter. *0*. absent. *1*. present.

45. Iliac fossa for M. cuppedicus (= M. iliofemoralis internus). *0*. present. *1*. absent.

46. Ischiadic terminal processes. *0*. in contact. *1*. lacking contact.

47. Pubic apex. *0*. in contact. *1*. lacking contact.

48. Pubis shaft laterally compressed throughout its length. *0*. absent. *1*. present.

49. Pubic foot. *0*. present. *1*. absent.

50. Femur with distinct fossa for capital ligament. *0*. absent. *1*. present.

51. Femoral anterior trochanter. *0*. nearly confluent with the greater trochanter. *1*. or fused to it forming the trochanteric crest.

52. Femur with prominent patellar groove. *0*. absent. *1*. present.

53. Femoral popliteal fossa distally bounded by a complete transverse ridge. *0*. absent. *1*. present.

54. Tibiofibular crest in the lateral condyle of femur. *0*. absent. *1*. poorly developed. *2*. prominent.

55. Femoral posterior trochanter. *0*. present. *1*. absent.

56. Tibia, calcaneum and astragalus. *0*. unfused or poorly coossified (sutures still visible). *1*. complete calcaneo-astragalar-tibial fusion.

57. Cranial cnemial crest on tibiotarsus. *0*. absent. *1*. present.

58. Extensor canal on tibiotarsus. *0*. absent. *1*. present.

59. Fibula with tubercle directed, for M. iliofibularis. *0*. anterolaterally. *1*. laterally. *2*. caudolaterally or caudally.

Taxa\characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Velociraptorinae	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Archaeopteryx	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	?	0	0	0
Mononykus	0	0	0	0	0	?	0	?	0	0	?	?	1	?	1	0	0	0	1	?	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1
Alvarezsaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	0	?	0	0	0	?	0	?	?	?	?	?	?	?	?	?
Patagonikus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?	?	?	0	0	0	0	0	?	0	?	?	?	1	0	?	0	0	1
Iberomesornis	?	?	?	?	?	?	?	?	?	?	?	1	1	?	0	0	1	1	0	?	?	2	?	1	?	1	0	?	?	?	1	0	?	0	0	1
Enantiornithes	1	0	1	0	1	?	1	0	?	?	0	1	?	1	1	1	1	?	0	1	0	2	1	1	1	1	0	1	1	0	1	0	2	1	1	1
Patagopteryx	?	?	?	?	?	?	?	0	1	1	0	1	1	1	1	1	?	?	0	1	0	2	1	1	1	1	1	?	?	1	0	0	?	?	?	1
Hesperornithiformes	1	1	1	1	1	1	1	1	1	0	1	1	1	2	1	1	1	1	2	1	1	2	1	1	1	1	1	1	0	1	0	0	?	?	?	1
Ichthyornithiformes	1	?	1	?	?	?	?	1	1	1	1	1	1	2	1	0	1	?	?	1	1	2	1	1	1	1	1	1	1	1	1	1	2	1	1	1
Neornithes	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	2	1	1	1

Taxa\characters	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69
Velociraptorinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Archaeopteryx	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	?	0	0	0	0	?	0	0	0	0	0	0	0	?	?	0
Mononykus	0	0	1	0	1	0	0	1	1	1	1	1	1	0	1	0	0	0	1	0	0	0	1	1	0	?	0	1	0	0	0	1	1
Alvarezsaurus	?	?	?	?	?	0	?	?	1	?	?	?	?	?	?	?	?	?	1	0	?	0	?	0	0	?	?	0	?	0	0	?	?
Patagonikus	0	0	1	0	0	?	0	1	1	?	1	1	0	?	0	0	0	0	1	0	0	0	?	0	0	?	?	0	0	?	?	?	?
Iberomesornis	?	1	?	?	1	0	0	?	?	?	?	0	?	?	0	0	?	?	?	0	0	0	?	0	0	?	0	0	?	0	0	?	?
Enantiornithes	1	1	1	1	1	0	?	1	0	1	0	0	0	0	1	1	0	1	1	0	1	0	?	1	0	1	1	0	0	0	1	?	1
Patagopteryx	?	1	1	?	1	0	0	1	1	1	1	0	1	?	?	0	1	2	1	1	0	0	1	1	1	1	1	0	0	1	0	1	1
Hesperornithiformes	?	1	?	?	1	1	1	1	1	1	1	1	1	?	?	1	1	?	1	1	1	1	2	1	1	1	1	2	1	1	1	1	1
Ichthyornithiformes	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	1	1	1	1	2	1	1	1	1	1
Neornithes	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	1	1	1	1	2	1	1	1	1	1

Taxa\characters	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
Velociraptorinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Archaeopteryx	0	1	1	0	?	0	?	0	0	0	1	1	1	1	?	?	1	1	0	?	?	1	0	0	?	?	0	0	0	0
Mononykus	0	1	0	0	1	1	1	1	1	1	1	1	?	?	1	1	0	?	?	1	1	?	1	0	0	1	?	0	?	?
Alvarezsaurus	?	?	0	0	?	?	0	0	?	?	?	?	?	?	?	1	0	?	?	1	?	?	?	?	?	?	?	?	?	?
Patagonikus	?	?	0	?	?	1	1	1	1	1	1	?	?	?	0	?	?	?	?	1	?	?	?	?	0	?	?	?	?	?
Iberomesornis	?	?	?	0	?	0	0	0	0	0	?	?	?	?	1	?	?	1	?	0	?	?	?	?	?	?	?	?	?	?
Enantiornithes	1	1	1	1	1	0	1	0	0	0	0	?	0	1	1	1	1	?	0	0	0	?	?	0	?	1	?	1	?	0
Patagopteryx	?	?	0	1	1	0	1	0	1	0	0	?	1	1	1	2	1	0	?	1	1	0	?	?	?	?	1	?	?	0
Hesperornithiformes	0	1	1	1	1	0	0	0	0	0	?	1	1	1	1	2	0	0	1	0	1	?	1	1	1	1	0	1	0	?
Ichthyornithiformes	?	1	1	1	?	0	?	0	0	0	0	?	?	?	1	1	1	?	?	0	1	1	0	1	?	1	1	?	0	1
Neornithes	1	?	1	1	1	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	1	2	1	1	1	1	1	1	1

Character data matrix.

60. Fibular articulation. *0.* with the calcaneum. *1.* greatly reduced distally, without articulation with the calcaneum.

61. Metatarsals II-IV completely fused one to each other. *0.* absent. *1.* present.

62. Distal tarsals. *0.* free. *1.* completely fused to the metatarsals.

63. Metatarsal V. *0.* present. *1.* absent.

64. Proximal end of metatarsal III. *0.* in the same plane as metatarsals II & IV. *1.* reduced, not reaching the tarsals (arctometatarsalian condition). *2.* plantarily displaced with respect metatarsals II & IV.

65. Well developed tarsometatarsal intercondylar eminence. *0.* absent. *1.* present.

66. Tarsometatarsal distal vascular foramen. *0.* absent. *1.* present.

67. Iliac brevis fossa. *0.* present. *1.* absent.

68. Quadratojugal-squamosal contact. *0.* present. *1.* absent.

69. Ischium. *0.* less than two-thirds. *1.* two-thirds or more of pubis length.

70. Lateral processes on the sternum. *0.* absent. *1.* present.

71. Teeth (adult). *0.* with serrated crowns. *1.* unserrated crowns.

72. Supracetabular lip. *0.* present. *1.* absent.

73. Cervical ribs. *0.* articulated with vertebrae. *1.* fused to vertebrae forming the costal processes.

74. Proximal end of fibula. *0.* excavated by a medial fossa. *1.* nearly flat.

75. Hypertrophied olecranon process. *0.* absent. *1.* present.

76. Synsacrum procoelous. *0.* absent. *1.* present.

77. Caudal portion of the synsacrum forming a prominent ventral keel. *0.* absent. *1.* present.

78. Caudal articular surface of synsacrum convex. *0.* absent. *1.* present.

79. Humerus. *0.* with two distal condyles. *1.* single condyle.

80. Prominent ventral projection of the lateroproximal margin of the proximal phalanx of digit I. *0.* absent. *1.* present.

81. Caudal tympanic recess. *0.* opens on the rostral margin of the paraoccipital process. *1.* opens into the collumelar recess.

82. Quadrate. *0.* with two distal condyles. *1.* with three condyles forming a triangle.

83. Basicranial fontanelle on the ventral surface of the basisphenoid. *0*. present. *1*. absent.

84. Hyposphene-hypantrum accesory intervertebral articulations in trunk vertebrae. *0*. present. *1*. absent.

85. Distal caudal prezygapophyses. *0*. elongate. *1*. short *2*. absent.

86. Prominent acromion in the scapula. *0*. absent. *1*. present.

87. Completely reverted hallux (arch of ungual phalanx of digit I oposing the arch of the unguals of digits II-IV). *0*. absent. *1*. present.

88. Caudal maxillary sinus. *0*. absent. *1*. present.

89. Procoelous caudals. *0*. absent. *1*. present.

90. Carotid processes in intermediate cervicals. *0*. absent. *1*. present.

91. Ungual phalanx on major digit (digit II). *0*. present. *1*. absent.

92. Dentary teeth. *0*. set in sockets. *1*. set in a groove *2*. absent.

93. Postorbital. *0*. present *1*. absent.

94. Fossa for the femoral origin of M. tibialis cranialis. *0*. absent. *1*. present.

95. Postorbital-jugal contact. *0*. present. *1*. absent.

96. Subequal cotyla of ulna. *0*. present. *1*. absent.

97. Costal facets in sternum. *0*. absent. *1*. present.

98. Bony mandibular symphysis. *0*. absent. *1*. present.

99. Proximal phalanx of manal major digit (digit II). *0*. of normal shape. *1*. flat and craniocaudally expanded.

NEW DATA ON THE ANKYLOSAURIAN DINOSAUR FROM THE LATE CRETACEOUS OF THE ANTARCTIC PENINSULA

ZULMA GASPARINI, XABIER PEREDA-SUBERBIOLA & RALPH E. MOLNAR

Ankylosaurian remains have been found in the Late Cretaceous (Campanian) of the Antarctic Peninsula (James Ross Island). The material includes a lower jaw, teeth, cervical, dorsal, sacral? and caudal vertebrae, ribs, parts of the scapula and ilium, autopodial bones, and armour from a single small individual. The Antarctic ankylosaur is probably a nodosaurid, based on the tooth form. The fragmentary material doesn't permit accurate identification at the generic or specific levels, so the specimens are referred to Nodosauridae indet. Current data on ankylosaurian distribution supports the hypothesis of a late dispersal of nodosaurids from the northern hemisphere to the Antarctic Peninsula via South America, although an early migration during Late Jurassic or Early Cretaceous time is possible. The Antarctic ankylosaur was small and lived in a high-latitude, although rather mild climate. □ *Dinosauria, Ankylosauria, Late Cretaceous, Antarctic Peninsula, Gondwana, palaeobiogeography.*

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In January 1986, ankylosaurian remains were recovered during fieldwork by the Instituto Antártico Argentino in Late Cretaceous (Campanian) sediments of James Ross Island, northeast of the Antarctic Peninsula (Gasparini et al., 1987). This was the first dinosaur to be discovered on the Antarctic continent (Olivero et al., 1991). Subsequently, other dinosaur remains have been collected from the Late Cretaceous of the Antarctic Peninsula, including a hypsilophodont ornithopod from the Campanian or Maastrichtian of Seymour Island (Hooker et al., 1991; Milner et al., 1992) and a theropod from the Coniacian or Santonian of James Ross Island (Molnar et al., this volume). Other occurrences of dinosaurs in Antarctica include a large crested theropod, *Cryolophosaurus ellioti*, and a *Plateosaurus*-like prosauropod from the Lower Jurassic of Mount Kirkpatrick, nearer the South Pole (Hammer & Hickerson, 1994).

A preliminary description of the ankylosaurian material and a discussion of its palaeobiogeographical implications were given by Gasparini et al. (1987) and Olivero et al. (1991). As a result of the preparation of the matrix in which the fossils were imbedded, two additional teeth were found. A latex cast was made from a mould of three articulated cervical vertebrae. Other material not described in the first account includes parts of the scapula and ilium, vertebral pieces, metapodials and phalanges. In this paper, we discuss the affinities of the Antarctic ankylosaur in the light of the known material. New palaeobiogeographical data allow us to comment further on ankylosaurian distribution during the Late Cretaceous.

GEOGRAPHICAL AND GEOLOGICAL FRAMEWORK

The ankylosaurian material was discovered by the Argentinian geologists E. Olivero and R. Scasso about 2km inside Santa Marta Cove, in the north of James Ross Island (Olivero et al., 1991). The remains come from the Gamma Member of the Santa Marta Formation, in the lowermost part of the Marambio Group (Gasparini et al., 1987). They were recovered from locality D6-1, about 90m above the base of the Gamma Member. The lithology consists of massive green silty sandstones with abundant trace fossils. The ankylosaurian bones were associated with fish vertebrae and marine invertebrates, including bivalves, gastropods and nautiloid cephalopods (e.g., *Cymatoceras*). The unusual association of nautiloid phragmocones with the vertebrate bones could be explained as the result of stranding of shells along a beach (Woodburne & Zinsmeister, 1984). The ammonite assemblages

found above and below the dinosaur beds suggest a probably Late Campanian age (Olivero et al., 1991; Olivero, 1992).

The ankylosaurian remains could belong to a single specimen, as previously reported, although size differences between the bones suggest the possibility of two distinct individuals. The fossils were recovered from a small area about 6 meters square (Olivero et al., 1991). Most bones are fragmentary and have been much shattered by frost action. Preparation of the remains was carried out in the laboratory of the Museo de La Plata using mechanical techniques.

Collection designations. MLP, Museo de La Plata, La Plata; QM, Queensland Museum, Brisbane; ROM, Royal Ontario Museum, Toronto.

SYSTEMATIC PALAEONTOLOGY
Subclass DINOSAURIA Owen, 1842
Order ORNITHISCHIA Seeley, 1888
Suborder ANKYLOSAURIA Osborn, 1923
Family NODOSAURIDAE Marsh, 1890
Genus and species indet.

MATERIAL EXAMINED. A partial lower jaw with a tooth in situ, two isolated teeth, a cervical vertebra and a latex cast prepared from a natural mould of three articulated cervical vertebrae, two dorsal centra from the presacral rod, parts of the ?sacrum, three fragmentary caudal vertebrae, rib fragments, a fragmentary scapula, a fragment of ilium, four metapodials and two phalanges, and a collection of dermal elements, representing five different kinds of armour. All the remains are kept at the Departamento de Paleontología de Vertebrados, Museo de La Plata with the registration number MLP 86-X-28-1.

PROVENANCE AND AGE. Santa Marta Cove, northern James Ross Island, northeast of the Antarctic Peninsula; locality D6-1, lower section of the Gamma Member, Santa Marta Formation, Marambio Group; Late Cretaceous, Upper Campanian (Gasparini et al., 1987; Olivero et al., 1991; Olivero, 1992).

DESCRIPTION

A preliminary description of the specimens was given by Gasparini et al. (1987) and Olivero et al. (1991). Here we describe for the first time additional bones, including teeth, vertebrae, parts of the pectoral and pelvic girdles, and autopodial elements. Because the only other reasonably well known ankylosaur from the southern hemisphere is the specimen of *Minmi* described in this volume (QM F18101), detailed comparison will be made where possible with that specimen.

Lower jaw (Fig. 1I-J). The only preserved portion of the lower jaw is a section of the left dentary,

including the sides and upper margin, but lacking the ventral margin (Gasparini et al., 1987). Nine alveoli are visible, including the foramina for tooth emplacement on the lingual side. The anterior and posterior parts of the tooth row are missing. The specimen is about 15mm thick and about 60mm long, as preserved. In occlusal view, the tooth row is slightly curved. One replacement tooth remains in place in the fifth preserved alveolus. The crown is broken but it looks like those of two isolated teeth described below. The dentary is a thick bone, as usual in ankylosaurs (Galton, 1983). It bears no armour. Four foramina are present on the labial side of the dentary. Medially, the splenial is missing and so the Meckelian canal is open. The lack of fusion of the splenial suggests that the lower jaw does not belong to a fully grown ankylosaur.

Teeth (Fig. 1A-H). In addition to the tooth preserved in situ in the lower jaw, there are two isolated teeth. Both teeth retain the crown and part of the root. The maximum crown width is about 7mm and the crown height about 7.5mm. As preserved, the more complete tooth is 20mm high. The teeth are typically ankylosaurian, with a leaf-shaped, laterally compressed crown (Coombs, 1990). They bear seven or eight denticles on the anterior margin and five on the posterior, each row of denticles separated from the other by a small apical cusp. The teeth are of about the same size as those of *Minmi* (QM F18101), but in *Minmi* the crowns are relatively higher (7.5 × 6mm rather than 7.5 × 7mm) and only have five or six anterior and three posterior denticles. A prominent, rugose basal cingulum is visible on each side of the crown. The cingulum is better developed and more basally placed on the labial side than on the other. Moreover, the lingual cingulum is arched apically and thicker posteriorly. The presence of a two-faced asymmetrical cingulum is a common feature among nodosaurids, e.g., *Sauropelta* (Ostrom, 1970) and *Edmontonia* (Carpenter, 1990). The cingula are more nearly symmetrical in *Minmi*, with one only slightly more basal than the other, and the lingual cingulum lacks the arch seen here. On the lingual side of the crown there are a set of small ridges (or sulci) that do not correspond with the denticles, but extend from the bases of the denticles to the cingulum, and may be continuous with the vertical wrinkles of the cingulum. There seem to be slight ridges on the labial side as well that are continuous with the denticles, but these extend only a short distance below them, and do not extend across the entire crown. The pattern of
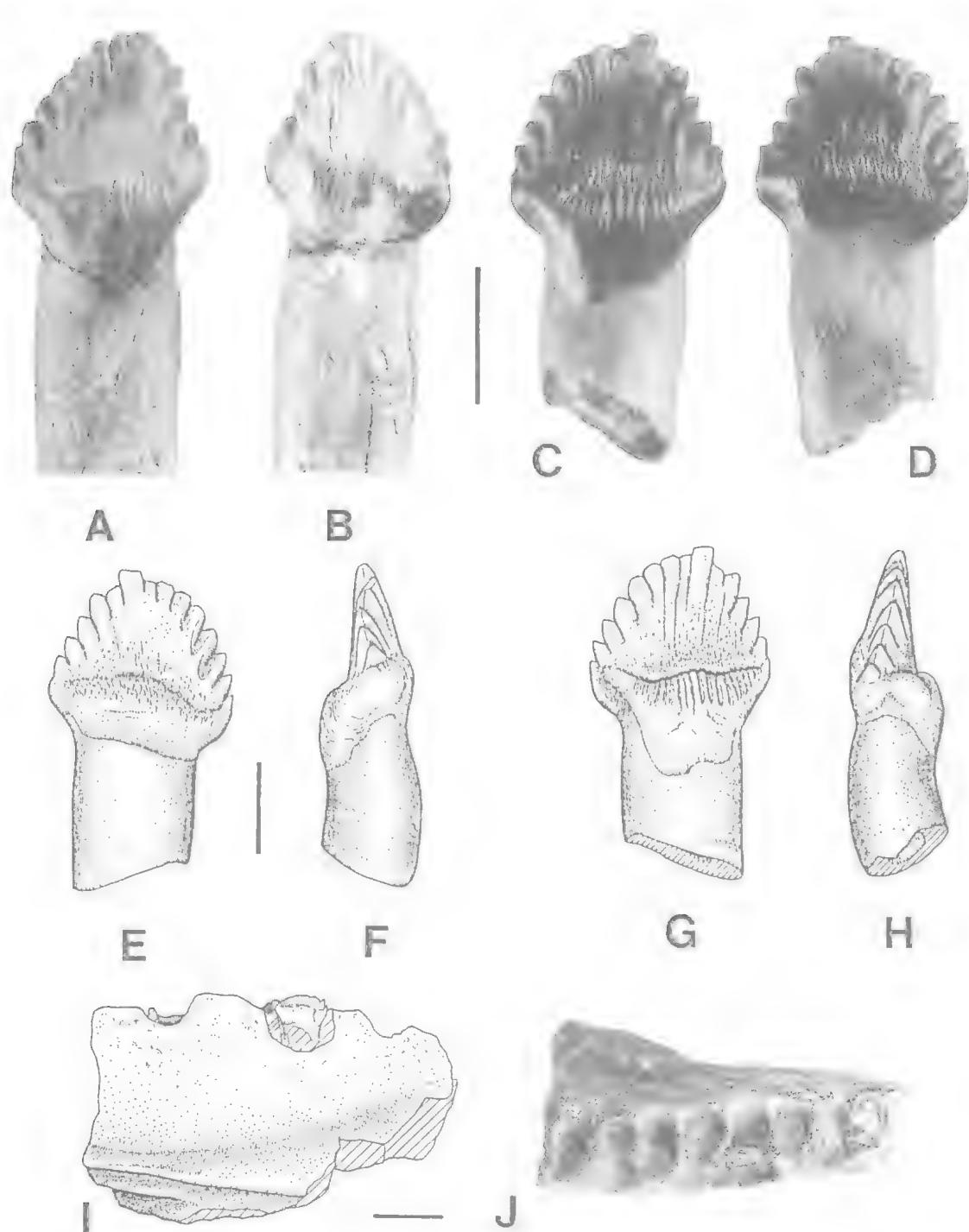
FIG. 1. MLP 86-X-28-1, ankylosaur cranial remains from the Late Cretaceous (Campanian) of James Ross Island, Antarctic Peninsula. A, C, two teeth in labial view; and B, D, lingual view; scale = 5mm (4x). E, tooth in lingual view; F, distal; G, labial; and H, mesial views; scale = 5mm. I, Left dentary with a tooth in situ in medial view; scale 10mm; and J, in occlusal view.
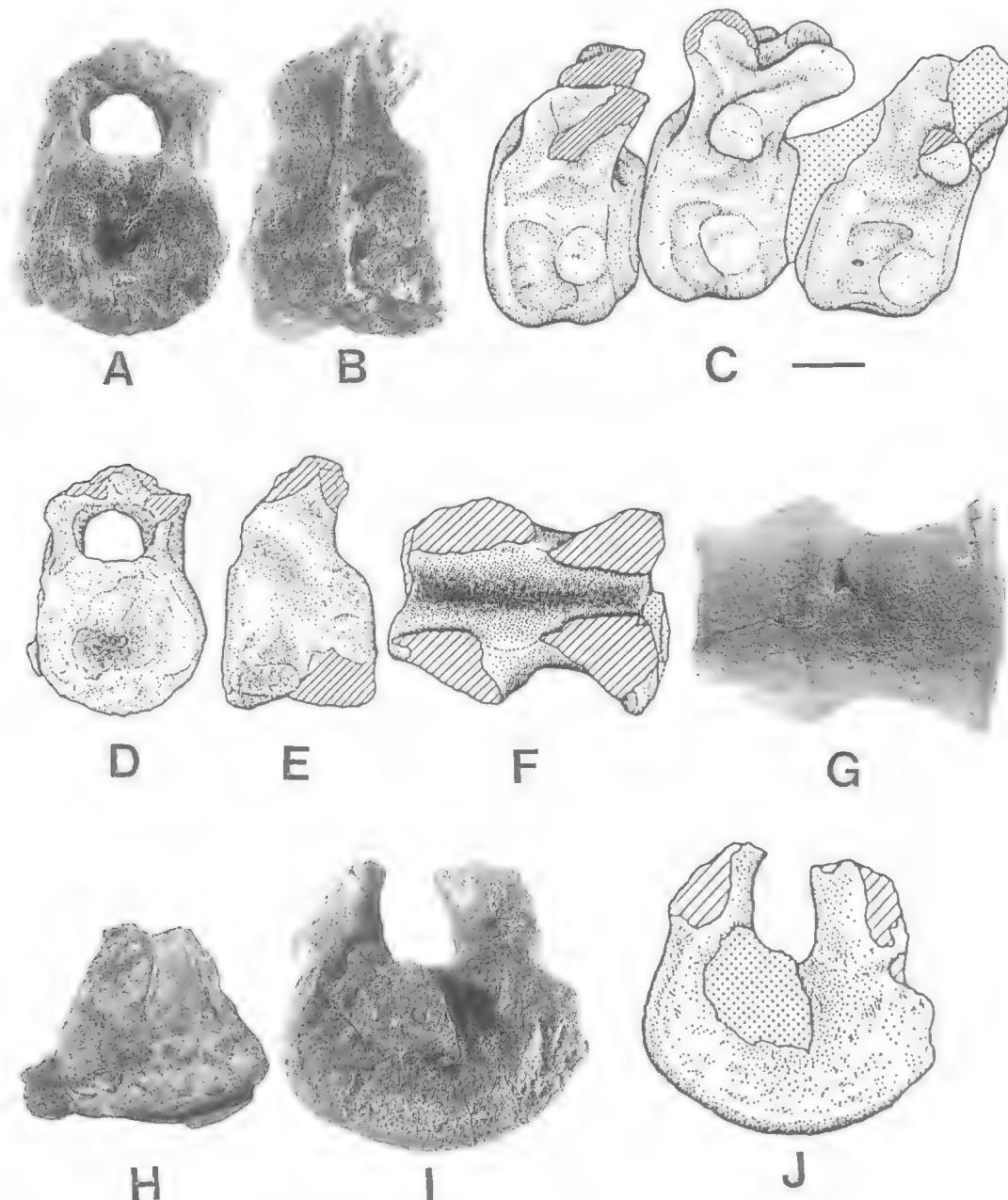
FIG. 2. MLP 86-X-28-1, ankylosaur vertebrae from the Late Cretaceous (Campanian) of James Ross Island, Antarctic Peninsula. A, D, anterior cervical vertebra in anterior view; and B, E, left lateral view. C, Latex cast from a mould of three articulated vertebrae in right lateral view (0.67x). F, two fused dorsal vertebrae from the ?presacral rod in dorsal view: G, ventral; and I, J, anterior views. H, Caudal vertebra in anterior view. Scale = 20mm.

vertical ridges on the crown is different from that of *Edmontonia*. In the latter, the ridges are continuous with the denticles, i.e., at the margin of the crown the ridges terminate in denticles (Coombs, 1990; Coombs & Maryanska, 1990). The root is slightly incurved and lingually convex in anterior and posterior views. It is separated from the crown by a slight constriction. If the
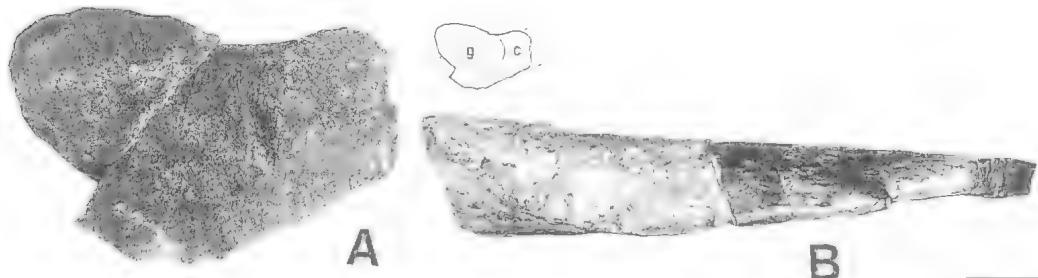
FIG. 3. MLP 86-X-28-1, ankylosaur limb girdle remains from the Late Cretaceous (Campanian) of the James Ross Island, Antarctic Peninsula. A, Scapula in articular (ventral) view. The inset indicates the humeral (g) and coracoid (c) articular surfaces. Medial is to the top. B, Ilium in lateral view. Scale = 20mm.

teeth belong to the lower jaw, they come from the left dentary (it is likely that they belong to the same individual).

Vertebrae and ribs (Fig. 2). About twelve more or less fragmentary vertebrae have been recognised. Most are quite damaged and shattered. A latex cast was made from a mould of three articulated cervical vertebrae (Fig. 2C). These vertebrae are small, with a total length of the series of about 123mm. The fusion of the neural archs to the centra suggests that they do not belong to a juvenile individual. The best preserved vertebra consists of part of the centrum, neural arch pedicles, transverse processes, prezygapophyses and the base of the neural spine. The centra are slightly amphicoelous, wider than long, and high as is common in ankylosaurs (Coombs & Maryanska, 1990). The parapophyses are placed near the anterior border, at mid-height of the centrum in the first preserved vertebra and become moderately higher in those further back. The neural canal is circular to slightly oval, and its diameter reaches a third of the width of the centrum. The transverse processes are short and oriented almost horizontally. The prezygapophyses are well-developed and form an angle with each other of about 60°. On the basis of these characters, the vertebrae are interpreted as coming from the middle of the cervical series (see Eaton, 1960).

In addition, an isolated cervical vertebra is known (Fig. 2F-G, I-J). This vertebra is about the same size or slightly smaller than the articulated cervicals. The centrum is also amphicoelous and wider than long. The neural canal is broader than high anteriorly, but higher than broad posteriorly. The parapophyses appear to be on the lower half of the lateral side. This suggests that the vertebra comes from the anterior half of the neck and was possibly situated anterior to the articulated series. The cervicals are similar to those of *Minmi*, but

differ in detail. The pedicles of the neural arches seem anteroposteriorly thinner in *Minmi*, and the centra are basically amphiplatyan with only slightly concave (or convex) central articular faces.

Two co-ossified centra (Fig. 2F-G) which preserve parts of the neural arches were originally described as sacral vertebrae (Gasparini et al., 1987: pl. 2, fig. 3). However, the neural canal of the vertebrae, as exposed dorsally, seems to be very narrow for the sacral region. In addition, the centra are only slightly compressed dorsoventrally and there is no fusion of the diapophyses and parapophyses lateroventrally, as occurs in the sacrals. Accordingly, these vertebrae probably come from the presacral rod, not the sacrum. They are tentatively regarded as the first and second vertebrae from the rod because the articular face of the best preserved centrum shows no trace of fusion with another vertebra. Vertebrae from the front of the presacral rod of *Minmi paravertebra* (QM F10329) differ in having a neural canal that is less laterally compressed, but centra that more compressed.

On the other hand, the other fragmentary fused elements may belong to the sacral region. The more complete specimen preserves parts of two possible co-ossified vertebrae, with broken lateral and dorsal attachments. The ventral surface is flat and narrower in the articular region between the elements. The specimen is too fragmentary for accurate identification, but it may be part of the sacral neural arches.

About eight fragments of dorsal ribs are known. The ribs are T-shaped to L-shaped in cross section proximally, a common morphology among ankylosaurs (Coombs, 1978), although found in some other dinosaurs as well.

At least three fragmentary caudal vertebrae are present. One of them contains a centrum with a fragmentary transverse process projecting

ventrolaterally (Fig. 2H), in anterior view this
caudal superficially resembles that of a mosasaur.
However it is amphicoelous, not procoelous. Two
other caudals retain only the lower face of the
centrum. A shallow, median groove and articular
surfaces for chevrons are visible ventrally. The
centra are very short and probably come from the
anterior part of the tail. The caudal vertebrae are
all similar in size and could belong to the same
individual.

Scapula (Fig. 3A). A fragmentary left scapula is
the only recognisable part of the pectoral girdle.
It includes the glenoid region but the scapular
spine is not preserved. The scapula and coracoid
were not co-ossified. This, together with small
size of the scapula, suggests that it could belong
to an immature individual.

Ilium (Fig. 3B). The pelvic girdle is represented
by a fragment of ilium. The specimen shows a
slightly sigmoid lateral border. The dorsal surface
is convex but the ventral surface is flat. The piece
probably comes from the central portion of the
preacetabular process of a right ilium which in
ankylosaurs — differently to other dinosaurs —
is unusually twisted laterally to lie in a horizontal
plane (Coombs, 1978; Coombs & Maryanska,
1990).

Metapodials and phalanges (Fig. 4). Four frag-
mentary metapodials and two phalanges are
known. The metapodials are broken and lack
proximal articular regions. They are relatively
broad and bear massive distal articulations, which
are approximately perpendicular to the long axis
of the shaft (Fig. 4A-B). The moderate robustness
of the metapodials suggests that they could
belong to the pes rather than to the manus; al-
though in fact, ankylosaurian metatarsals are
more slender than metacarpals (Coombs &
Maryanska, 1990). Three of the metapodials
seem roughly similar in shape but comparatively
smaller than metatarsals II, III and IV of the
nodosaurid *Sauropelta* (see Ostrom, 1970: pl.
26). The phalanges are very different in form.
One is cube-shaped, slightly asymmetrical in
ventral view, and longer than wide (Fig. 4C). It
probably comes from digit I. The other is a very
short, disc-like bone (Fig. 4D). It is tentatively
identified as the second phalanx of digit II or III.
The disc-like phalanx is about 1.5 times as wide
as the other. This difference in size can be inter-
preted in two ways: either one phalanx was from
the manus and the other from the pes, or they are
from two different individuals.

Armour (Fig. 5). Dermal elements are repre-
sented by five different types (Gasparini et al.,
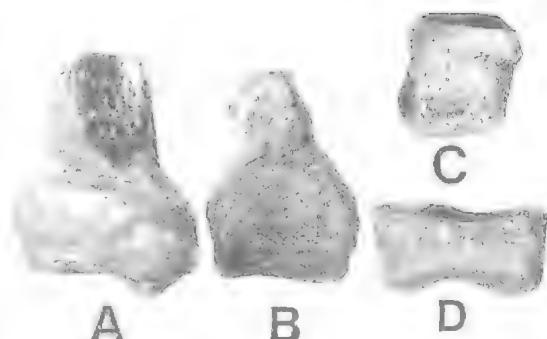
FIG. 4. MLP 86-X-28-1, ankylosaur manual or pedal
remains from the Late Cretaceous (Campanian) of the
James Ross Island, Antarctic Peninsula. A, B, two
metapodials; and C, D, two phalanges in anterior
view. Scale = 20mm.

1987): a) keeled, hollow-based scutes; b) massive
bulging plates; c) co-ossified flat scutes, overlap-
ping each other; d) oval, low-keeled scutes; and
e) tiny button-like ossicles.

Several fragmentary plates of the first type (a)
are known. These are massive, with an irregular
dorsal surface and prominent keel. Ventrally, the
surface is deeply hollowed in the largest
preserved specimen (Olivero et al. 1991, fig. 2c).
These plates were originally regarded as cranial
ossifications and so tentatively referred to the
Ankylosauridae (Gasparini et al., 1987). The
specimens are too fragmentary to confirm this.
The occurrence of prominent lateral horny plates
on the skull roof is a conspicuous character of
ankylosaurids (Maryanska, 1977; Coombs &
Maryanska, 1990) but similar structures could be
sporadically present in nodosaurids (Kirkland,
pers. comm., 1995).

The second type (b) of armour consists of large,
rough-surfaced plates (Gasparini et al., 1987, pl.
I, fig. 6; Olivero et al., 1991, fig. 2d). The dorsal
surface is sculptured with numerous small pits
and rugosities. The ventral face is irregular and
hollowed. These plates were originally inter-
preted as a possible tail-club but there is no direct
evidence (i.e. fusion to distal caudal vertebrae)
confirming this.

The third kind (c) of armour consists of co-os-
sified flat scutes overlapping each other and
enclosed by small polygonal ossicles (Fig. 5C-D:
Gasparini et al., 1987, pl. II, fig. 4). The scutes are
subcircular to oval in form, irregular in outline
and devoid of a dorsal keel. This pattern resembles
that of the sacral armour of *Polacanthus*-like
nodosaurids, which are characterised by the
fusion of a mosaic of plates into a rigid shield

FIG. 5. MLP 86-X-28-l, ankylosaur dermal plates from the Late Cretaceous (Campanian) of James Ross Island, Antarctic Peninsula. Osteoderms, including A-D, overlapped flat plates; and E, F, an oval low-keeled scute in dorsal view. G, skull roof ossification? Scale = 20mm (0.5x).

(Gasparini et al., 1987, pl. II, fig. 6). These ossicles probably floated in the skin and formed a continuous pavement between the large dermal elements permitting supple movements of the body (Carpenter, 1984). A histological study of these ossicles is currently in progress (de Ricqlés and collaborators, in preparation).

The new specimen of *Minmi* (QM F18101) also shows five types of dermal armor, but only two of them (types d and e given here) clearly match those of the James Ross Island ankylosaur. These kinds seem to be found in many ankylosaurian taxa. *Minmi* clearly lacked *Polacanthus*-like sacral armor, and had larger (5-6mm diameter) dermal ossicles.

DISCUSSION

The general morphology of the lower jaw, teeth, vertebrae, ilium and armour allow confident attribution of the dinosaur from James Ross Island to the Ankylosauria. At least three derived characters of ankylosaurs (Sereno 1986; Coombs & Maryanska 1990) are present: posterior dorsal vertebrae fused to form a presacral rod, ilium rotated into the horizontal plane, and body covered by a mosaic of armour plates of several shapes.

In a preliminary account, Gasparini et al. (1987) tentatively assigned the material to the family Ankylosauridae on the following characters: skull co-ossifications with lateral projections, teeth with cingula, and tail-club. However, our redescription of the material advises caution in regard to these features. In fact, on the basis of tooth form the ankylosaurian remains from the Antarctic Peninsula look more likely to be nodosaurid than ankylosaurid. Coombs & Maryanska (1990) pointed out that the two families can usually be distinguished on dental features. These authors cited several characters that are useful in this regard, e.g., conspicuous basal cingulum, cingulum typically higher on the

(Hulke, 1888; Kirkland & Carpenter, 1994; Pereda-Suberbiola, 1994). As far as known, a synsacral shield could be present in the Antarctic ankylosaur but further material is need to confirm it.

The small to medium-sized scutes (d) are oval in shape and bear a low dorsal keel (Fig. 5E-F: Gasparini et al., 1987, pl. II, fig. 5). They were probably situated in longitudinal rows on the body, as diagnostic for thyreophorans (Sereno, 1986). The ventral surfaces of the scutes are generally flat as in nodosaurids (Coombs, 1978). Together with small ossicles, one of these scutes has been preserved associated with a dorsal rib and ossified tendons (Gasparini et al., 1987, pl. I, figs 3,4). This suggests that the small scutes were arranged in an intercostal position along the trunk, as in *Minmi* and generally among ankylosaurs.

Finally, there are numerous polygonal ossicles (e) of very small size, less than 4mm in diameter

TABLE 1. Gondwanan ankylosaurs.

TAXON	AGE	PROVENANCE
Nodosauridae indet. (Coria, 1994)	Campanian-Maastrichtian	Patagonia, Argentina
Nodosauridae indet. (Molnar & Wiffen, 1994)	Campanian-Maastrichtian	North Island, New Zealand
Nodosauridae indet. (this paper; Gasparini et al., 1987; Olivero et al., 1991)	Campanian	James Ross I., Antarctic Peninsula
Minmi paravertebra Molnar, 1980 (Molnar, 1980, 1991, this volume: Molnar & Frey, 1987)	Aptian-Albian	Queensland, Australia
Ankylosauria indet. (Rich & Rich, 1989)	Aptian-Albian	Victoria, Australia
Ankylosauria (Chatterjee & Rudra, this volume)	Maastrichtian	Gujarat, India

lingual face, and grooves on crown generally better developed (Coombs & Maryanska, 1990). All of these features are present in the teeth from James Ross Island and this suggests that they belong to a nodosaurid ankylosaur. The differences in tooth form and the absence of a sacral 'buckler' in *Minmi* are the clearest distinctions between the Antarctic beast and *Minmi*. Thus they seem not to be closely related — insofar as we can tell when many corresponding elements are either missing (in the Antarctic specimen) or not yet exposed (in *Minmi*). The currently-known material from James Ross Island is too fragmentary for generic or specific identification and is here provisionally referred to Nodosauridae indet. Further material is needed to accurately define the affinities of the Antarctic ankylosaur.

The geologists who discovered the material thought it derived from a single partial skeleton of small size (Olivero, pers. comm.). Only some of the bone fragments were recovered because the ice was very thick around the fossils and the bones were broken by frost action. However, revision of the material at La Plata raised the possibility that two individuals were represented. Thus size differences between some of the bones, e.g., phalanges, would be accounted for. Also, on the one hand the neural arches are fused to the centra, which supports the idea that the vertebrae do not belong to a juvenile. But, on the other, the scapula and coracoid (not found) were not fused, in contrast to the usual condition of adult ankylosaurs (Coombs & Maryanska, 1990). Nonetheless these conditions are both seen in the skeleton of *Minmi* (QM F18101) which clearly derives from a single (articulated) individual. The differences in size between the phalanges may be due to one being manual and the other pedal. So there is no strong evidence that two individuals are represented.

The absence of fusion of the scapula to the coracoid suggests immaturity, although fusion does not take place in *Hylaeosaurus* (Pereda-Suberbiola, 1993) nor *Edmontonia* (Carpenter, 1990). So the absence of fusion of the splenial and dentary is perhaps more convincing. Fusion of the neural arches to the centra indicates that the animal was not very young. So most of the skeletal remains from James Ross Island are tentatively regarded as those of an immature, small individual. The estimated body length of the Antarctic ankylosaur is 3 or 4m.

PALAEOBIOGEOGRAPHICAL SIGNIFICANCE

Ankylosaurs were quadrupedal, armoured dinosaurs that lived from the Middle Jurassic to the Late Cretaceous (Coombs & Maryanska, 1990). The distribution of the two families is probably vicariant. The more conservative Nodosauridae are known in Europe from the Callovian to the Maastrichtian (Galton, 1983; Pereda-Suberbiola, 1992), and in North America from the Tithonian to the Maastrichtian (Carpenter & Breithaupt, 1986; Kirkland & Carpenter, 1994). The club-tailed Ankylosauridae are present in Asia from the Bathonian-Callovian to the Maastrichtian (Maryanska, 1977; Dong, 1993), and in North America during Campanian-Maastrichtian times (Coombs, 1986).

Unquestionable ankylosaurs from Gondwanaland include discoveries from the Lower Cretaceous of Australia and from the Late Cretaceous of New Zealand, South America and Antarctica (Table 1). Chatterjee & Rudra (this volume) also report an ankylosaur from India. In Australia, there are five Aptian-Albian occurrences in Queensland, including the holotype of *Minmi paravertebra* (Molnar, 1980; Molnar & Frey 1987) and a nearly complete, articulated skeleton referable to *Minmi* (Molnar, 1991, this volume), and two occurrences in Victoria (Rich & Rich, 1989). Ankylosaurs are also present in the Campanian-Maastrichtian of North Island, New Zealand (Molnar & Wiffen, 1994) and that

TABLE 2. Specimens from Gondwanaland incorrectly referred to the Ankylosauria.

TAXON	AGE	PROVENANCE	STATUS
Loricosaurus scutatus Huene 1929 (Huene, 1929)	Maastrichtian	Argentina	Titanosaurid sauropod (Powell, 1980; Bonaparte & Powell, 1980)
Lametasaurus indicus Matley 1923 (Matley, 1923; Huene & Matley, 1933)	Maastrichtian	India	Composiite theropod, sauropod and crocodilan (Chakravarti, 1935; Walker, 1964, Molnar & Frey, 1987)
Brachypodosaurus gravis Chakravarti 1934 (Chakravrati, 1934)	Maastrichtian	India	Stegosaur? (Galton, 1981)
Stegosaurus madagascariensis Piveteau 1923 (Piveteau, 1923; Russell et al., 1976)	Campanian	Madagascar	unknown
Acanthopholidae indet (Lapparent, 1960)	Albian	Niger	Stegosaur? (Molnar & Frey, 1980; X. Pereda-S., pers. obs.)

of Río Negro Province, Patagonia, Argentina (Coria, 1994; Salgado & Coria, in press). The list is completed with these remains from the Campanian of the Antarctic Peninsula (Gasparini et al., 1987; Olivero et al., 1991).

Ankylosaurs have also previously been reported from the Early Cretaceous of North Africa (Lapparent, 1960) and the Late Cretaceous of India (Matley, 1923; Huene & Matley, 1933; Chakravarti, 1934; Coombs, 1978) and Madagascar (Piveteau, 1923; Russell et al., 1976). Nevertheless, these remains are probably not ankylosaurian and can be assigned to other groups of dinosaurs or archosaurs (Table 2; see Molnar & Frey, 1987, for a discussion). As far as known, no conclusive evidence confirms the occurrence of ankylosaurs in Africa (Molnar & Frey, 1987; X. P.-S., pers. obs.), India (Chakravarti, 1935; Walker, 1964; Galton, 1981; Molnar & Frey, 1987) other than that reported by Chatterjee & Rudra, nor Madagascar (Sues, 1980). Dermal scutes from Argentina (*Loricosaurus scutatus* Huene, 1929) have been removed from the ankylosaurs to the titanosaurid sauropods (Powell, 1980; Bonaparte & Powell, 1980).

The presence of ankylosaurs in Antarctica during the Late Cretaceous can be explained as the result of dispersal from the northern continents to southern Gondwana (see discussion in Gasparini et al., 1987; Olivero et al., 1991). The time of this passage is not well known but two hypotheses may be considered:

First, an early migration during the Late Jurassic via Africa or South America. At this time, nodosaurids were present in Europe and North America and palaeobiogeographical evidence shows that passage to Gondwanaland was possible (Galton, 1977). If so, ankylosaurs were present in southern continents before the breakup of Gondwana (Bonaparte 1986). According to Molnar (1980, 1991, this volume), the mixture of primitive and specialised characters in *Minmi* could be the result of endemic evolution (because of geographical isolation) of this lineage of ankylosaurs in Australia during the Early Cretaceous. There is no evidence of Jurassic ankylosaurs in Gondwanaland and there seems no close affinity between the Antarctic ankylosaur and *Minmi*. On the other hand, the Late Cretaceous polar dinosaur fauna from New Zealand, that includes an ankylosaur, has been interpreted as probably representative of the terrestrial assemblages that inhabited Late Cretaceous Antarctica (Molnar & Wiffen, 1994). Unfortunately, a comparison between the Antarctic ankylosaur and that from New Zealand is not possible with the available material.

Second, a late dispersal, during the Late Cretaceous, via South America. The vertebrate interchange between North America and South America in the Campanian is well documented (Bonaparte, 1986; Gayet et al., 1992). Ankylosaurs could have traversed South America and reach Antarctica. This hypothesis is supported by the presence of a nodosaurid in Patagonia at this time (Coria, 1994; Salgado & Coria, in press). A continuous or intermittant land connection between Antarctica and South America is likely for some period during the Late Cretaceous (Olivero et al., 1991) and the Early Paleogene (Woodburne & Zinsmeister, 1984; Gasparini et al.,1986; Marenssi et al., 1994).

The occurrence of an armoured dinosaur in the Antarctic Peninsula is also interesting because it is one of the rare occurrences of ankylosaurs in high latitudes. During the Late Cretaceous, the Antarctic Peninsula was situated near its present position, at about 64°S (Zinsmeister, 1987). Other reports of ankylosaurs in high palaeo-

latitudes are of the nodosaurid *Edmontonia* from the Late Cretaceous of Alaska (Gangloff, 1995) at about 70°N, *Minmi* from the uppermost Early Cretaceous of Australia (Molnar, 1980, 1991, this volume) between 70° and 80°S (Veevers et al., 1991), and an indeterminate ankylosaur from the Late Cretaceous of New Zealand (Molnar & Wiffen, 1994) at least 66°S (see Barron, 1986 and Veevers et al., 1991, for palaeogeographical maps). In addition to the ocurrence of the Antarctic ankylosaur in high latitudes, there is independent evidence of a diversified flora suggesting a rather mild climate and a relatively high humidity, at least in the area where the dinosaur remains were found (Baldoni, 1992).

As noted by Molnar & Wiffen (1994), although large ankylosaurs (up to 9m) are known from both Asia and North America, there is no indication of any from the Gondwanan continents more than 4m long, including Australia, New Zealand, Antarctica, and South America. With the exception of the latter find, all the others probably represent components of insular, near-polar faunas.

Finally, the ankylosaur remains from James Ross Island were recovered from shallow marine deposits associated with marine invertebrates (Olivero et al., 1991). It should be noted that among ankylosaurs, ankylosaurid specimens are known only from continental deposits (Table 22.1 of Coombs & Maryanska, 1990) although articulated nodosaurid bones have (occasionally) been reported from marine formations (Horner, 1979; Carpenter et al., 1995; Coombs & Deméré, 1996). In addition there have been several recent discoveries of disarticulated nodosaurid specimens in marine formations as well (Coombs, 1995; Gangloff, 1995; Holden, 1996; Lee, 1996). This taphonomic difference suggests that by the Late Cretaceous nodosaurids preferred nearshore environments, whereas ankylosaurids probably lived in more inland habitats. A similar ecological segregation has been suggested among hadrosaurid dinosaurs (Horner, 1979; Carpenter et al., 1995). Walter Coombs (pers. comm., 1996) pointed out that recent discoveries of specimens from southern Califoria (Coombs & Deméré, 1996), Alaska (Gangloff, 1995) and, reportedly, Hokkaido (Holden, 1996) suggest a circum-Pacific distribution of nodosaurids, reminiscent of that of desmostylians. He also noted that the Alaskan specimen (referred to *Edmontonia* sp.) is a skull very like that of ROM 1215 from the continental Campanian of Alberta. This suggests that nodosaurids were not restricted to marginal marine habitats — and nodosaurids show no am-

phibious features in their morphology — but perhaps had a broader tolerance of habitats than ankylosaurids. To sum up, the Antarctic ankylosaur remains were found in shallow marine sediments and in high palaeolatitudes, a typical condition among nodosaurids but unknown in ankylosaurids. This indirectly supports the nodosaurid affinities of the Antarctic dinosaur.

ACKNOWLEDGEMENTS

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CRETACEOUS DINOSAURS OF AFRICA: EXAMPLES FROM CAMEROON AND MALAWI

LOUIS L. JACOBS, DALE A. WINKLER & ELIZABETH M. GOMANI

Africa became progressively isolated during the middle portion of the Cretaceous Period as it rifted apart from other Gondwana continents and the southern Atlantic Ocean was completed. Within this geological context, which controls the occurrence and distribution of Cretaceous fossil localities over most of Africa, there is considerable variety in composition and occurrence of fossils. In the Koum Basin of Cameroon in western Africa, abundant footprints of five morphotypes, but scrappy skeletal remains and teeth of the ornithopod *Ouranosaurus* and other taxa are found. In the Karonga area of northern Malawi, in southeastern Africa, more complete skeletal remains are known, including the sauropod *Malawisaurus*, which shows affinity to South American titanosaurids, and an undescribed sauropod taxon. These may demonstrate a range of morphological diversity in sub-Saharan Cretaceous sauropods comparable to that found in South America. ☐ *Cretaceous, Africa, Sauropoda, palaeobiogeography, crocodilia, stratigraphy.*

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Africa is a vast continent with a sporadic fossil record, remarkably good for some time intervals in some regions, yet dismally bad in others, yielding a disjointed and sketchy picture of past life on the continent. Our research into the African Cretaceous is focused on sub-Saharan Africa, a largely tropical to subtropical Precambrian shield area, heavily vegetated for the most part, and deeply weathered, often into fossil-destroying lateritic soils. In this paper we are primarily concerned with two areas of Lower Cretaceous outcrop: one in Cameroon and the other in Malawi. Both are associated with extensional tectonics along reactivated Precambrian mobile belts (Mateer et al., 1992). Our primary objective in this paper is to provide a general comparison between the two; that is, between eastern and western African dinosaur faunas of the Early Cretaceous using the Koum Basin, Cameroon, and the Dinosaur Beds of Karonga, Malawi, as examples (Fig. 1). We will also take this opportunity to examine briefly African Cretaceous dinosaurs and their relationship to those of South America.

Africa became isolated from Madagascar, India, Australia and Antarctica during the Late Jurassic (Pittman et al., 1993). One of the most profound events affecting the physical geography of the Cretaceous world was the opening of the southern Atlantic Ocean by the rifting of South America and Africa. Beginning in the earliest Cretaceous, tectonic rifting that culminated in the isolation of Africa began in the south between the continents. By the Late Albian to Cenomanian the African terrestrial fauna may have been isolated from that of South America by the Atlantic (Pittman et al., 1993). These geographic changes would have precipitated climatic change by modifying oceanic and atmospheric currents distributing heat across the Cretaceous world.

In the Early Cretaceous, volcanism in southern Africa and the reactivation of the Precambrian East African mobile belt resulted in Cretaceous fossil deposits in Malawi, and along the Zambezi River and its tributaries (Eby et al., 1995). Also in the Early Cretaceous, as noted above, on the west side of the continent, South America and Africa were rifting apart along a fault-rift-rift triple junction (Popoff, 1988), completing the Atlantic Ocean by Cenomanian or earlier time.

Thus, the Cretaceous fossil record is largely controlled by the tectonic framework of the continent, which provided the geologic setting in which fossil deposits formed. The chronology of African Cretaceous localities has yet to be documented in detail. Many identifications as presented in the literature are preliminary or based on incomplete material. Table 1 is a compilation of published records of Cretaceous dinosaurs from Africa. This is provided as a guide to published literature only, in recognition of the rather tentative nature of most of the entries.

KOUM BASIN, CAMEROON

The Koum Basin is an isolated basin associated with the Benue Trough, a major structural feature of West Africa (Figs 1, 2). The Benue Trough is an aulacogen, the failed arm of the triple junction that led to the completion of the Atlantic Ocean, extending from the Gulf of Guinea through Nigeria, then dividing into northern and southern branches. The southern branch is called the Yola Arm, which passes into Cameroon. While the Koum Basin is not the only fossiliferous basin associated with the Yola Arm (see also Brunet et al., 1988; Dejax et al., 1989; Michard et al., 1990), it is of interest here because of the dinosaur fauna it contains.

The most complete study of the Koum Basin (also referred to as Mayo Rey Basin in Flynn et al., 1987) and its fauna to date is that of Congleton (1990). The Koum Basin (Figs 2, 3) is an 80km long half-graben oriented east-west, bounded to the north by a fault, and filled with up to 3,000m of fluviatile, overbank, and lacustrine Cretaceous sediments (Tillement, 1971). It is surrounded by Precambrian metamorphic rocks. Cretaceous sediments are exposed primarily along the Mayo Rey, an east to west flowing tributary to the Benue River.

Congleton (1990) referred to the Cretaceous sediments as the Koum Formation, in which he recognised two areally restricted and well-defined members. The Mbissirri Member is composed of reddish fine-grained silty mudstones, clay shales, thin limestones and sandstones. There appear to be cyclical repetitions of cross-bedded sandstones and thicker mudstones within a sequence generally coarsening upwards. Congleton (1990) suggested that the Mbissirri Member represented lacustrine and aggraded meandering stream sediments within a fine-grained meander belt. Carbonised plant fragments, conchostracans, turtle carapace fragments and dinosaur footprint localities (designated KB-3, KB-17, KB-18, KB-23 in Fig. 3) have been found in the Mbissirri Member.

The Mbissirri Member is overlain along the northern margin of the basin by the coarse-grained Grés de Gaba Member. The contact is gradational. The sediments of the Grés de Gaba Member are medium to coarse-grained cross-bedded arkosic sandstones, conglomerates, and interbedded mudstones and palaeosols. Congleton (1990) interpreted the Grés de Gaba Member as representing a coarsegrained, braided fluvial system. Bone-bearing localities (KB-6,

FIG. 1. Location map of Koum Basin, Cameroon and the Dinosaur Beds, Mwakasyunguti area, Karonga, Malawi. Lakes Chad and Malawi indicated in black.

KB-8, KB-13), but no footprints, are known from the Grés de Gaba Member. Congleton et al. (1992) present a section measured at locality KB-6, the most productive bone locality. The base of the locality is coarse sand containing fragmentary scattered bones and teeth representing predominantly, in order of abundance, iguanodontian, theropod and sauropodomorph dinosaurs. One tooth was identified as thyreophoran(?); we consider that identification dubious and the specimen possibly confused with a crocodilian. The iguanodontian teeth resemble those of *Ouranosaurus*. The section fines upwards and small bones, representing particularly anurans and the crocodyliform *Araripesuchus*, but also mammals (Brunet et al., 1990, Jacobs et al., 1988), are concentrated in the lower portion of a mudstone, at the top of which a calcareous palaeosol is developed. Insect trace fossils resembling hymenopteran larval cases are found in the palaeosol. The sequence is succeeded by a coarse sandstone representing the initiation of the next fluvial cycle. A neural arch and neural spine attributed to the region of the sixteenth dorsal vertebra of *Ouranosaurus* (based on height of spine and position of the transverse processes) was found in conglomeratic sandstone at locality KB-13, overlying KB-6 by approximately 5 meters.
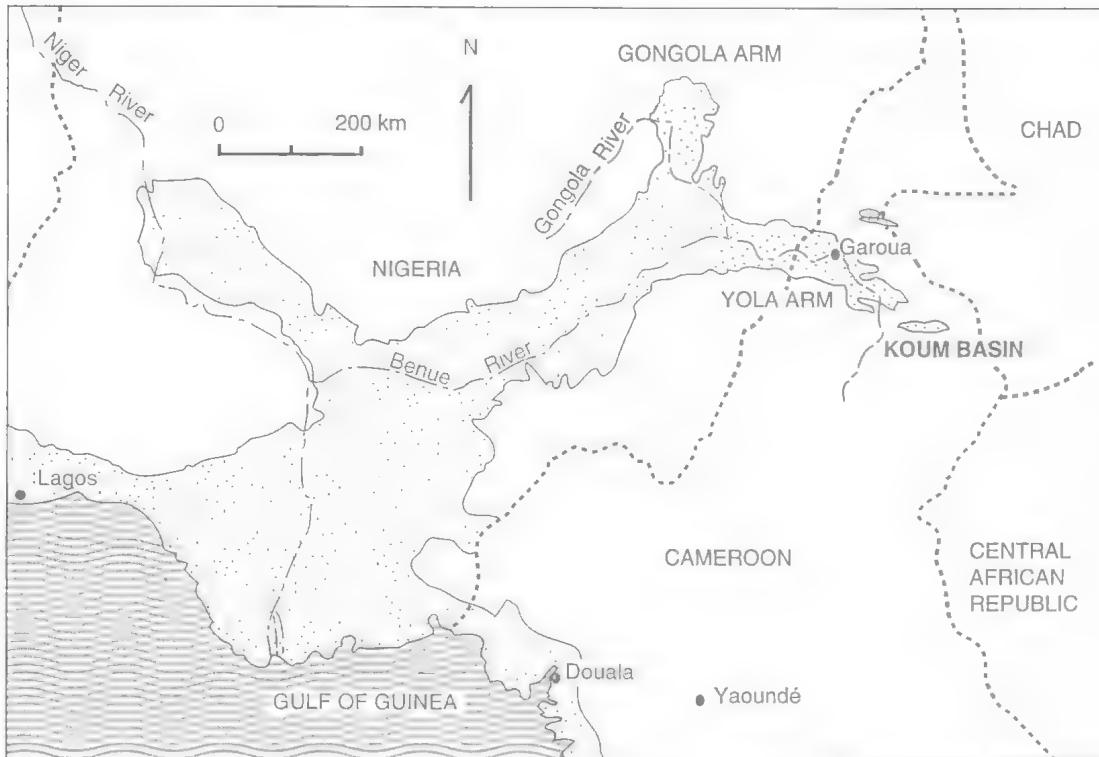
FIG. 2. Distribution of Cretaceous and younger sediments (stippled pattern) in the Benue trough (redrawn from Allix, 1983).

Congleton et al. (1992) suggested that faunas of the Koum Basin were correlative with the locality of Gadoufaoua, Niger, based on the common occurrence of *Araripesuchus* and *Ouranosaurus*. The age of Gadoufaoua is usually considered Aptian (Taquet, 1976). Colin et al. (1992) report the ostracode *Cypridea minuscula* from the Koum Basin (locality KB-24, Mbissirri Member). This genus was originally described from the Candeias Formation, Reconcavo Basin, Brazil. The Candeias Formation is placed within the Rio da Serra local stage (Moura et al., 1994), which ranges from the lower Berriasian to the lower Hauterivian stages (Ponte, 1994). Brunet et al. (1988) estimated the age of the nearby Mayo Oulo Léré Basin to be approximately around the Hauterivian-Barremian transition based on plants, particularly the palynomorph *Dicheiropollis etruscus*. A similar age is suggested for the Babouri-Figil Basin, which also contains dinosaur tracks, for the same reason (Dejax et al., 1989). It appears likely that the Koum Basin is Early Cretaceous in age, no younger than Aptian, but perhaps older.

Dinosaur footprints are relatively abundant in the Koum Basin. Congleton (1990) recognized five morphotypes of tracks corresponding to theropod, ornithopod and sauropod, consistent with incomplete skeletal remains from elsewhere in the basin. The most prolific trackway site is KB-17 in the Mbissirri Member, where tracks occur in four successive sandstone strata. Small theropod prints are the most abundant morphotype. Taken together, the trackways are directed north-northeast or south-southwest consistently, suggesting that the pathways remained constant over the flooding events that deposited the track-bearing strata and that a consistent barrier guided the movements of the dinosaurs.

A considerable amount of variation in stride length and other indicators of relative speed or inferred behavior is reported by Congleton (1990). Interpreted gaits include walking, trotting, sprinting, acceleration, deceleration and hobbling. The majority of the trackmakers appear to have been walking, however, based on relative stride length and pace angle. Smaller trackmakers appear relatively more energetic than larger
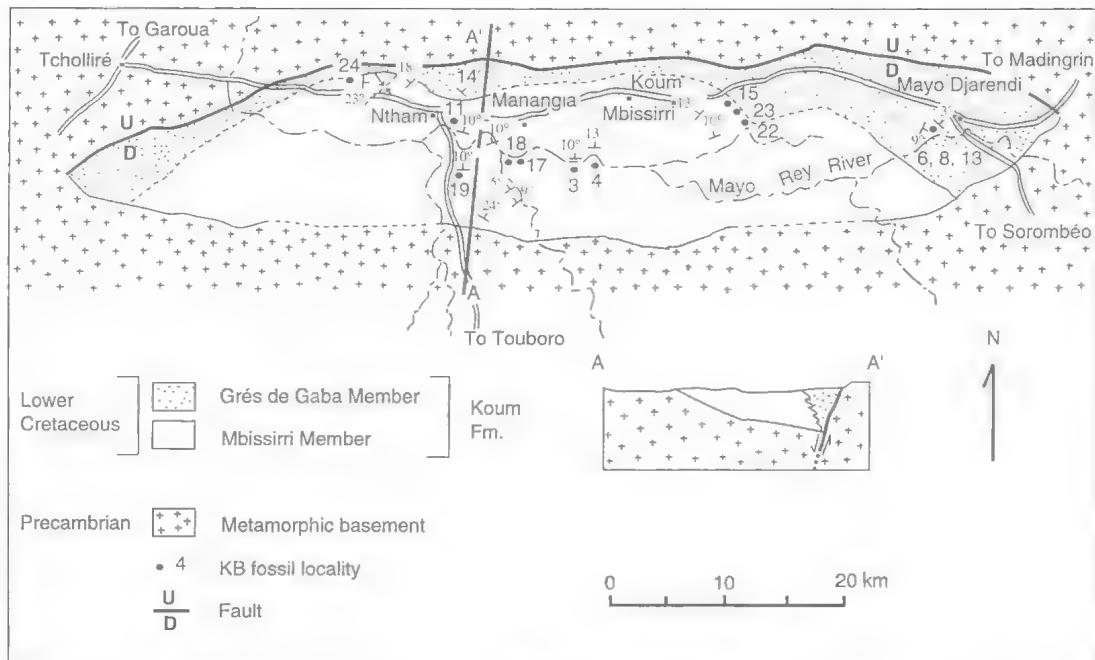
FIG. 3. Geological map of the Koum Basin, northern Cameroon (redrawn from Congleton, 1990).

trackmakers, as interpreted from inferred stride rates.

KARONGA, MALAWI

The Dinosaur Beds of northern Malawi are located along the Sitwe River in the Mwakasyunguti area of Karonga District. Malawi is a long, narrow country located in the southern portion of the East African Rift. Karonga is the northernmost province and Mwakasyunguti is located approximately 70km southwest of Karonga District Headquarters. Jacobs et al. (1992) provided an overview of previous palaeontological research in Malawi.

The Sitwe River near Mwakasyunguti flows through a north-south trending half graben, paralleling the Malawi Rift System (Kaufulu, 1989; Tiercelin et al., 1988) and bordered by Precambrian metamorphic basement. Three sedimentary formations are exposed in the half graben (Fig. 4): the Dinosaur Beds are deposited on the basement and are unconformably overlain by the Plio-Pleistocene Chiwondo Beds, which are in turn unconformably overlain by the Pleistocene Chitemwe Beds.

The Dinosaur Beds are commonly tilted to the northeast with dips ranging from 14-25° northeast. They are cut by two obvious faults (Fig. 4).

One fault trends north-south, cutting across almost the entire study area. It juxtaposes sediments of the upper Dinosaur Beds against the lower Dinosaur Beds and the Precambrian basement. Drag on this fault results in southwesterly dips for the upper part of the Dinosaur Beds. The second clearly visible fault cuts across Cretaceous and Cenozoic sediments, juxtaposing the entire package against Precambrian basement.

Dixey (1928; see also Gomani, 1993) divided the Dinosaur Beds into an upper and a lower member based mainly on color. The lower member is unfossiliferous red and purple mud and calcite-cemented sandstone, locally conglomeratic with some mottling and dessication cracks. The upper member is composed primarily of fossiliferous alternating red and white crossbedded fluvial sandstones deposited along braided streams. At least two distinct modes of bone preservation are found in the Dinosaur Beds. Nearly complete and articulated notosuchid crocodyliforms (Clark et al., 1989; Gomani, 1993, in press) are found within burrows in abandoned channel sediments. A more diverse suite of dinosaurs and other taxa occur as isolated bones, associated clusters, or articulated elements in course poorly-sorted sandstone (Gomani, 1993). Plant macrofossils are rare with only two diaspores
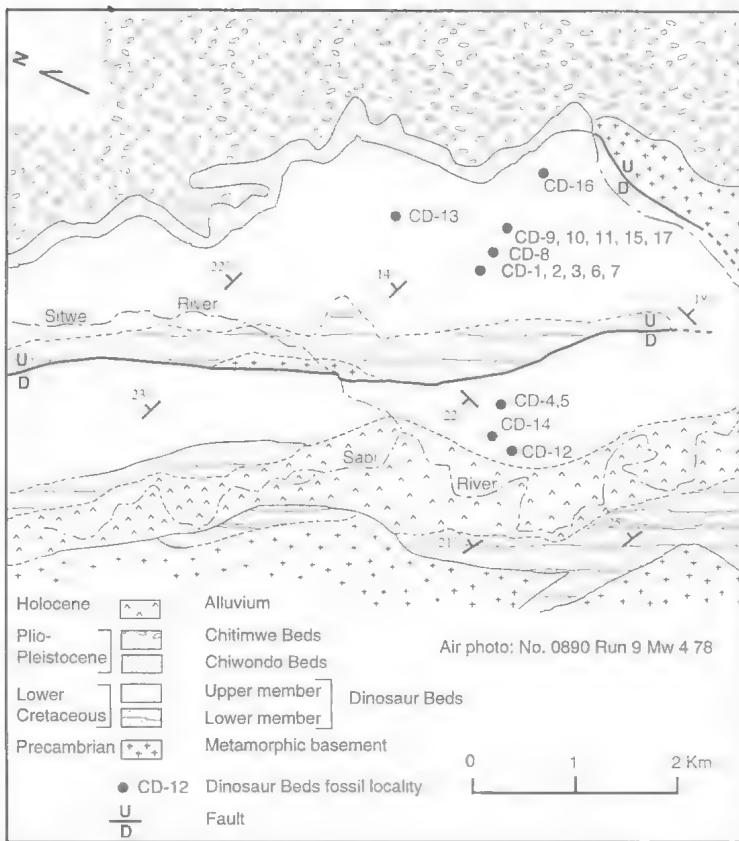
FIG. 4. Geological map of Mwakasyunguti area, Karonga District, Malawi (redrawn from Gomani, 1993).

having been recovered (Jacobs, 1990), and pollen is not preserved. The vertebrate fauna indicates an Early Cretaceous age (Jacobs et al., 1990).

The vertebrate fauna, including fish (but not lungfish), anurans, turtles, crocodyliforms and dinosaurs (Jacobs et al., 1990, 1992; Gomani, 1993), has been collected from localities designated as CD-l to CD-17 (Fig. 4). Anurans are represented by two skull fragments: one has rugose dermal bones and the other one has no sculpturing (Jacobs et al., 1990). The crocodyliforms include an interesting notosuchid (Gomani, in press), aff. *Araripesuchus* sp., and teeth of an unidentified taxon. Aff. *Araripesuchus* is represented by isolated ziphodont teeth which are indistinguishable from specimens from Cameroon (Congleton, 1990). The latter resemble the type of *Araripesuchus wegeneri* from Niger (Buffetaut, 1981), which Kellner (1994) argues may be generically distinct from the genotypic South American species. The notosuchid species is represented by complete

skeletons, which apparently died in burrows (Gomani, in press). It has a long and flat jaw articulation surface and a heterodont dentition with multicusped teeth (Clark et al., 1989; Gomani, in press) that appear to be similar to *Candidodon* from Brazil (Carvalho & Campos, 1988; Carvalho, 1994) and *Chimaerasuchus* from China (Wu et al., 1995). Although distinct, a close phylogenetic relationship of the Malawi notosuchid to *Candidodon* and *Chimaerasuchus* appears likely, but cannot be tested until better material of these genera is found (Gomani, in press). The crus and tarsal bone articulations of the Malawi notosuchid are vertical and the distal condyles of the femur are posteriorly directed. These indicate an erect posture. The ventral position of the occipital condyle and foramen magnum indicates that the head was held perpendicular to the neck (Gomani, in press).

Based on field identifications, it was suggested that the Malawi dinosaur fauna consists of at least five taxa including a titanosaurid, a diplodocid, two morphs of theropods and a stegosaur. However, examination of Argentinean dinosaur specimens and further preparation of the Malawian material necessitate re-evaluation. There are at least two species of sauropods, one of which is *Malawisaurus dixeyi* (Haughton, 1928; Jacobs et al., 1990, 1992, 1993; Gomani, 1993), the other of which is undescribed and has 'pencil-like' teeth. At least two species of theropods are present, based on teeth (Jacobs et al., 1990, 1992). The most abundant elements belong to *Malawisaurus*, a titanosaurid.

Malawisaurus is a titanosaurid because it has a transversely expanded ischium and strongly procoelous anterior caudal vertebrae, derived characters that are considered diagnostic for the Titanosauridae, or possibly a more inclusive monophyletic group containing *Malawisaurus*. Titanosaurids are known to have dermal armor (Depéret, 1896; Bonaparte & Powell, 1980).

Malawisaurus lacks direct evidence of dermal armor, but calcite pseudomorphs shaped like dermal armor were found associated with the bones in the same quarry (Jacobs et al., 1993).

One cervical vertebra referred to *Malawisaurus* (Mal-180, Fig. 5A) has a low neural spine that is not bifurcated. The prezygapophyses extend 10cm beyond the anterior end of the centrum but the postzygapophyses do not extend posteriorly beyond the centrum. The centrum lacks pleurocentral cavities. The cervical ribs are coossified to the centrum and have cranial processes that terminate at the anterior limit of the centrum. The shafts of the ribs extend beyond the centrum posteriorly. In *Saltasaurus loricatus* (PVL 4017-139) of Argentina and in cf. *Titanosaurus* from Brazil (Powell, 1986), the prezygapophyses do not extend beyond the centrum while the postzygapophyses do extend beyond the centrum. In addition, *Saltasaurus* and cf. *Titanosaurus* cervical vertebrae have pleurocentral cavities on the centra. In anterior cervicals of *Saltasaurus* neural spines do not rise above the neural arches while in posterior cervicals low neural spines rise above the neural arches. Based on comparison with *Saltasaurus*, this vertebra of *Malawisaurus* (Mal-180) is probably posterior to the fourth cervical in position.

Dorsal vertebrae attributed to *Malawisaurus* (Mal-181, and Mal-182, Figs 5B-D) indicate no evidence of hyposphene-hypantrum articular surfaces. The centra are opisthocoelous and pleurocoels are anteriorly restricted. The transverse processes of Mal-181 are wide and slightly inclined dorsally. The broad-based, undivided neural spine has elongate anterolateral depressions that are at the same level as the postzygapophyses. A well-developed thin prespinal lamina occurs at the anterior base. The postspinal lamina is thicker than the prespinal lamina.

The base of the undivided neural spine in Mal-182 is narrower than in Mal-181. The prespinal lamina is well-developed. In anterior dorsals (dorsals 1-4) of sauropods the parapophyses are located on the centra while on the posterior dorsals, the parapophyses are high on the centrodiapophysial lamina that extends from the diapophysis (McIntosh, 1990). Mal-181 and Mal-182 are not anterior dorsals because the centra lack parapophyses. In *Epachthosaurus*, the parapophyses become progressively higher posteriorly on dorsals. The transverse processes of Mal-182 are broken, thus the height of the parapophyses and relative vertebral position cannot be determined. The prezygapophyses in Mal-

182 are closer together than in Mal-181. The undivided neural spine is high and inclined caudally in Mal-181, but it is vertical in Mal-182. Supradiapophysial laminae in Mal-181 and Mal-182 are well-developed. Deep lateral excavations and high prespinal laminae also occur in *Saltasaurus loricatus, Andesaurus delgadoi* and *Argyrosaurus superbus* from Argentina (Bonaparte & Powell, 1980; Calvo & Bonaparte, 1991). In *Saltasaurus*, caudally inclined neural spines occur in more anterior dorsal vertebrae and vertical neural spines occur in posterior dorsal vertebrae (Powell, 1986). Based on comparison with these taxa, Mal-182 probably is more posterior in the vertebral column of *Malawisaurus* than Mal-181.

Caudal vertebrae of *Malawisaurus* are described by Jacobs et al. (1993). The vertebrae progress from procoelous to gently amphicoelous posteriorly. The anterior caudals are strongly procoelous, the prezygapophyses extend slightly beyond the centrum as in *Titanosaurus* sp. from Argentina (Powell, 1986) and *Alamosaurus* from North America (Gilmore, 1946). However, *Alamosaurus* and *Titanosaurus* are more derived because all their posterior caudal vertebrae are procoelous. *Malawisaurus* also shares low caudal neural spines with *Andesaurus* and derived titanosaurids. *Malawisaurus* is distinct from *Andesaurus* and *Epachthosaurus* because these genera have hyposphene-hypantrum articular surfaces on dorsal vertebrae (Calvo & Bonaparte, 1991) that are absent in *Malawisaurus*. All caudal vertebrae of *Epachthosaurus* are procoelous.

Isolated teeth similar to those associated with titanosaurids from Argentina (Huene, 1929 Pl. 1. Figs 12-13; Powell, 1986), Brazil (Kellner, this volume) and to those associated with *Alamosaurus* from North America (Kues et al., 1980; Lucas & Hunt, 1989) occur in the Dinosaur Beds. These teeth are slender and conical. Presence of relatively long slender and conical (peglike) teeth is one of the diagnostic features of Titanosauridae and Diplodocidae (McIntosh, 1990; Titanosauroidea and Diplodocoidea of Upchurch, 1995). Thus, the slender teeth in the Dinosaur Beds may be titanosaurid or diplodocid. The presence of diplodocids in the Dinosaur Beds is suggested by the derived features of an undescribed mandible. It has a short tooth row and the ramus turns at a sharp angle towards the symphysis where the dorsal margin of the mandible flares outward. These characters are also present in South American *Antarctosaurus* (Huene, 1929; Huene & Matley, 1833; Powell,
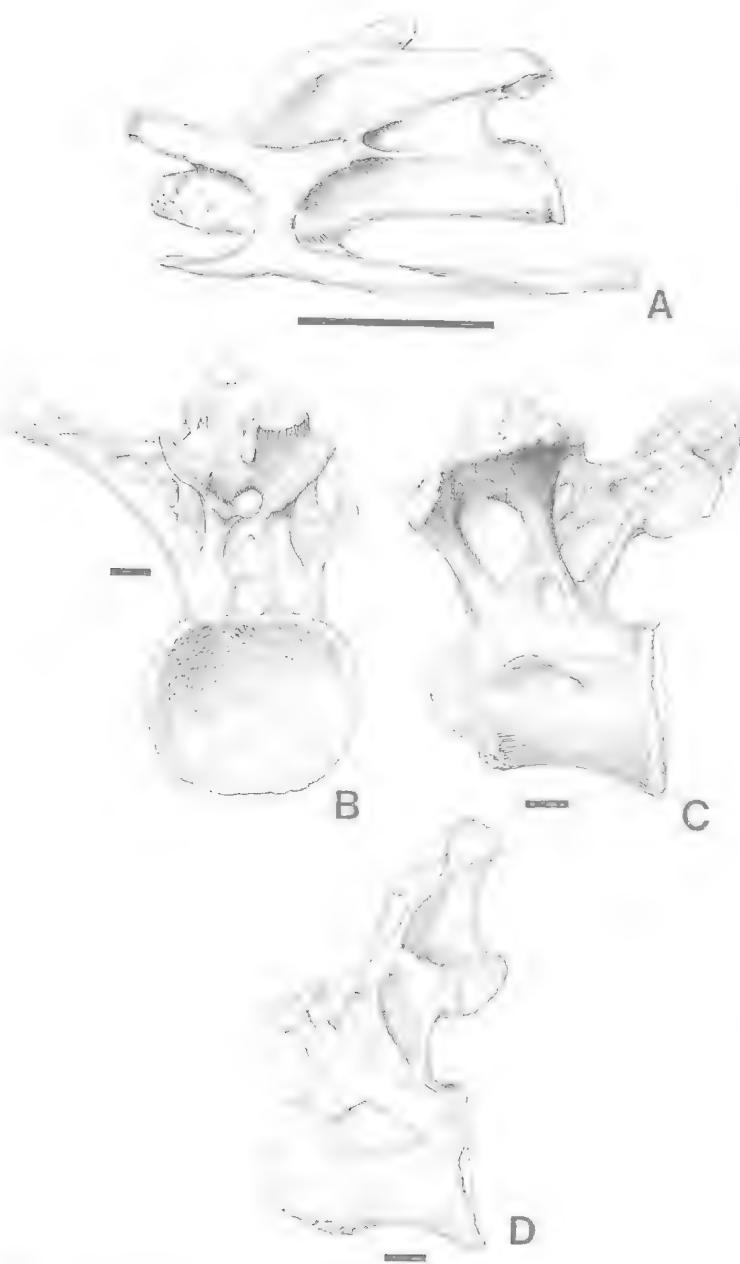
FIG. 5. Vertebrae of *Malawisaurus*. A, middle cervical, Mal-180, left lateral view; scale = 10cm. B, C, D, dorsals of *Malawisaurus* (B, C, Mal-181, right lateral and posterior view, respectively). D, Mal-182, left lateral view. B-D scales = 3cm.

Diplodocoidea of Upchurch, 1995), it is clear that the morphological diversity of both South American and African saurpods may be greater than we previously anticipated.

A pelvis from CD-10 is a titanosaurid as suggested by the pelvis of *Epachthosaurus* and *Saltasaurus*. The anterior blade of the ilium of these titanosaurids is curved anterolaterally, a feature that may be derived for this group of sauropods. Further description of the pelvis from Malawi awaits complete preparation.

DISCUSSION AND CONCLUSION

Dinosaurs of Cretaceous age in Africa are widely distributed geographically (Table 1). The data used in the compilation of Table 1 were derived from Broom (1904), Haughton (1928), Dixey & Smith (1929), Dixey (1937, 1939), Greigert et al. (1954), Lavocat (1954), Lapparent (1960), Said (1962), Broin et al. (1971,1974), Kennedy & Klinger (1972), Russell et al. (1976), McLachlan & McMillan (1976), Taquet (1976,1982,1984), El-Khashab (1977), Monbaron (1978), Klitzsch et al. (1979), Pentel'kov & Voronovsky (1979), Sues & Taquet (1979), Dutuit & Ouazzou (1980), Sues (1980), Galton & Coombs (1981), Rich et al. (1983), Cooper (1985), Kent & Gradstein (1985, 1986), William & Savage (1986), Flynn et al. (1987), Handford (1987), Kennedy et al. (1987), Mateer (1987), Shrank (1987), Bouaziz et al. (1988), Brunet et al. (1988), Carroll (1988), Buffetaut (1989a, 1989b), Dejax et al. (1989), Jacobs et al. (1989, 1990, 1992, 1993), Colin & Jacobs (1990), Congleton (1990), Jacobs (1990), Klitzsch & Squyres (1990), Lefranc & Guiraud (1990), Weishampel (1990), Wycisk

1986). Those authors consider *Antarctosaurus* a titanosaurid, but others have suggested diplodocid or diplodocoid relationships (Jacobs et al., 1993; Hunt et al., 1994; Upchurch, 1994, 1995). While these are given as characters of Diplodocidae (Berman & McIntosh, 1978;

(1990), Moody & Sutcliffe (1991), Colin et al. (1992), Congleton et al. (1992), Mateer et al. (1992), Werner (1993a, 1993b), Wescott et al. (1993), Krause & Dodson, (1994); Sereno et al. (1994, 1996), Rauhut & Werner (1995), Forster (1996), Sampson et al. (1996), Krause et al. (in press), and the references therein. The most widely distributed sauropods in Africa are titanosaurids. This is important for palaeobiogeographical comparison between Africa and South America because titanosaurids are also the most widely distributed geographically and most numerous sauropods in South America (Huene, 1929; Huene & Matley, 1933; Bonaparte & Powell, 1980; Powell, 1986; Weishampel, 1990). In Africa, Cretaceous titanosaurids are reported from the Campanian of Madagascar (Russell et al., 1976; Sues & Taquet, 1979; Sues, 1980; Forster, 1996; Sampson et al., 1996; Krause et al., in press), the Senonian of Sudan (Werner, 1993a, 1993b), the Turonian-Santonian of Kenya (Arambourg & Wolff, 1969; Weishampel, 1990; Westcott et al., 1993), the Cenomanian of Egypt (Stromer, 1932), the Albian of Niger (Lapparent, 1960), the Aptian of Malawi (Jacobs et al., 1992, 1993).

Titanosaurid sauropods are clearly important elements in the Cretaceous fauna of both South America and Africa. Titanosaurids are considered to include *Aegyptosaurus*, *Aeolosaurus*, *Alamosaurus*, *Andesaurus*, *Antarctosaurus*, *Argentinosaurus*, *Argyrosaurus*, *Epachthosaurus*, *Hypselosaurus*, *Janenschia*, *Laplatasaurus*, *Macrurosaurus*, *Magyarosaurus*, *Malawisaurus*, *Saltasaurus*, *Titanosaurus* and questionably *Campylodoniscus*. The most diagnostic and most commonly used synapomorphy of titanosaurids is strongly procoelous caudal vertebrae. Having all caudal vertebrae procoelous is derived relative to having posterior caudals amphicoelous.

Malawisaurus has gently amphicoelous posterior caudals. This feature is also seen in *Janenschia* from Tanzania (Janensch, 1922; 1961), *Aeolosaurus rionegrinus* from Argentina (Powell, 1986; 1987) and *Macrurosaurus* from England (Seeley, 1876). No anterior caudal vertebrae are known for *Andesaurus* (Calvo & Bonaparte, 1991). The posterior caudal (Calvo & Bonaparte, 1991, Figs 4A-C) of the latter is described as amphiplatyan. Huene & Matley (1933) described an amphiplatyan posterior caudal and associated it with *Titanosaurus indicus*. The use of the terms gently amphicoelous as compared to amphiplatyan in this case may be a distinction without a difference. Having gently

amphicoelous posterior caudal vertebrae may be fairly common among titanosaurids and taxa cannot be excluded from the group because of amphicoelous posterior caudals.

Diplodocids in the Cretaceous of Africa are reported from the Cenomanian of Morocco and the Albian of Niger, Algeria and Morocco (Lavocat, 1954; Lapparent, 1960; Taquet, 1976). These are represented by dorsal vertebrae, humerus, sacrum and teeth of *Rebbachisaurus* and isolated pencil-like teeth (not figured) of an unnamed taxon from Niger (Taquet, 1976). The identification of the unnamed taxon is based on comparison with *Dicraeosaurus* teeth from the Kimmeridgian of Tanzania. Because some pencil-like teeth are referred to titanosaurids, the teeth from Niger require further study for confident assignment to taxon. In the Cretaceous of South America, diplodocids (diplodocoids of Upchurch, 1995) are represented by *Rebbachisaurus* (recently reported by Calvo & Salgado, 1995, in a paper we have not yet had the opportunity to evaluate) and *Amargasaurus* (Salgado & Bonaparte, 1991). *Amargasaurus* is most closely related to the Late Jurassic *Dicraeosaurus* from Tendaguru, Tanzania (Upchurch, 1995). The African titanosaurid *Malawisaurus* is more derived than *Janenschia* from Tendaguru and more similar to South American *Andesaurus*. The undescribed jaw from the Dinosaur Beds of Malawi may be diplodocid but the phylogenetic relationships to other sauropods will be presented elsewhere.

Early Cretaceous sediments and fauna from Cameroon and Malawi are depositionally different and taxonomically distinct. In Cameroon, fossils occur in lacustrine, meanderbelt channel, overbank and braided stream deposits, while in Malawi dinosaur fossils occur predominantly in course-grained, braided fluvial sediments lacking finegrained overbank deposits. Footprints occur in Cameroon but not Malawi. Bones are more complete in Malawi. Cameroon appears to have a more diverse total fauna than Malawi. In Cameroon, the ornithopod *Ouranosaurus* is present while Malawi has no ornithopods. In Malawi, sauropods are the best represented elements, while they are rare in Cameroon. In neither area do we have a reasonably complete understanding of the fauna because of inadequate sampling, but both contribute to the palaeontological baseline for Africa. Compared to other African localities, the Koum Basin appears most similar to Gadoufaoua, Niger, which is close in proximity and probably in age; but neither Koum

TABLE 1. Cretaceous dinosaurs of Africa.

TAXON	STAGE	LOCALITY (ROCK UNIT)	REFERENCE
Theropoda			
Elaphrosaurus	Cenomanian	Marsa Matruh, Egypt (Baharija Fm)	Lapparent, 1960; Said, 1962; El-Khashab, 1977
	Albian	Kasr-es-Souk, Morocco (Tegana Fm)	Lapparent, 1960; Monbaron, 1978
Afrovenator	Hauterivian-Barremian	Southern Sahara, Niger	Sereno et al., 1994
Majungasaurus	Campanian-Maastrichtian	Marsa Matruth, Egypt (Phosphatic Beds)	Lapparent, 1960; Said, 1962; El-Khashab, 1977
	Campanian	Majunga District, Madagascar (Maevarano Fm)	Russell et al., 1976; Sues & Taquet, 1979; Sues, 1980; Foster, 1996; Sampson et al., 1996; Krause et al., in press
Bahariasaurus	Turonian-Santonian	Agadez, Niger (In Beceten Fm)	Greigert et al., 1954; Broin et al., 1974
	Cenomanian	Marsa Matruh, Egypt (Baharija Fm); Tahoua, Niger (Farak Fm); Northern Province, Sudan (Wadi Milk Fm)	Greigert et al., 1954; Lapparent, 1960; Said, 1962; Taquet, 1976; El-Khashab, 1977; Werner, 1993a
	Albian	Agadez, Niger (Continental Intercalaire)	Lapparent, 1960
Carcharodonto-saurus	Cenomanian	Marsa Matruh, Egypt (Baharija Fm); Northern Province, Sudan, (Wadi Milk Fm); Kem Kem, Morocco, (Kem Kem Beds)	Lavocat, 1954; Lapparent, 1960; Said, 1962; El-Khashab, 1977; Werner, 1993a; Sereno et al., 1996
	Albian-Cenomanian	Hammada du Guir, Morocco (Continental Red Beds)	Buffetaut, 1989a, 1989b
	Albian	Tamenghest, Wargla, & Adrar, Algeria; Agadez, Niger (Continental Intercalaire); Kasr-es-Souk, Morocco (Tegana Fm); Gharyan, Libya (Continental Intercalaire) Medenine, Tunisia (Chenini Fm)	Lapparent, 1960; Monbaron, 1978; Bouaziz et al., 1988
	Aptian	Medenine, Tunisia (Chenini Fm)	Bouaziz et al., 1988
Deltadromeus	Cenomanian	Kem Kem, Morocco, (Kem Kem Beds)	Sereno et al., 1996
Spinosaurus	Turonian-Santonian	Rift Valley Province, Kenya (Turkana Grits)	Weishampel, 1990; Wescott et al., 1993
	Cenomanian	Marsa Matruh, Egypt (Baharija Fm)	Lapparent, 1960; Said, 1962; El-Khashab, 1977
	Albian-Cenomanian	Hammada du Guir, Morocco (Continental Red Beds)	Buffetaut, 1989a, 1989b
	Albian	Medenine, Tunisia (Chenini Fm)	Bouaziz et al., 1988; Weishampel, 1990
	Aptian	Gadoufaoa, Niger (Elrhaz Fm)	Taquet, 1976; 1982; 1984
	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin)	Congleton, 1990; Congleton et al., 1992; Colin et al., 1992
? Spinosaurid indet.	Aptian	Agadez, Niger (Elrhaz Fm)	Lapparent, 1960
	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin)	Congleton 1990; Colin et al., 1992
Dromaeosaurid	Cenomanian	Northern Province, Sudan (Wadi Milk Fm)	Rauhut & Werner, 1995
Theropoda undescribed and indet.	Campanian	Marsa Matruh, Egypt (Nubian sandstone); Majunga District, Madagascar (Maevarano Fm)	Said, 1962; Weishampel, 1990; Forster, 1996; Sampson et al., 1996
	Turonian-Santonian	Rift Valley Province, Kenya (Turkana Grits)	Weishampel, 1990; Wescott et al., 1993
	Albian	Wargla and Adrar, Algeria (Continental Intercalaire); Gharyan, Libya (Continental Intercalaire); Agadez, Niger (Continental Intercalaire); Medenini, Tunisia (Chenini Fm)	Lapparent, 1960; Broin et al., 1971
	Aptian	Agadez, Niger (Elrhaz Fm)	Lapparent, 1960; Broin et al., 1974
	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin)	Congleton, 1990; Colin et al., 1992
	Barremian	Cape Province, South Africa (Sundays River Fm)	Rich et al., 1983; Weishampel, 1990

TABLE 1 (*cont.*)

TAXON	STAGE	LOCALITY (ROCK UNIT)	REFERENCE
	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood; Enon Fm)	Rich et al., 1983; Mateer, 1987
Theropod footprints	Maastrichtian	Agadir, Morocco (Unnamed unit)	Weishampel, 1990
	Cenomanian	Laghout, Algeria (Unnamed unit)	Weishampel, 1990
	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin)	Flynn et al., 1989; Congleton, 1990; Congleton et al., 1992; Colin et al., 1992
Sauropoda - Diplodocidae			
cf. *Dicraeosaurus*	Cenomanian	Marsa Matruh, Egypt (Baharija Fm)	Lapparent, 1960; Said, 1962; El-Khashab, 1977
Rebbachisaurus	Cenomanian	Kem Kem, Morocco, (Kem Kem Beds)	Lavocat, 1954; Sereno et al., 1996
	Albian	Adrar, Wargla and Tamenghest, Algeria (Continental Intercalaire); Agadez, Niger (Continental Intercalaire); Tahoua, Niger (Farak Fm); Kasr-es-Souk, Morocco (Tegana Fm); Medenini, Tunisia (Chenini Fm)	Greigert et al., 1954; Lavocat, 1954; Lapparent, 1960; Taquet, 1976; Monbaron, 1978
Algoasaurus	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	Broom, 1904; McLachlan & McMillan, 1976
Diplodocid indet. and undescribed	Aptian	Agadez, Niger (Elrhaz Fm)	Lapparent, 1960; Taquet, 1976, 1982, 1984
Titanosauridae			
Titanosaurus	Campanian	Majunga District, Madagascar (Maevarano Fm)	Sues & Taquet, 1979; Sues, 1980; Forster, 1996; Sampson et al., 1996; Krause et al., in press
	Turonian-Santonian	Rift Valley Province, Kenya (Turkana Grits)	Weishampel, 1990; Wescott et al., 1993
Aegyptosaurus	Cenomanian	Marsa Matruh, Egypt (Baharija Fm); Tahoua, Niger (Farak Fm)	Greigert et al., 1954; Lapparent, 1960; Said, 1962; El-Khashab, 1977
	Albian	Agadez, Niger (Continental Intercalaire)	Greigert et al., 1954; Lapparent, 1960; Taquet, 1976
Malawisaurus	Aptian	Karonga, Malawi (Dinosaur Beds)	Haughton, 1928; Jacobs et al., 1990, 1992, 1993
Titanosaurid indet.	Maastrichtian	Agadir, Morocco (Unnamed unit)	Weishampel, 1990
	Campanian	Majunga District, Madagascar (Maevarano Fm)	Suez & Taquet, 1979; Sues, 1980; Forster, 1996
	Santonian	Natal, South Africa (Unnamed unit)	Kennedy et al., 1987
	Turonian-Santonian	Agadez, Niger (Unnamed unit);	Broin et al., 1974
	Cenomanian	Northern Province, Sudan (Wadi Milk Fm)	Schrank, 1987; Werner, 1993a; 1993b; Rauhut & Werner, 1995
	Aptian	Agadez, Niger (In Beceten Fm); Gadoufaoa, Niger (Elrhaz Fm)	Greigert et al., 1954; Broin et al., 1974; Taquet, 1976, 1982
	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	Forster, 1996
Brachiosauridae			
Brachiosaurus	Albian	Wargla and Adrar, Algeria (Continental Intercalaire)	Lapparent, 1960
?*Pleurocoelus*	Albian	Agadez, Niger (Continental Intercalaire)	Lapparent, 1960
	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	McLachlan & McMillan, 1976; Rich et al., 1983
Brachiosaurid indet.	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	Forster, 1996
Camarasauridae			
Camarasaurid indet.	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	Rich et al., 1983

TABLE 1 (*cont.*)

TAXON	STAGE	LOCALITY (ROCK UNIT)	REFERENCE
Sauropoda indet. and undescribed	Turonian-Santonian	Rift Valley Province, Kenya (TurkanaGrits)	Weishampel, 1990; Wescott et al., 1993
	Cenomanian	Marsa Matruh, Egypt (Baharija Fm); Madagascar (Ankarafantsika Fm)	Lapparent, 1960; Said, 1962; El-Khashab, 1977; Mateer et al., 1992
	Albian	Adrar, Algeria (Continental Intercalaire and Unnamed unit); Medenine, Tunisia (Chenini Fm); Gao, Mali (Continental Intercalaire)	Lapparent, 1960; Broin et al., 1971; Bouaziz et al., 1988
	Aptian	Karonga, Malawi (Dinosaur Beds); Chirunda Hill, Mozambique (Lupata Series); Luangwa Valley, Zambia (Dinosaur Beds)	Dixey & Smith, 1929; Dixey, 1937, 1939; Pentel'kov & Voronovsky, 1979; Colin & Jacobs, 1990; Jacobs et al., 1990, 1992, 1993
	Barremian-Aptian	Mayo Djarendi, (Koum Basin)	Brunet et al., 1990
	Hauterivian-Barremian	Southern Sahara, Niger	Sereno et al., 1994
Sauropod footprints	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin)	Flynn et al., 1989; Congleton, 1990; Congleton et al., 1992
	Tithonian-Berriasian	Marrakech, Morocco (Unnamed unit)	Dutuit & Ouazzou, 1980
Ornithopoda - Iguanodontidae			
Ouranosaurus	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin); Agadez, Niger (Elrhaz Fm)	Lapparent, 1960; Taquet, 1976, 1982, 1984; Brunet et al., 1990; Congleton, 1990; Congleton et al., 1992
Iguanodontian indet.	Cenomanian	Northern Province, Sudan (Wadi Milk Fm); Kem Kem, Morocco, (Kem Kem Beds)	Rauhut & Werner, 1995; Sereno et al., 1996
	Aptian	Medenini, Tunisia (Continental Intercalaire); Agadez, Niger (Elrhaz Fm)	Lapparent, 1960; Taquet, 1976
	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	Rich et al., 1983; Foster, 1996
Hypsilophodontidae			
Valdosaurus	Aptian	Agadez, Niger (Elrhaz Fm)	Lapparent, 1960; Taquet, 1976, 1982, 1984
Kangnasaurus	Tithonian-Hauterivian	Cape Province, South Africa (Kalahari Deposits)	Cooper, 1985
Hypsilophodontid indet.	Cenomanian	Northern Province, Sudan (Wadi Milk Fm)	Rauhut & Werner, 1995
Ornithopoda indet.	Turonian-Santonian	Rift Valley Province, Kenya (Turkana Grits)	Weishampel, 1990; Wescott et al., 1993
	Cenomanian	Northern Province, Sudan (Wadi Milk Fm)	Werner, 1993a; Rauhut & Werner, 1995
	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	McLachlan & McMillan, 1976
Ornithopod footprints	Cenomanian	Kem Kem, Morocco, (Kem Kem Beds)	Sereno et al., 1996
	Barremian-Aptian	Mayo Djarendi (Koum Basin)	Flynn et al., 1989; Congleton, 1990; Congleton et al., 1992
? Pachycephalosauria - ?Pachycephalosauridae			
Majungatholus (? = *Majungasaurus*)	Campanian	Majunga District, Madagascar (Maevarano Fm)	Sues & Taquet, 1979; Sues, 1980; Sampson et al., 1996a,b; Krause et al., in press
Thyreophora - Stegosauridae			
Paranthodon	Tithonian-Hauterivian	Cape Province, South Africa (Upper Kirkwood Fm)	Galton & Coombs, 1981; Rich et al., 1983
Nodosauridae			
Nodosaurid indet.	Albian	Gao, Mali; Agadez, Niger (Continental Intercalaire)	Lapparent, 1960; Weishampel, 1990
? Thyreophora indet.	Barremian-Aptian	Mayo Djarendi, Cameroon (Koum Basin)	Congleton, 1990; Congleton et al., 1992

nor the Dinosaur Beds of Malawi can be shown to be particularly similar to other African localities. This is interesting with respect to the differentiation and development of endemism in the African dinosaur fauna in that it highlights both the chronological and geographic shortcomings of the record as we now know it.

Ongoing work by groups of researchers in the Sahara, southeast Africa and Madagascar is elucidating further the history of dinosaurs on this great continent. For example, Sereno et al. (1994) described the theropod *Afrovenator*, a tetanuran more primitive than *Spinosaurus*, and mentions sauropod remains with unclear affinities, but not diplodocid or titanosaurid, from the Early Cretaceous of Niger. The bones were found in channel fills and show evidence of fluvial transport. They interpret the area to have had a uniform climatic regime because of the absence of caliche and fossil wood without growth rings. Work in the Cenomanian of Morocco (Sereno et al., 1996) led to the discovery of the coelurosaur *Deltadromeus* and the description of the skull of the large allosauroid *Carcharodontosaurus*. Sereno et al. (1996) and Sereno (1996) concluded that dinosaurian endemism began abruptly in the Late Cretaceous.

Late Cretaceous work in Madagascar recently by field parties led by David Krause have resulted in significant new discoveries, particularly of titanosaurids, the theropod *Majungasaurus* and birds. These discoveries, and the ones that are sure to follow, may prove to be particularily enlightening because Madagascar remained joined to the Gondwana landmass including India, Australia, Antarctica and South America into the Early Cretaceous, long after it had rifted from the west coast of Africa (Krause & Dodson, 1994; Forster, 1996; Sampson et al., 1996; Krause et al., in press).

ACKNOWLEDGMENTS

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REMARKS ON BRAZILIAN DINOSAURS

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To date the dinosaur record in Brazil is limited to saurischians and no confirmed evidence (except probably footprints) of ornithischians is presently known. Two dinosaur taxa were described from the Triassic Santa Maria Formation: *Spondylosoma absconditum* and *Staurikosaurus pricei*. The dinosaurian affinities of *Spondylosoma* are questioned in the literature; *Staurikosaurus* is regarded by some authors as closely related to *Herrerasaurus* from Argentina. No Jurassic dinosaurs are known from Brazil, but there are several Cretaceous occurrences. Titanosaurid sauropods (*Antarctosaurus brasiliensis*, several undescribed postcranials and teeth) and theropods (teeth) are present in the Late Cretaceous strata of the Bauru Group. Spinosaurid theropods have been found in the Albian strata of northeast Brazil and are apparently closely related to some African forms. This distribution pattern may be a product of an Early Cretaceous vicariant event. Spinosaurids as regarded here are not an exclusive Gondwanan group and are also present in Europe (*Baryonyx*). A literal interpretation of the stratigraphic record, therefore, suggests that dinosaur faunal interchanges between Europe and Gondwana may have occurred not only from South to North as previously supposed, but in the opposite direction as well. This hypothesis is very preliminary and can be tested by new and more complete dinosaur material from Brazil and Africa. ☐ *Brasil, dinosaurs, Triassic, Cretaceous, spinosaurid, soft tissue.*

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Dinosaur remains are recorded from several localities in Brazil (Fig. 1). To date only remains of saurischian dinosaurs are known in this country and no confirmed evidence (except some possibly ichnofossils) of ornithischian taxa have been found (see Campos & Kellner, 1991, for a review). Many specimens have been collected, but most are still undescribed. Apart from the considerable work done on footprints and trackways, (e.g., Leonardi, 1984), little is actually known from the Brazilian dinosaur fauna.

This paper reviews the most important dinosaur occurrences in Brazil, particularly those from the Santa Maria Formation (Triassic), Santana Formation (Early Cretaceous) and Bauru Group (Late Cretaceous). The preliminary description of new specimens (mostly teeth) and the palaeobiogeographic information that can be inferred based on the present knowledge of the Brazilian dinosaurs is also discussed.

SANTA MARIA FORMATION

Triassic dinosaurs in Brazil are only found in the Santa Maria Formation (Parana Basin, south Brazil) which is the most fossiliferous unit of that period in this country. Rhynchosaurs, cynodonts and dicynodonts are frequently found preserved in red sandstones and siltstones. The age of this unit is regarded as ranging from Anisian to Carnian based essentially on the fossil vertebrate assemblages (Barberena et al., 1985).

Two supposed dinosaurs have been reported from the Santa Maria Formation. The first one is *Spondylosoma absconditum* named by Huene (1942) based on some postcranial elements. Colbert (1970) mentioned that two small and compressed teeth with serrated edges may also belong to the same specimen. Romer (1956) listed *Spondylosoma* within Prosauropoda, which was followed by others (e.g., Colbert, 1970). Unfortunately no recent detailed description of this material is available which could provide more evidence about the systematic position of this taxon. According to Sues (1990), the dinosaurian affinity of *Spondylosoma* has not been conclusively presented so far.

A second dinosaur from this unit, *Staurikosaurus pricei*, is only known by the type specimen. This taxon was named by Colbert (1970) on the basis of an incomplete skeleton. Another partial postcranial skeleton found in the Late Triassic Ischigualasto Formation from Argentina was attributed to cf. *Staurikosaurus* sp. (Brinkman & Sues, 1987), but is now referred to *Herrerasaurus* (Novas, 1994).

FIG. 1. Map showing the most important Brazilian dinosaur localities known so far (after Campos & Kellner, 1991). In Rio Grande Do Sul: 1, Santa Maria. In São Paulo: 2, Presidente Bernardes; 3, Adamantina; 4, Pacaembu Paulista; 5, Guararapes; 6, São José do Rio Preto; 7, Ibirá; 8, Colina; 9, Monte Alto. In Minas Gerais: 10, Uberaba/Peirópolis. In Mato Grosso: 11, Morro do Cambambe. In Ceará: 12, Sobradinho; 13, Chapada do Araripe. In Paraíba: 14, Rio do Peixe. In Maranhão: 15, Bacia de São Marcos. In Amazonas: 16, Nova Olinda do Norte.

The phylogenetic position of *Staurikosaurus* has been controversial. In the original description, Colbert (1970) placed this taxon in the Saurischia, regarding it as possibly a carnivorous prosauropod (see Galton,1977). Benedetto (1973) considered *Staurikosaurus* closely related to *Herrerasaurus* from the Ischigualasto Formation (Argentina) and classified both in the Her-

rerasauridae, which he excluded from Theropoda. Galton (1973) suggested that *Staurikosaurus* was probably a primitive theropod, but classified this taxon as Saurischia incertae sedis. Later, Galton (1977) placed *Staurikosaurus* in its own higher taxonomic unit (Staurikosauridae), separating the Brazilian species from *Herrerasaurus*, and considered both
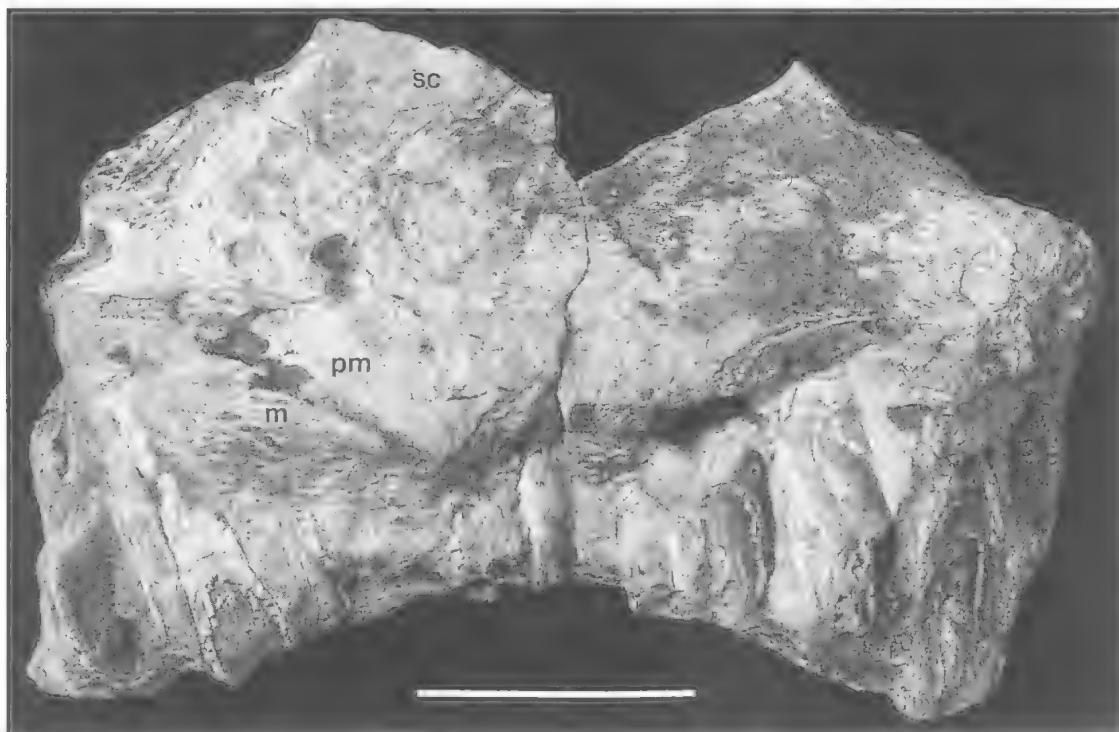
FIG. 2. Brazilian spinosaurid *Angaturama limai*; right lateral view of the anterior portion of the skull (Universidade de São Paulo - USP, São Paulo: GP/2T-5). m=maxilla, pm=premaxilla, sc=sagittal crest; scale = 50mm.

as Saurischia incertae sedis. Brinkman & Sues (1987) also disagreed with the hypothesis of close relationship between *Staurikosaurus* and *Herrerasaurus*, regarding both taxa as successive outgroups for Saurischia + Ornithischia. More recently Novas (1992, 1994) and Sereno & Novas (1992), based on the study of new material of *Herrerasaurus*, suggested that the Argentinean form was closely related to *Staurikosaurus*, and considered both as basal theropods of the monophyletic group Herrerasauridae.

SANTANA FORMATION

The Santana Formation (Araripe Basin, northeast Brazil) is one of the most fossiliferous units in the world. This formation is divided into three members, named from bottom to top: Crato, Ipubi and Romualdo (Beurlen, 1971). According to palynological data (Pons et al., 1990), the age of those strata varies from Aptian-Albian (Crato Member) to middle Albian (Romualdo Member).

The palaeontological content of the Santana Formation is very diverse. The Crato Member is very rich in plants, insects and fishes, but includes pterosaurs (Frey & Martill, 1994; Campos &

Kellner, 1996) and birds (so far only feathers). The Romualdo Member is well known for the variety and quantity of fishes, but plants, pterosaurs and crocodilians are also found (see Maisey, 1991). Dinosaur material is rare and presently restricted to the calcareous nodules of the Romualdo Member.

The first dinosaur reported from the Santana Formation is an isolated bone, tentatively identified as an ischium of an ornithischian dinosaur (Leonardi & Borgomanero, 1981). Although probably dinosaurian, the fragmentary nature of this specimen casts doubt about its anatomical identification. This material needs further preparation and at this point should be regarded as Dinosauria incertae sedis.

Another dinosaur specimen reported from the Romualdo Member is the anterior portion of a skull (incomplete premaxilla-maxilla; Figs 2, 3) and represents a new theropod (Kellner, 1994a), *Angaturama limai* (Kellner & Campos, 1996). The rostrum of this dinosaur is very compressed (more than in any other theropod) and the distal portion is expanded ('spoon-shaped'). A sagittal crest formed by the premaxillae is present on the anterior part of the snout. This specimen repre-
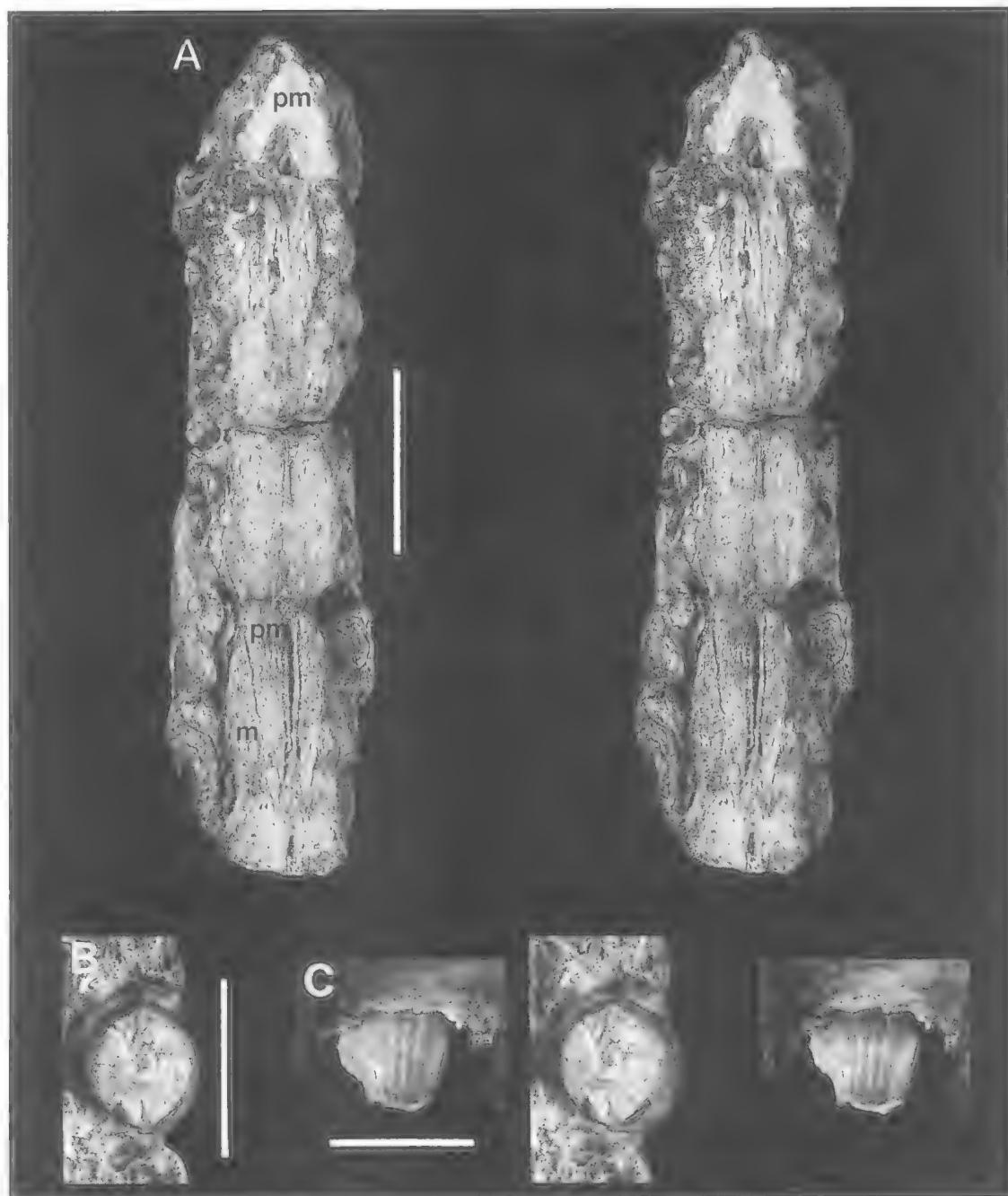
FIG. 3. Spinosaurid *Angaturama limai* (USP GP/2T-5). A, Stereopair of the palatal view. pm=premaxilla; scale = 50mm. B, Right 6th premaxillary tooth, stereopair of the transverse section; scale = 10mm. C, Lingual view; scale = 10mm.

sents the first occurrence of a spinosaurid in Brazil.

Spinosauridae is considered a group of unusual theropods that includes *Spinosaurus aegyptiacus* found in the Cenomanian rocks of Egypt (Stromer, 1915) and the spinosaurids found in Early Cretaceous strata of Gadoufaoua, Niger (Taquet, 1984). *Baryonyx* found in the Barremian
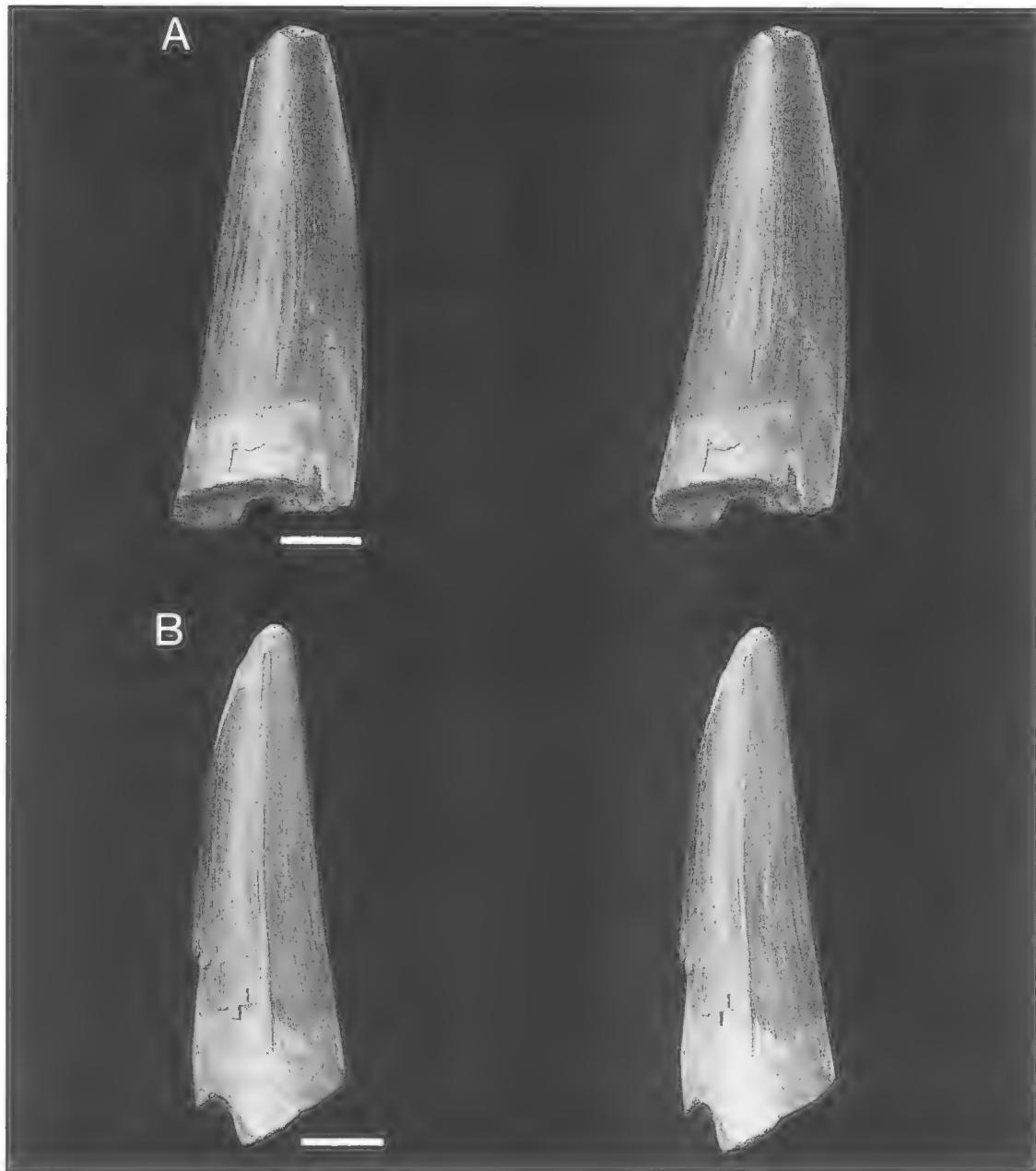
FIG. 4. Isolated spinosaurid tooth from Cretaceous strata of Morocco, housed in the Departamento Nacional da Produção Mineral (DNPM), Rio de Janeiro. A, Stereopair of the lingual view; scale = 10mm. B, Posterior view; note the wear surface on the basal portion of the tooth; scale = 10mm.

of England (Charig & Milner, 1986) is considered a spinosaurid too (Paul, 1988; Buffetaut, 1989a; Kellner, 1994a; Kellner & Campos, 1996; but see Charig & Milner, 1990). Buffetaut (1989a) also attributed to Spinosauridae (*Spinosaurus* cf. *S. aegyptiacus*) a fragmentary maxilla with almost circular alveoli (no teeth were preserved) found in continental red beds of Albian-Cenomanian age in the Taouz region, southern Morocco. More materials from Morocco referable to Spinosauridae are isolated teeth, preserved in reddish sandstone (Fig. 4) that were collected near

the region of Ksar-es Souk (Henry Galiano, pers. comm. 1994) and come possibly from the Tegana Formation (Albian-Cenomanian?). Those teeth are very similar to the ones reported from Albian strata of Southern Tunisia, which are attributed to *Spinosaurus* sp. (Bouaziz et al., 1988).

A potential synapomorphy of Spinosauridae that can be observed in the Brazilian specimen is the 'crocodilian-like' teeth, with subcircular transverse sections and striated enamel. The anterior and posterior keels of the teeth in the Brazilian spinosaurid are unserrated, which is the same condition as in *Spinosaurus aegyptiacus* and the teeth found in Tunisia and Morocco (Fig. 4), but different from the finely serrated teeth in *Baryonyx* (Charig & Milner, 1986; 1990). Other derived characters shared by spinosaurids are: the particular shape of the rostrum (concave ventral margin of the upper jaw, which corresponds to a convex dorsal margin of the lower jaw); the presence of seven premaxillary teeth; and, the external naris displaced backwards (observed in *Baryonyx* and indicated in the specimens found in Gadoufaoua and in Brazil). The last two features cannot be observed in *Spinosaurus aegyptiacus* since the upper jaw of this species remains unknown.

Recently Martill et al. (1996) described another theropod from the Romualdo Member, *Irritator challengeri*, which they regarded as representing a new clade (Irritatoridae) of maniraptoran dinosaurs. The material includes an almost complete skull and mandible which lacks the rostral portion.

Judging from the published picture, this specimen was still unprepared at the time of their study (Martill et al., 1996: 6). It is also not clear if the matrix from several cranial openings has been completely removed or if those openings are only indicated on the picture of the specimen (compare Martill et al., 1996, Figs 2 & 3).

Despite listing several characters that *I. challengeri* apparently shares with different theropods, the authors have not made clear why they regard it as a maniraptoran. The only cranial character used by Gauthier (1986) to diagnose the Maniraptora is the absence or reduction of the prefrontal. The presence or absence of this bone cannot be verified in *I. challengeri* since Martill et al. (1996, Fig. 3) listed this bone but failed to indicate its presence (and consequently its shape and proportions) in the skull. Holtz (1994: 1107), reviewing the phylogeny of theropods, listed as a cranial synapomorphy of maniraptorans the '*jugal expressed on the rim of the antorbital*

fenestra'. If the cranial sutures indicated by Martill et al. (1996) are correct, the jugal of *I. challengeri* does not participate in the antorbital fenestra. All other synapomorphies of the Maniraptora are based on postcranial bones (Gauthier, 1986; Holtz, 1994).

Curiously, Martill et al. (1996) did not compare the skull of *I. challengeri* with the spinosaurid, *Angaturama limai*, from the same deposit (Kellner, 1994a; Kellner & Campos, 1996). Nor did Martill et al. (1996) compare their specimen with *Baryonyx* described by Charig & Milner (1986; 1990). They did, however, notice similarities between the dentitions of *I. challengeri* and *Spinosaurus* from Egypt (Stromer, 1915), but pointed out that the '*mandible of Spinosaurus would certainly not fit with the dental margin of the maxilla and premaxilla*' of their material (Martill et al., 1996: 8). It is intriguing how this conclusion was reached, since their specimen lacks the rostral part of the skull.

Preliminary comparison of *I. challengeri* with other spinosaurid taxa indicates that they share at least two synapomorphies: transverse section of the teeth sub-circular and external nares displaced backwards. Those features suggest that *I. challengeri* is a spinosaurid and so there seems no justifiation for the Irritatoridae, here considered a junior synonym of the Spinosauridae.

The comparison of *I. challengeri* with *Angaturama limai* is difficult since they are based on different parts of the skull. Both, however, have unserrated teeth. This feature, associated with the fact that they come from the same deposit, raises the possibility that they represent the same taxon. The preserved posterior portion of the skull of *A. limai*, however, is apparently higher and more laterally compressed than the preserved anterior portion of the skull of *I. challengeri*. Although there is a good possibility that the specimens belong to the same taxon, regarding them as synonymous is premature until more complete material is found.

Another dinosaur specimen from the Santana Formation mentioned in the literature is an incomplete sacrum (Frey & Martill, 1995). The material, only partially prepared, was attributed to a possible oviraptorosaurid on the basis of the presence of pleurocoels. Since oviraptorosaurids are a highly specialised group of theropods whose presence has only definitely been recorded from North America and Asia (Barsbold et al., 1993), the assignment of this incomplete material to this group should be viewed with caution, as indeed was pointed out by Frey & Martill (1995).
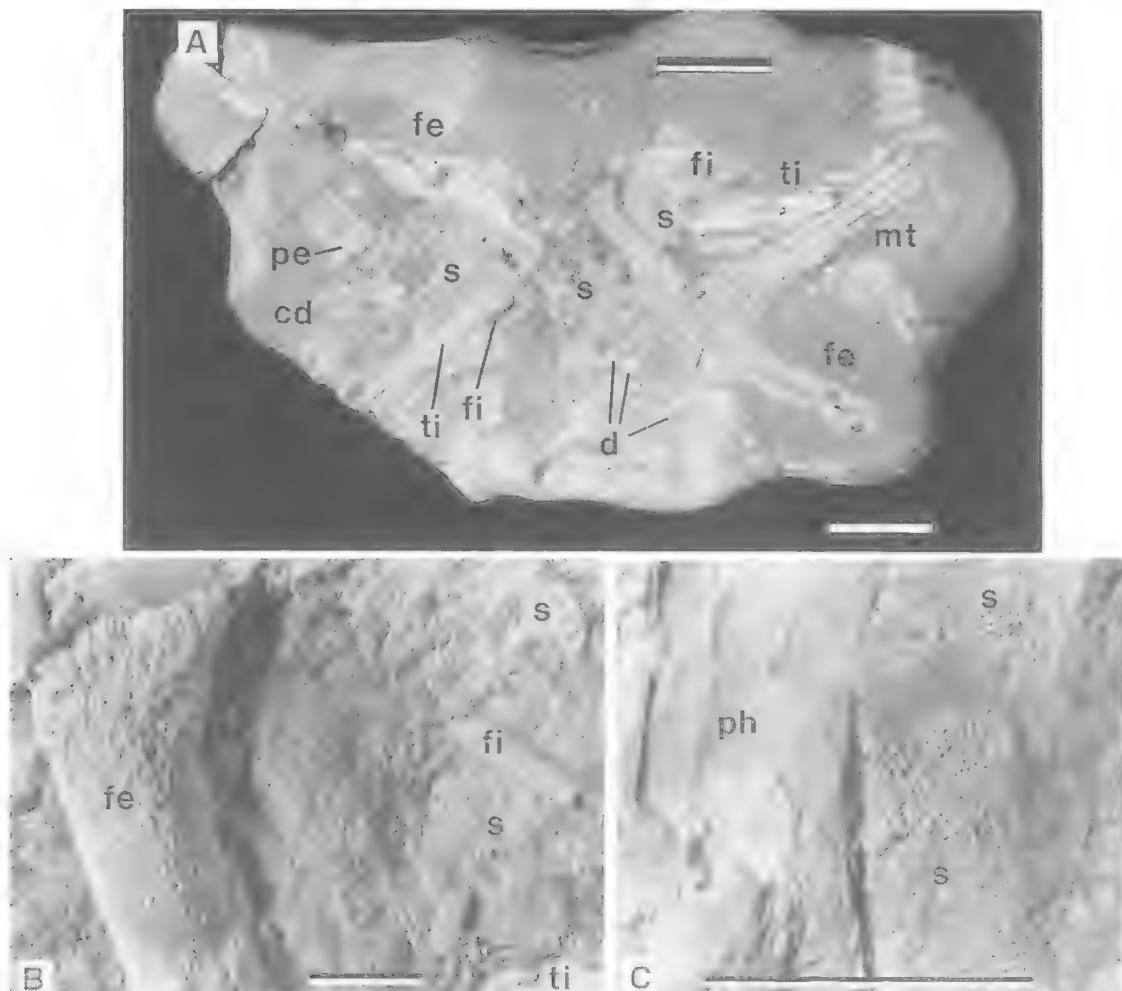
FIG. 5. Small theropod from the Santana Formation, Araripe Basin (MCT 1502-R). A, Complete nodule; scale = 50mm. B, Detail of soft tissue between femur, tibia and fibula; scale = 10mm. C, Detail of soft tissue near one pedal phalanx; scale = 10mm. cd=caudal vertebrae, d=digits of pes, fe=femur, fi=fibula, mt=metatarsals, pe=remains of pelvis, ph=phalanx of pes, s=soft tissue, ti=tibia.

Further dinosaur material from the Santana Formation includes limb bones, one series of nine vertebrae (three sacrals and six caudals), and a complete pelvis with articulated posterior limb elements and several vertebrae (dorsal, sacral and caudal). Recently a calcareous nodule containing both hindlimbs, partial pelvis and several vertebrae of a small theropod (length of femur approximately 175mm) was found (Figs 5, 6). This specimen is particularly striking because of the soft tissue associated with many bones. Since epidermis and muscle fibers are preserved in three dimensions, this might be the best fossilised soft tissue of a dinosaur known so far (Kellner, 1996). Furthermore, longitudinal and transverse sections through a fragment of one femur showed the presence of rod-like structures filling the channels for blood vessels. These structures might be either mineralisations filling those channels or they could represent the replacement of the actual blood vessels. All this material is currently being prepared and will be described elsewhere.

BAURU GROUP

The Bauru Group comprises one of the most extensive continental sedimentary sequences in South America. Outcrops of this unit are found in many Brazilian States (Parana, São Paulo, Minas Gerais, Goiás and Mato Grosso do Sul) and ex-
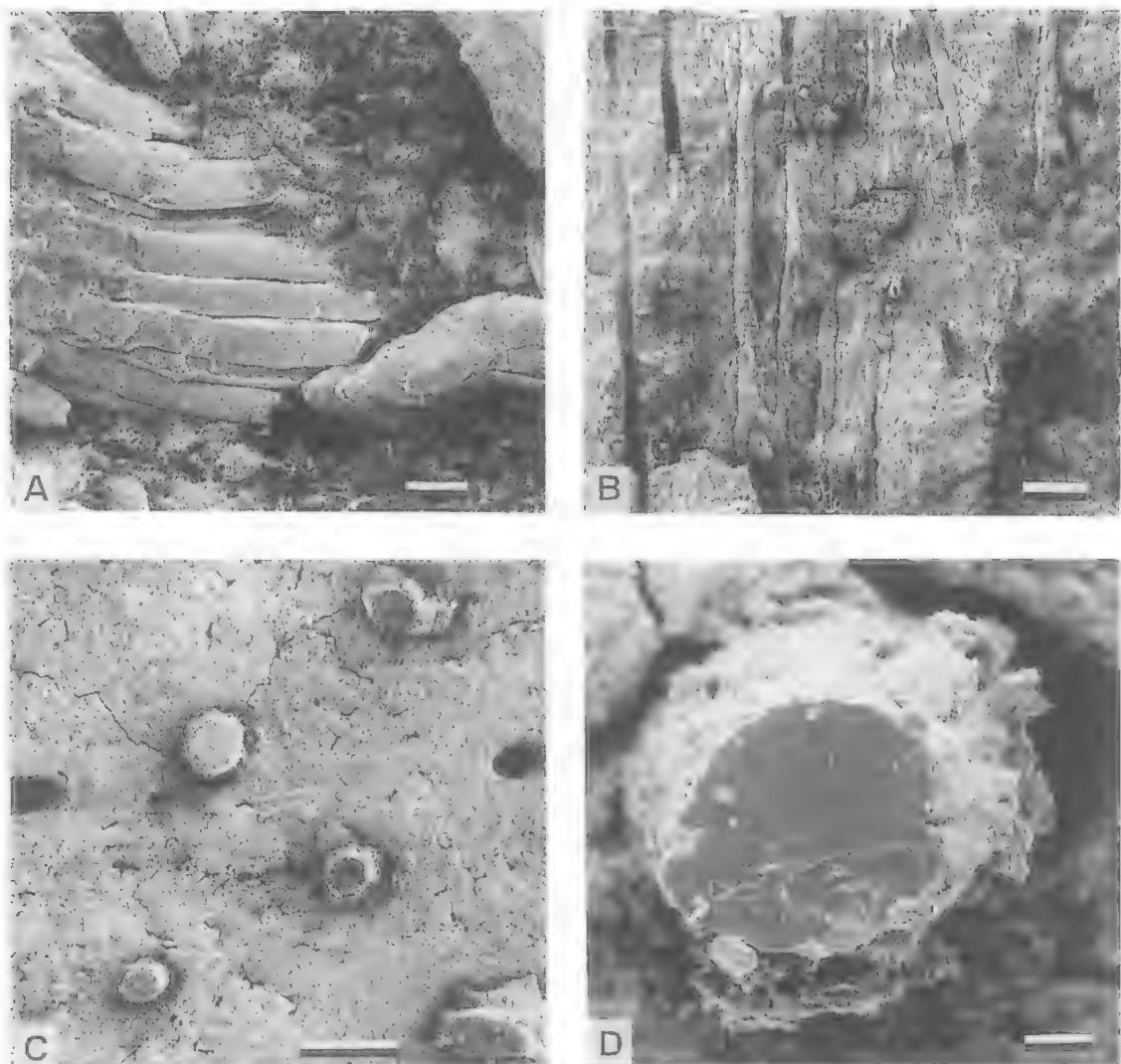
FIG. 6. Scanning electron micrographs of soft tissue preserved in the small theropod (MCT 1502-R) from the Santana Formation. A, Muscle fibres; scale = 50μm. B, Longitudinal section through a fragment of the femur showing rod-like structures preserved in the channels for the capillary blood vessels of the bone; scale = 100μm; C, Transverse section through the same bone showing the rod-like structures; scale = 50μm; D, Detail of one of the rod-like structures; scale = 5μm.

tend into Paraguay. The most widely accepted stratigraphic subdivision for those strata was proposed by Soares et al. (1980), who recognised four formations: Caiuá, Santo Anastácio, Adamantina and Marília. To these, Souza (1984) included the Uberaba Formation, which is interdigitated with the Adamantina Formation. Essentially all these stratigraphical units are composed by sandstones and siltstones, deposited in a semi-arid environment by a meandering river system, and all are of Late Cretaceous age. Among the

fossil vertebrates reported are crocodilians, dinosaurs, turtles and fishes, most of which came from the upper layers (Adamantina/Uberaba, Marília formations).

Although dinosaur remains from the Bauru strata were reported at the beginning of this century (Ihering, 1911) and more specimens were collected since, very little is known about the dinosaurian fauna of this unit. A few incomplete specimens were assigned to European and North American taxa, which may be erroneous (Cam-

pos & Kellner, 1991). The only new species described is the sauropod *Antarctosaurus brasiliensis*, based on very fragmentary material (incomplete humerus, femur and dorsal vertebra) collected in São Paulo (Arid & Vizotto, 1971). *Antarctosaurus* was first reported in Cretaceous sediments of Argentina and regarded as a titanosaurid (Huene, 1929; McIntosh, 1990a). More recently, based on the jaw morphology, Jacobs et al. (1993) questioned the titanosaurid affinities of the Argentinean genus, and regarded *Antarctosaurus* as a diplodocid. Due to the fragmentary nature of the material referred to *Antarctosaurus brasiliensis*, there is no particular feature that would support any particular generic affinity of the Brazilian species.

Recently Bertin et al. (1993) reported the presence of an incomplete upper jaw and one tooth referred to Abelisauridae, and an incomplete dentary of a coelurosaur. These potentially important specimens, however, were not described or figured and no diagnostic feature was presented that could support their assignment. The presence of an abelisaur in the Bauru group would be of considerable interest for the palaeobiogeography, since Abelisauridae are considered to have a Gondwanan distribution (Bonaparte & Novas, 1985).

Most of the dinosaur collecting in the Bauru strata was done by Llewellyn Ivor Price near Uberaba and Peirópolis in Minas Gerais where an ongoing excavation is currently being carried out (Campos, 1993). The work resulted in an extensive collection of postcranial dinosaur material which has yet to be described.

The most common dinosaur remains found near Peiropolis are sauropod and theropod teeth (Kellner, 1994b). The sauropod teeth are typically pencil-like: long, slender and subcircular in cross-section. The labial side is slightly more inflated than the lingual side. The enamel has a brownish colour and a rough surface (Fig. 7). Small, unserrated carinae can be observed in well preserved specimens, although in most they are absent (possibly worn down). In some teeth the enamel is almost completely lost, exposing the dentine that has a light color and a smooth surface. Wear surfaces are present and vary possibly according to the tooth's position in the jaw and its age. Based on wear surfaces, the following tooth classes have been recognised:

1) teeth with wear surfaces present on the lingual side and either absent or very limited on the labial side (Figs 7D-F);

2) teeth with wear surfaces present on the lingual and labial side (Figs 7A-C);

3) teeth with wear surfaces present on different parts of the tooth.

Most teeth are of class two, with the lingual wear surface always more developed than the labial one. Some teeth exhibit a combination of wear surfaces (class three), most on the labial and lateral side of the tooth.

The curvature of the teeth changes from almost straight to slightly curved. This variation may also be related to the tooth's position in the jaw. The roots of the teeth can be distinguished from the enamel by their smooth texture and white color. All roots are very small, suggesting that most of the preserved teeth were replaced during the animal's life.

The pencil-like shaped teeth are typical of two sauropod groups: Titanosauridae and Diplodocidae (McIntosh, 1990a, 1990b). Since all sauropod postcranial bones so far reported from the Bauru strata (no skull material is known from this unit) are typical of titanosaurids (e.g., Powell, 1987; Kellner & Borgomanero, 1989), I assume that the teeth described here belong to this group.

There is, however, some morphological variation regarding tooth morphology in titanosaurids. The teeth from the Bauru strata are very similar to those reported by Kues et al. (1980) in *Alamosaurus*, but both differ from the ones described in *Malawisaurus* which, according to Jacobs et al. (1993), are more flattened labial-lingually.

As far as tooth morphology can suggest, there is no evidence of more than one titanosaurid sauropod taxa in the Bauru Group. There are two almost complete pelves, however, of different morphology that indicate the presence of at least two sauropod taxa. The same applies to postcranial elements, all collected in Minas Gerais (Campos, 1993).

Theropod teeth are found in greater abundance than sauropod ones. There are several teeth with distinct morphologies among the material collected near Peirópolis, which range from large blade-like, symmetrical teeth to small, inflated and asymmetrical teeth (Figs 8, 9). The carinae are always serrated, although their configuration might change according to the position of the tooth in the jaw and its age. In one tooth, the middle portion of the posterior carina follows a sigmoid curve (Figs 9A-B), which might have been pathological. Another tooth has a split anterior carina (Figs 9C-D). Split carinae were recently observed in tyrannosaurids (Erickson, 1995) and in one theropod tooth from the Fruit-

land Formation of the San Juan Basin, housed in the New Mexico Museum of Natural History, Albuquerque (NMMNH P-25068; pers. observ.).

The potential for identifying theropods at different taxonomic levels using the morphology of the teeth was already demonstrated elsewhere (e.g., Currie et al., 1990), and is certainly worth investigating in the Bauru material. In a preliminary study of the theropod teeth found in the region of Peirópolis, Kellner (1995) identified six categories:

1) teeth very compressed laterally (blade-like); anterior margin curved distally and posterior margin straight; anterior and posterior carinae with 3 (base) and 2.5 (tip) denticles per mm; denticles straight, longer than wide, and chisel-like (Figs 8C-D);

2) teeth similar to those of category 1 but less compressed laterally; anterior and posterior carinae with 3 (base) and 2 (tip) denticles per mm; denticles straight, longer than wide, and slightly hooked on the basal part of the crown (Figs 9A-B);

3) teeth curved labial-lingually with oval cross-section at the base; anterior carina with 2-3 denticles per mm and posterior with 2.5 (base) to 1.5 (tip) denticles per mm; denticles on posterior carina larger than on anterior; denticles straight, tend to be wider towards the tip of the crown, and are proportionately longer than in categories 1 and 2, but smaller than in categories 5 and 6 (not figured);

4) very similar to those of category 3, but with split anterior carina (only one specimen, Figs 9C-D);

5) recurved and laterally compressed teeth smaller than in category 1; anterior carina with 3 denticles per mm and posterior with 3-4 denticles per mm; denticles on posterior carina larger than those on anterior; denticles pointed, inclined and hooked; blood grooves extend from between the bases of adjacent denticles onto the surface of the crown, particularly on the posterior basal portion (not figured);

6) slightly recurved teeth with labial portion inflated and lingual portion flattened; basal cross-section oval to sub-circular; carinae with 2 denticles per mm; denticles on posterior carina larger than on anterior; denticles inclined, hooked, and wider than those of category 5 (Figs 8A-B).

Based on their morphologies Kellner (1995) suggested that the teeth described in categories 1, 3, 5 and probably 6, represent different theropod taxa, unless the theropods in this unit present accentuated heterodonty. The finding of complete theropod jaws from those layers is needed to confirm this hypothesis.

Other dinosaur remains reported from the Bauru strata include eggs. The first was described by Price (1951) and regarded as belonging to a sauropod dinosaur. The material is not very well preserved and only the impression of the inner portion of the egg shell can be identified in some parts of the specimen.

Further dinosaur eggs were reported by Campos & Bertini (1985) and referred to Ceratopsia (Ornithischia) because of their general similar shape with those found in the Cretaceous rocks of the Gobi Desert, Mongolia. Recently, Norell et al. (1994) have found theropod remains associated with eggs very similar to ones previously attributed to Ceratopsia in a new locality of the Gobi Desert. This raises the possibility that the eggs reported by Campos & Bertini (1985) also belong to theropods.

Until detailed descriptions and comparisons of the fossil eggs found in the Bauru strata are available, including an analysis of the microstructure of the egg shell — which may or may not turn out to be of systematic value — those specimens should only be considered Dinosauria incertae sedis.

DISCUSSION

Mesozoic sedimentary strata, especially of Cretaceous age, are well represented in Brazil and provide a high potential for the preservation of dinosaur remains. Despite this fact very few specimens have been recovered, reflecting the lack of collected fossils in this country. This limited information on the Brazilian dinosaur faunas seriously restricts our knowledge of dinosaur diversity and distribution in this part of South America. Nevertheless, the few studies done so far allow some preliminary considerations.

The dinosaurian affinities of the Triassic *Spondylosoma* are not clear (Sues, 1990). *Staurikosaurus*, the other Brazilian dinosaur of that period, is now regarded as a primitive theropod

FIG. 7. A-C, Titanosaurid tooth from the upper portion of the Late Cretaceous Bauru group. A, Stereopair of the labial view; note wear surface. B, Lingual view; note wear surface. C, Lateral view. D-F, Smaller titanosaurid tooth from the upper portion of the Late Cretaceous Bauru group. D, Stereopair of the labial view; almost no wear surface. E, Lingual view; note wear surface. F, Lateral view. Scale = 10 mm.
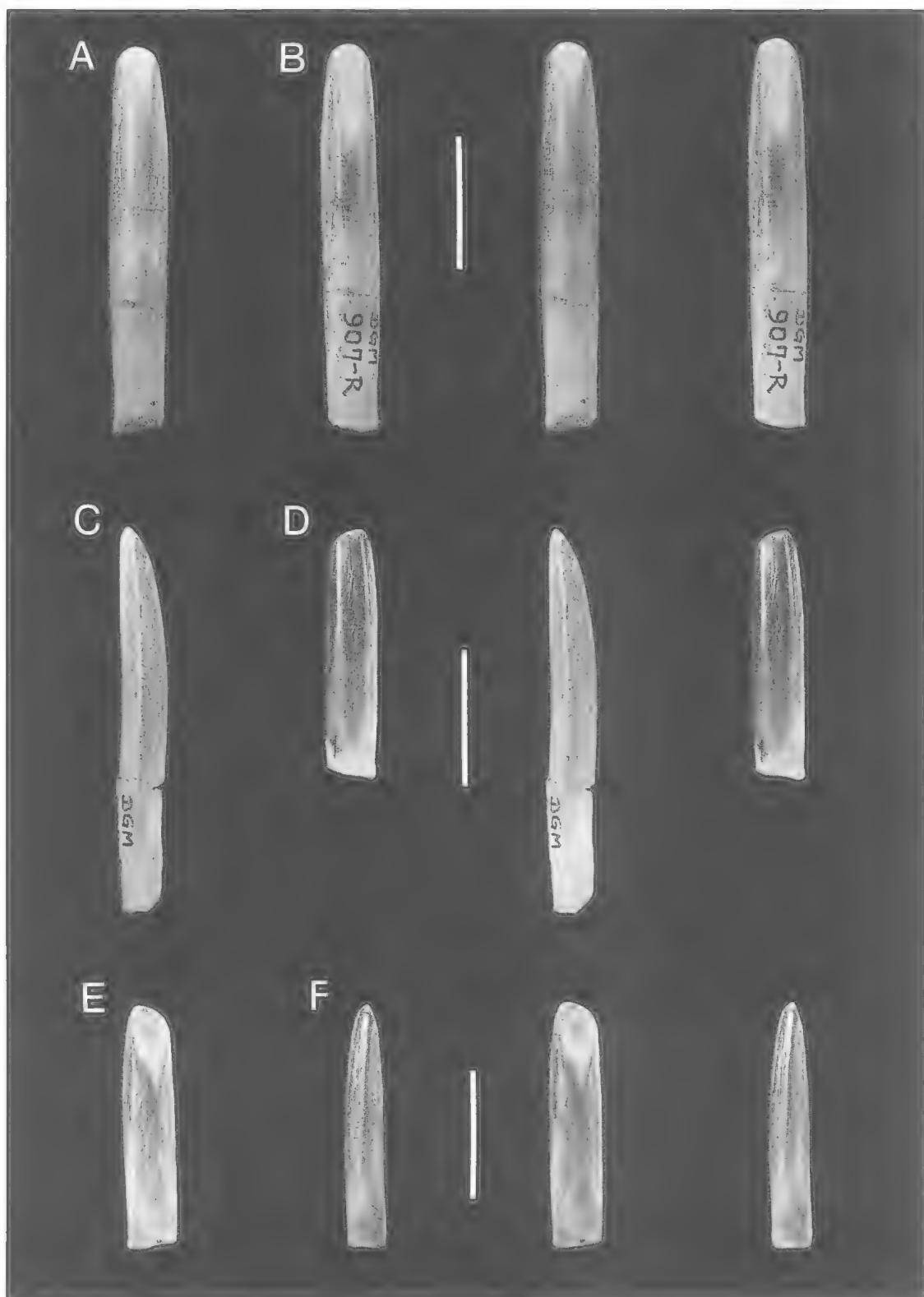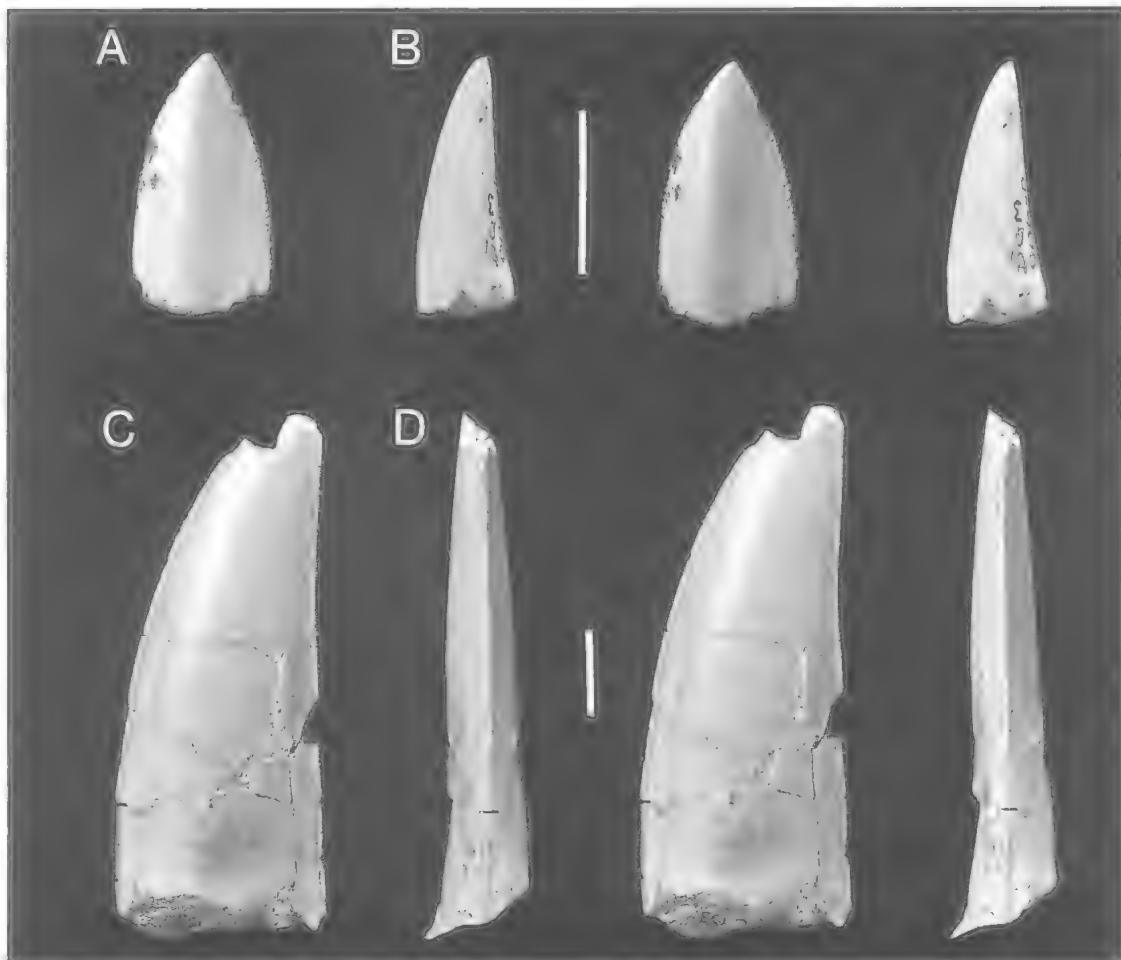
FIG. 8. A-B, Theropod tooth from the upper portion of the Late Cretaceous Bauru group. A, Stereopair of the labial view. B, Posterior view; scale = 10mm. C-D, Large theropod tooth from the upper portion of the Late Cretaceous Bauru group. C, Stereopair of the lingual view. D, Posterior view; scale = 10mm.

and has been referred to the Herrerasauridae (Novas, 1992; 1994). So far no palaeo-biogeographical pattern is apparent from these occurrences other than a possible faunistic link between the Southern part of Brazil and Argentina during the Triassic.

The Late Cretaceous *Antarctosaurus brasiliensis* is regarded as a titanosaurid sauropod (Arid & Vizotto, 1971), although the fragmentary nature of the type specimen makes it difficult to establish its phylogenetic position within Titanosauridae. Titanosaurid sauropods in Late Cretaceous strata of Brazil are not unexpected, since they occur widely in other parts of South America (Huene, 1929; Bonaparte, 1986; Powell, 1987; McIntosh, 1990a). Although titanosaurids have been regarded as 'typical' Gondwanan sauropods (e.g.,

Bonaparte, 1984), they are also reported from Europe and North America (e.g., McIntosh 1990a). This has been used to suggest that faunal interchanges between northern continents and Gondwana happened during the Late Cretaceous (e.g., Bonaparte, 1984; Buffetaut, 1989b). A better understanding of the ingroup relationships among titanosaurid taxa is needed to test this hypothesis.

The occurrence of spinosaurids from Albian strata of Brazil (Kellner, 1994a; Martill et al., 1996; Kellner & Campos, 1996) is very interesting from the palaeobiogeographical point of view. Due to the fragmentary nature of most specimens attributed to Spinosauridae, their ingroup relationships are very difficult to establish. Nonetheless, the Brazilian and some African spinosaurids (*Spinosaurus aegyptiacus* and iso-

FIG. 9. A-B, Theropod tooth from the upper portion of the Late Cretaceous Bauru group. A, Stereopair of the labial view. B, Posterior view; note the irregular carina; scale = 10mm. C-D, Theropod tooth from the upper portion of the Late Cretaceous Bauru group. C, Stereopair of the lingual view. D, Anterior view; note the split carinae; scale = 10mm.

lated teeth found in Tunisia and Morocco) have developed teeth with unserrated carinae. This synapomorphic character suggests a close relationship between the Brazilian and those African spinosaurids.

Baryonyx, known only from Europe, lacks this derived dental feature. Despite the discussion whether this European taxon should be classified in its own higher taxonomic unit (i.e., Baryonychidae), there is a consensus view that *Baryonyx* and spinosaurids are closely related (Charig & Milner, 1986, 1990; Buffetaut, 1989a; Paul, 1988). The morphological features of the anterior portion of the rostrum and the particular structure of the teeth shared by *Baryonyx* and spinosaurids supports this hypothesis. I suggest that *Baryonyx* is a primitive member of the spinosaurid clade, lacking the dental character which seems to unite at least some of the Gondwanan forms.

The above phylogenetic hypothesis supports two biogeographic points:

a) that Brazilian and African spinosaurid distribution may be the result of an Early Cretaceous vicariant event (i.e., opening of the South Atlantic Ocean);

b) that the spinosaurid clade is not an exclusively Gondwanan group as previously proposed (e.g., Bonaparte, 1986; Russell, 1993), but was originally more widespread. In the middle part of the Cretaceous an apparently monophyletic group of spinosaurids occupied western Gondwana, where they diversified and eventually gave rise to the African and Brazilian taxa.

In addition, a literal interpretation of stratigraphic data suggests that dinosaur dispersal events in the Cretaceous were not only directed from Gondwana to Europe as proposed by Russell (1993), but may also have occurred in the reverse direction. All spinosaurids from Brazil and Africa are Albian or younger, while *Baryonyx*, here regarded as a primitive member of this clade, is Barremian. The limited information about the taxa mentioned, particularly regarding the African and Brazilian forms, makes the previous suggestion only a very preliminary hypothesis. Note that it is still possible that spinosaurids arose in Gondwana at an even earlier time, and that *Baryonyx* may represent a plesiomorphic lineage which migrated into Europe prior to the break-up of western Gondwana. More complete dinosaur material from Brazil and from Africa are needed to test this hypothesis.

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GONDWANAN DINOSAURS OF INDIA: AFFINITIES AND PALAEOBIOGEOGRAPHY

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The record of Indian dinosaurs is now well known and extends from Late Triassic to the terminal Cretaceous. The Indian dinosaurs are based on fragmentary cranial, skeletal and egg material which is a cause of some uncertainty in the analysis of their taxonomic affinities, age and palaeobiogeography. The Indian dinosaurian record starts with the Triassic Maleri Formation, which yields *Alwalkeria maleriensis*, a coelurosaur. The overlying Dharmaram Formation contains phytosaurs, aetosaurs, plateosaurids and a sphenosuchid. The early Jurassic Kota Formation has yielded numerous bones (cranial and postcranial) of *Barapasaurus tagorei*, besides semionotid fishes, coelacanths, pleurosaurs, crocodiles and mammals. The Cretaceous dinosaurian record is from sedimentary sequences associated with the Deccan volcanics and is dominated by skeletal remains of titanosaurid sauropods and theropods, such as *Indosuchus raptorius* and *Indosaurus matleyi*. The Kallamedu Bone Bed (Ariyalur Formation) has yielded bones and a tooth of *Megalosaurus*. The cranial and postcranial skeleton of a stegosaur *Dravidosaurus blanfordi* is known from the Trichinopoly Group. Khosla & Sahni (1995) have classified Indian dinosaur eggs and eggshell fragments into eight new oospecies (in the oofamilies Megaloolithidae and Subtiliolithidae): *Megaloolithus cylindricus, M. jabalpurensis, M. mohabeyi, M. baghensis, M. dholiyaensis, M. walpurensis, M. padiyalensis* and *Subtiliolithus kachchhensis*. Besides these Late Cretaceous eggshells, footprints are known from the Bhuj Formation of Early Cretaceous age (Ghevariya & Srikarni, 1990). Coprolites of dinosaurs and (probable) chelonians are known from the Late Cretaceous of Pisdura, and include four categories of ribbed and non-ribbed forms. The palaeobiogeographic analysis of the Indian dinosaurs implies they are part of a cosmopolitan distribution. However, migrations through an earlier Madagascan connection and through island arcs in the Cretaceous (represented by Dras volcanics) and earlier collision arcs and microplates in Late Permian to Cretaceous (represented by north-ernmost Gondwana fragments of Tibet, Iran, Iraq and Afghanistan) led to an influx of some taxa. These paths of migration are significant in explaining the cosmopolitan character of the Indian biotas and their similarities to Laurasian faunas during the drift of the Indian Plate. ☐ *India, dinosaurs, Mesozoic, tracks, dinosaur nests, eggs.*

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Dinosaur remains in India are found in the Triassic-Cretaceous sequence of peninsular India (Table 1), however Middle Jurassic-Middle Cretaceous gaps are quite significant. In this context, the Pranhita-Godavari valley, where a thick continental vertebrate-rich sequence of Late Permian-Cretaceous age is exposed, has assumed considerable significance as a site for Gondwanan dinosaurs.

While the Pranhita-Godavari Valley (Fig. 1) represents a repository of dinosaurs of Triassic-Jurassic age, the younger terminal Cretaceous dinosaur fauna is most diverse. It occurs along the Narmada Valley of central India, associated with the Lameta Formation and is spread over more than 10,000 sq. km., below the Deccan vol-canosedimentary sequence (Sahni et al., 1994, Fig. 2). In addition, Cretaceous dinosaurs also occur towards the south, associated with the Ariyalur Formation.

TRIASSIC

The oldest record of Indian dinosaurs comes from the Late Triassic Maleri Formation, which is exposed near the village Maleri (near Tandur) in the district Adilabad, Andhra Pradesh. Lithologically, red clays are abundant, along with lime-pellet rocks (calcirudites, calcarenites) and quartzose sandstones (Kutty & Sengupta, 1989).

The biotic elements of Maleri Formation include vertebrates, coprolites, invertebrates and plants. Dominant in the Lower Maleri, is *Alwalkeria maleriensis*, which constitutes the earliest Indian dinosaur (Chatterjee, 1987) and is based on imperfectly known fragmentary material, a partial skull, vertebrae, a femur and

astragali. It is referred to the basal theropods, belonging to a group of slightly built predaceous dinosaurs.

The overlying Dharmaram Formation is composed of a basal thick sandstone followed by more sandstones and clay beds. The sandstones resemble the Maleri sandstones, but are more coarse-grained and gritty (Kutty et al., 1987). The lower part of the Dharmaram Formation — besides the occurrence of the fish *Xenacanthus* and *Ceratodus* — is characterised by the presence of a phytosaur (*Nicrosaurus*), dominant aetosaurs and a small prosauropod (Kutty & Sengupta, 1989). The Upper Dharmaram Formation, on the other hand, is far richer and contains a large plateosaurid, an ornithischian and a sphenosuchid (Kutty, 1969; Kutty et al., 1987). Although as the fauna remains undescribed as yet, a Late Norian-Rhaetian age is preferred by most workers for this fauna.

FIG. 1. Map of Pranhita-Godavari Valley with fossil- bearing localities (after Jain et al., 1975).

JURASSIC

The continental Kota Formation, of Early Jurassic age, lies conformably above the Dharmaram Formation and in turn is overlain by Gangapur Formation of Early Jurassic age (Kutty et al., 1987). The stratotype of this formation is named after Kota village, on the eastern bank of the Pranhita River. This formation has provided a vast amount of information about its exceedingly rich continental fauna, comprising fishes, reptiles, mammals, freshwater ostracodes, conchostrachans and land insects (Kutty et al., 1987).

The lithic units of the Kota Formation are characterised by sandstones (ferruginous arkoses), with cross-bedding, and limestones with desiccation polygons and worm-bored layers (Robinson, 1970; Jain, 1980; Yadagiri & Rao, 1987).

Field work conducted by palaeontologists of the Indian Statistical Institute in the Kota Formation during 1960-61 led to the recovery of about 300 sauropod bones from a bone bed occurring between a sandstone-clay lens. This vertebrate material was assiduously studied by Dr S.L. Jain and his colleagues, who established a new

sauropod, *Barapasaurus tagorei*, one of the best known Early Jurassic dinosaurs in the world (Jain, 1975, 1979). A complete mounted skeleton of this dinosaur is displayed at the Geology Museum, Indian Statistical Institute, Calcutta.

Barapasaurus tagorei was a large sauropod with slender limbs, spoon-shaped teeth with coarse denticles, opisthocoelous cervical and anterior dorsal centra, with the other centra platycoelous. Neural spines are not bifurcate and the centra are not cavernous, but have oval depressions in the lateral surface. The ilium possesses a well-developed anterior process, the ischium is relatively slender and rod-like distally and the pubis has a well-developed terminal expansion.

Jain et al. (1979) commented on the level of development of *Barapasaurus*, stating that it is intermediate between the prosauropod stage and that of known sauropods (e.g., the limbs, though graviportal, are slender). The anterior caudals have not developed procoelous centra. The sacrum is narrow, with the pelvic depression small in comparison to length of the pubis. McIntosh (1990) tentatively assigned *Barapasaurus*

TABLE 1. Gondwana stratigraphy of Pranhita-Godavari Valley (modified after Kutty et al., 1987).

LITHO-UNIT, AGE	CONTAINED FOSSILS	LITHOLOGY
Deccan volcano-sedimentary sequences Late Cretaceous	mammals, dinosaurs (titanosaurids), frogs, fishes, charophytes, ostracodes	sandstones, shales, marls, associated with Deccan basalts
Chikiala		ferruginous sandstones conglomerates
Gangapur Early Cretaceous	*Gleichenia, Pagiophyllum Ptilophyllum*	gritty sandstones, pink mudstones, ferruginous sandstones
Kota Early Jurassic	holostean fishes, sauropods, pterosaurs, early mammals	sandstones, siltstones, clays and a limestone band
Dharmaram late Late Triassic	prosauropods	sandstones, red clays
Maleri early Late Triassic	metoposaurs, aetosaurs, phytosaurs, rhynchosaurs	red clays, sandstones, lime-pellet rocks
Bhimaram Sandstone late Middle Triassic	labyrinthodont, dicynodont	sandstones (ferruginous in lower part), red clays
Yerrapalli early Middle Triassic	stahleckeriid, kannemeyeriid dicynodonts	red violet clays, sandstones, pellet rocks
Kamthi Late Permian-Early Triassic	dicynodonts from basal beds	ferruginous, non-felspathic sandstones, purple siltstones

to the Vulcanodontidae (Cooper, 1984) on the basis of the narrow sacrum, deeply furrowed caudals, long forelimbs, apron-like pubis, elongate metatarsals and teeth with coarse denticles.

The associated fauna of the Kota dinosaurs includes semionotid fishes (*Tetragonolepis, Lepidotes, Parapedium*), a coelacanth (*Indocoelacanthus robustus*), a pholidophorid fish (*Pholidophorus*), a pterosaur (*Campylognathoides*) and teleosaurid crocodiles (Kutty et al., 1987; Jain & Roy Chowdhury, 1987). Early Jurassic mammals from the Kota Formation are represented by *Kotatherium, Trishulotherium* and *Indotherium* (Datta, 1981; Yadagiri, 1984; 1985).

CRETACEOUS

SKELETAL MATERIAL. The Indian Cretaceous dinosaur record is associated with the non-marine post-Gondwana sequence of central and western India. This sequence is represented by Lameta Formation, which has received considerable attention for the last 70 years for its fairly extensive dinosaurian fauna. Stratigraphically, the dinosaur-rich vertebrate beds underlie the Deccan Traps, with an aerial extent of more than 10,000 sq. kms. As such, this vertebrate sequence is crucial to the dating and duration of the traps, more so as the Late Cretaceous extinction mechanisms might be related to the eruptions (Courtillot et al., 1986; Buffetaut, 1987).

The stratotype of the Lameta Formation is situated at Lametaghat, near Jabalpur on the banks of Narmada river. The classic dinosaur areas here are Bara Simla Hill and Chui Hill, in

addition to Pisdura in Maharashtra. The first detailed account of the geology of the Jabapur area was given by Matley (1921), who prepared an excellent map of the area on a scale measuring 8 inches to a mile, along with a description of various lithic units.

Huene & Matley (1933) described postcranial elements of the titanosaurid sauropods, viz. *Titanosaurus indicus* and *Antarctosaurus septentrionalis* from Bara Simla Hill, and a third sauropod *Laplatasaurus madgascariensis* from Pisdura. From the same locality carnosaurs were also described: *Indosuchus raptorius* and *Indosaurus matleyi*, along with coelurosaurs, such as *Compsosuchus solus, Laevisuchus indicus, Jubbulpuria tenuis, Coeluroides largus, Dryptosauroides grandis, Ornithomimoides mobilis* and *O.(?) barasimlensis*.

Of the aforementioned forms *Antarctosaurus septentrionalis* has been given a new generic name *Jainosaurus* by Hunt et al. (1994) because of its distinctness from the Argentinian form, the genotypic *A. wichmannianus*. The main differences are in braincase of the Indian and Argentinian forms. Earlier Indian braincase studies on '*Antarctosaurus' septentrionalis* were by Berman & Jain (1982) however the specimens were recovered from Dongargaon near Pisdura. Further, *Indosaurus* and *Indosuchus* regarded by Chatterjee (1978) as a megalosaur and tyrannosaurid (respectively), are now considered as abelisaurids (see Chatterjee, this volume).

As compared to the saurischian fauna, the information and taxonomic assignment of ornithischians have remained largely in doubt.
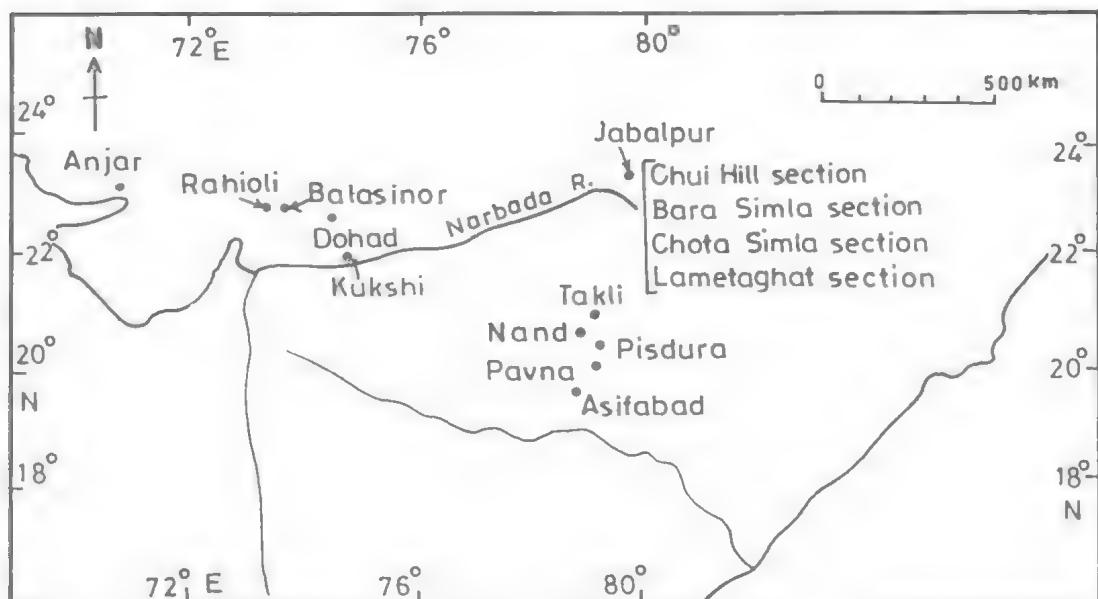
FIG. 2. Localities of dinosaur eggshells and nests in India.

Lametasaurus indicus described from Bara Simla Hill by Matley (1933) was at that time considered to be a stegosaurian. Later Chakarvarti (1934) and Walker (1964) opined that this genus could not be an ankylosaurian. Recently, works by Berman & Jain (1982), Buffetaut (1987) and Molnar & Frey (1987) opined that *Lametasaurus* could well have been a titanosaurid. Molnar (pers. comm., 1996) believes it to be a chimaera (based on bones and skeletons of saurischians and crocodilians). However a new ankylosaurian specimen is reported by Chattergee & Rudra (this volume).

From South India, the dinosaur studies were first conducted by Blanford (1862), who reported bones and a tooth of *Megalosaurus* from the same horizon in the Kallamedu Bone Bed (Ariyalur Formation, Late Cretaceous). Matley (1929) reported fragmentary bones of *Titanosaurus* along with teeth of a megalosaur and bones of a stegosaurian. Much later, Yadagiri & Ayyasami (1979) described cranial and postcranial skeleton of stegosaur *Dravidosaurus blanfordi* from the Trichinopoly Group (Turonian-Santonian). In this work, a brief mention is also made of the presence of bones of a sauropod, theropod and stegosaur from the Kallamedu Bone Bed.

EGGSHELLS. The Late Cretaceous eggshell material and nesting sites have been most abundant and have assumed considerable significance over the last decade, providing evidence of a large dinosaur hatchery (Figs 2, 3). The eggshells and nesting sites underlie the Deccan Trap flows and are uniformly found in a hard sandy carbonate with strong development of a calcretised palaeosol towards the top (Tandon et al., 1990; Jolly et al., 1990; Sahni et al., 1994, Fig. 3). In addition, Late Cretaceous eggshells are also known from the sandy limestones of the Kallankurichi Formation of the Ariyalur sequence (Kohring et al., 1996).

Up to now, considerable work has been done to categorise main eggshell morphotypes (discussed later) based on megascopic and microscopic characters (Mohabey, 1982; 1984; Srivastava et al., 1986; Vianey-Liaud et al., 1987; Jain 1989; Sahni, 1989; Mohabey & Mathur, 1989; Jolly et al., 1990; Sahni, 1993; Sahni et al., 1994 and many others). This research and the present work, have established five eggshell morphotypes, three of which have been assigned to titanosaurid sauropods (parataxonomic oofamily Megaloolithidae, Zhao, 1979) and the fourth to the ornithoid type. In a recent work, Khosla & Sahni (1995) established eight oospecies including seven of the oogenus *Megaloolithus* referable to sauropods and one, *Subtiliolithus*, an ornithoid. These oospecies are:

Megaloolithus cylindricus Khosla & Sahni (1995)(Pl. 1, Fig. A): spherical eggs 12-20cm in diameter; eggshell thickess varying from 1.7-
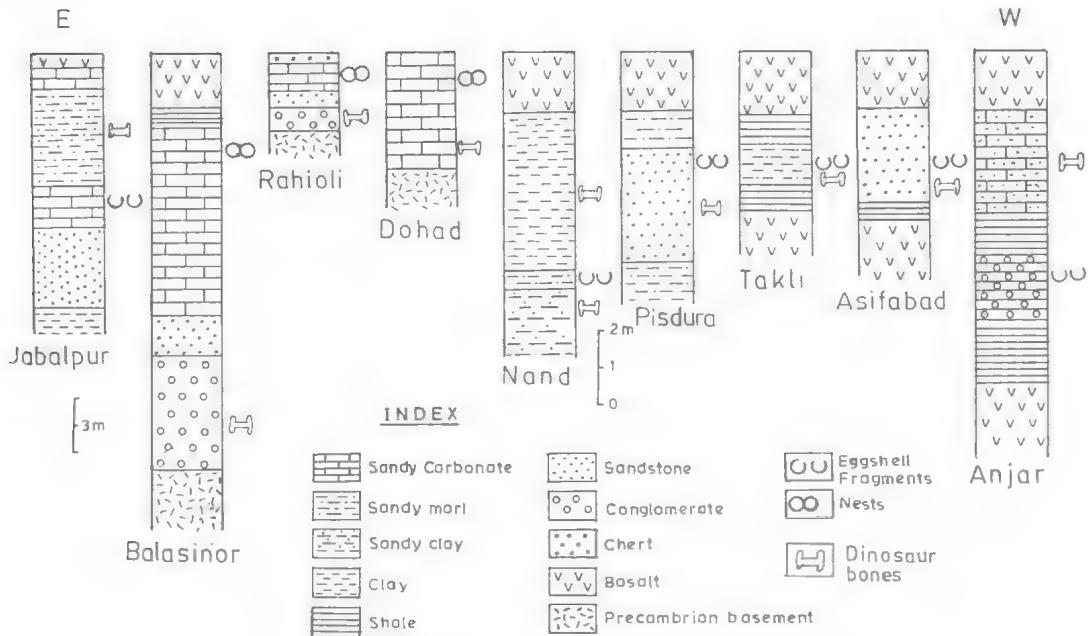
FIG. 3. Stratigraphic sections with associated eggshells and nests.

3.5mm; spheroliths cylindrical; pores subcircular; pore canals long and narrow; tightly packed subcircular basal caps, 0.2-0.5mm in diameter.

Megaloolithus jabalpurensis Khosla & Sahni (1995)(Pl. 1, Figs B, C): spherical eggs 14-16cm in diameter; eggshell thickness 1-2.3mm; nodose external surface; spheroliths with varying width and shapes; elongate to circular pores; tightly packed basal caps (more so than in *M. cylindricus*) 0.1-0.5mm in diameter.

Megaloolithus mohabeyi Khosla & Sahni (1995): spherical eggs 16-19cm in diameter; eggshell thickness 1.8-1.9mm; nodose external surface; spheroliths long and fused to adjacent ones; growth lines convex to undulating; pores elliptical; broad and semicircular basal caps, 0.14-0.21mm in diameter.

Megaloolithus baghensis Khosla & Sahni (1995)(Pl. 1, Fig. D): spherical eggs 14-20cm in diameter; eggshell thickness 1.0-1.7mm; nodes discrete to fused; spheroliths fan-shaped, distinct or partially fused and look more compressed when ending in multiple nodes; pores subcircular to elliptical; basal caps swollen-ended, 0.2-0.3mm in diameter.

Megaloolithus dholiyaensis Khosla & Sahni (1995): eggshell thickness 1.47-1.75mm; nodose outer surface; spheroliths cylindrical and fan-shaped; pore canals straight; basal caps subcir-

cular to conical, isolated to fused, 0.15-0.30mm in diameter. So far found only as fragments.

Megaloolithus walpurensis Khosla & Sahni (1995): eggshell 3.5-3.6mm thick; spheroliths irregularly fan-shaped and showing fusion towards the outer surface; pore canals short, thin, slender, with slit-like openings; basal caps conical to subcircular, 0.25-0.30mm in diameter. So far found only as fragments.

Megaloolithus padiyalensis Khosla & Sahni (1995): eggshells 1.12-1.68mm thick; nodose external surface; small irregular, slender spheroliths; small and large pore canals; basal caps circular to semicircular, 0.07-0.21mm in diameter. So far found only as fragments.

Subtiliolithus kachchhensis Khosla & Sahni (1995)(Pl. 1, Fig. E): eggshells extremely thin, 0.35-0.45mm; external surface exhibits irregularly spaced microtubercles; double layered; spongy layer poorly defined; mammillary layer 1/2-1/3 of the total eggshell thickness; mammillae tightly packed, 0.03-0.05mm in diameter. So far found only as fragments.

The eggshells referred to a new morphotype (Elongatoolithidae) were recovered from near Rahioli (district Kheda, Gujarat) and work on them is in progress. This morphotype is currently being described in detail with Dr D.M. Mohabey, GSI, who has also recovered the same type of
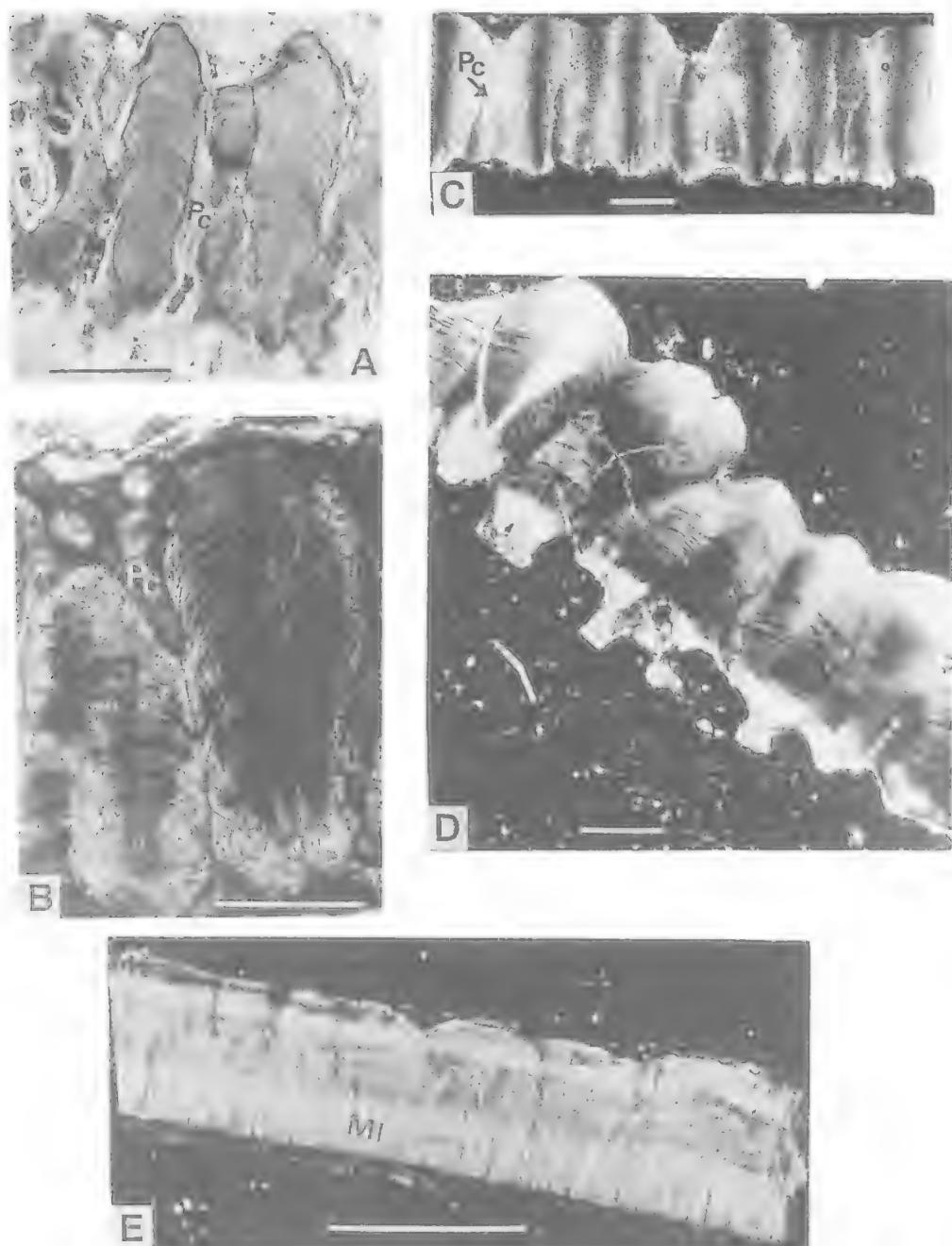
PLATE 1. A, Radial view of *Megaloolithus cylindricus* (VPL/AK 220), Pat Baba Mandir, Jabalpur (Madhya Pradesh). Note cylindrically shaped spheroliths. B, Radial view of *Megaloolithus jabapurensis* (VPL/AK 275), Bara Simla Hill, Jabalpur (Madhya Pradesh), showing small and large fan-shaped spheroliths. C, Radial view of *Megaloolithus jabalpurensis* (VPL/AK 276), Bara Simla Hill, Jabalpur (Madhya Pradesh). Note sweeping extinction pattern of spheroliths. D, Radial view of *Megaloolithus baghensis* (VPL/AK 556), Pisdura, Chandrapur district, Maharashtra. Note small and large fused spheroliths with moderately arched growth lines. E, Radial view of *Subtiliolithus kachchhensis* (VPL/AK 580), Anjar, District Kachchh, Gujarat. Note two-layered eggshell. Mammillary layer is well defined while spongy layer is faintly developed. ML=mammillary layer, Pc=pore canal; scale = 500μm. (VPL/AK=Vertebrate Palaeontology Lab./Ashu Khosla).

eggs. These eggshells are ellipsoid in shape, with a thickness of 1.2-1.6mm, and ornamentation varying from sagenotuberculate (at poles) to lineartuberculate in the equatorial region. The microstructure shows a double layer with radiating structures in the mammillary zone —the latter being about half of the total thickness. Gently curving growth striations are observed in the outer spongy layer. The spheroliths are slender and fused towards the upper part.

TRACKS. As well as the skeletal and eggshell material, dinosaur pedal tracks are also known from the Early Cretaceous Bhuj Formation exposed in the Pakhera and Fatehgarh areas of Kachchh (Ghevariya & Srikarni, 1990). From the Pakhera area, tracks belonging to a juvenile and an adult individual were reported. These types were interpreted as ornithopod, as claws were absent. From the Fatehgarh area, diversely shaped (rectangular, oval and diamond shaped) tracks were described from hard sandstone; the associated grey shale bears an Upper Gondwanan plant, *Ptilophyllum*.

PALAEOENVIRONMENTS

The Triassic Maleri Formation, has long been thought to have been deposited in a river valley system, the sandstones representing the channel deposits and clays suggesting an interchannel floodplain (Jain, 1990). The cross-bedded and lenticular sandstones represent cut-off meanders of the mainstream, with clays deposited on water-logged floodplains (Sengupta, 1970). Jain (1990) described the general environment of the Maleris as indicative of well-aerated country, inhabited by aquatic vertebrates, in a forest habitat. The waterholes and their environs were dominated by amphibians and arboreal vertebrates. The eosuchian *Malerisaurus* probably lived on floodplains or marshy land close to lakes.

The environment for the overlying Dharmaram Formation, from its base to the top of the lower Kota Formation is similar to that of an upwardly-fining sequence deposited under a laterally shifting meandering stream (Rudra, 1982).

As mentioned earlier, the overlying Kota Formation is a typical continental deposit. There were two kinds of depositional environment: sandstones and clays representing fluviatile conditions (river deltas), and thin limestones suggesting deposition in inland lakes (Robinson, 1970). Further, two different climatic conditions also prevailed; one with moderately high relief and rainfall and the other low relief and rainfall. Tasch

et al. (1975), on the basis of conchostracans, and Govindan (1975), on the presence of ostracodes, supported a fresh water environment for the deposition of the limestone within small basinal ponds. According to Rudra (1982) the Kota Limestone suggests periodic precipitation of impure lime muds in freshwater playa-type lakes. The presence of inclined and vertical burrows indicates quiet sedimentary episodes, and pelletoid-bearing laminations indicate a very slow rate of sedimentation (Maulik & Rudra, 1986). Periods of drought are also suggested by the presence of semionotid fish in cracked limestone — this circumstance has been explained by Jain (1980; 1983) as owing to the mortality of semionotids in the oxygen-deficient evaporating water of the Kota lakes. The large sauropods, such as *Barapasaurus*, inhabited land close to the Kota lake and fed upon the aquatic vegetation, while the crocodiles fed on fishes and lived on the banks (Jain & Roychowdhury, 1987). Broadly, the Kota lake environment is pictured as a shallow water body, with pholidophorids and coelacanths inhabiting its deeper parts.

The Late Cretaceous Lameta Formation has provided a fairly extensive record of terrestrial dinosaurs, ostracodes, charophytes and invertebrates; the environmental interpretation has therefore been of much fascination.

The marine interpretation of the Lameta Formation is based on the presence of algal-like structures, glauconite beds and thalassinoid burrows (Chanda, 1963; Chanda & Bhattacharya, 1966). Singh (1981) opined that both the Bagh and Lameta Formations are the product of a Turonian-Senonian marine transgression; wherein an estuarine tidal flat complex was indicated by crab burrows, bioturbated carbonate and marl facies.

The marine interpretation was first challenged by Brookfield & Sahni (1987) who believed that the evidence favouring a marine environment may have been misinterpreted, for instance the algal structures in the limestones are pedogenic carbonate structures of palaeosols. Further, on the basis of the dinosaur eggs, bones and associated freshwater biota (charophytes, ostracodes and other invertebrates), it was concluded that the entire Lameta sequence consists of pedogenically-modified piedmont calcrete deposited in a semi-arid environment dominated by a large river.

Subsequently, on the basis of Matley's (1921) map of the Jabalpur area, Tandon et al. (1990) studied the sedimentology and facies of sections
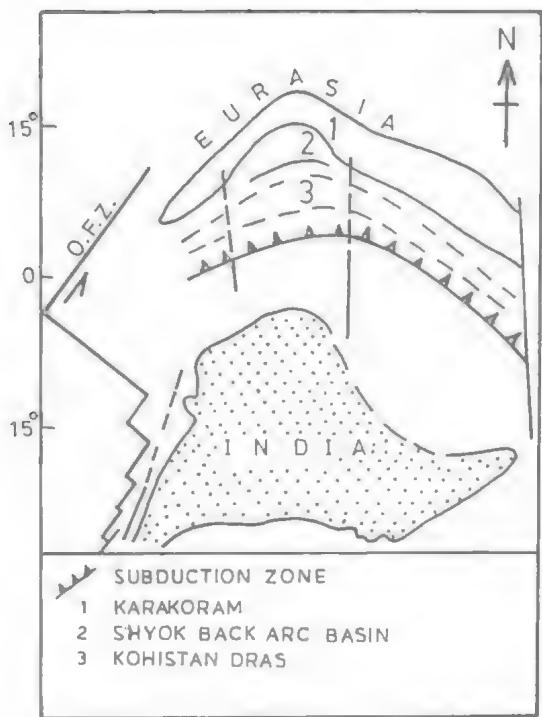
FIG. 4. Late Cretaceous palaeoposition of the Indian plate and Kohistan-Dras Island Arc (after Sharma, 1987; Sahni & Bajpai, 1991).

at Lametaghat, Chui Hill and Bara Simla Hill in detail. At Bara Simla Hill they identified several undulations associated with 'relief highs' and 'relief lows' — these were interpreted (through computer studies) to represent shoulders and ramps on an ancient geomorphic surface. The relief high characterises dinosaur nest-bearing nodular carbonates, while the relief lows are associated with a marly dinosaur bone-bearing horizon. Both these palaeo-relief surfaces form part of fanpalustrine flat system with repeated sheetwash activity, wherein the upper sandy carbonate represents emergent areas with high pedogenic modification, while the lower marly facies has low pedogenic modification (Tandon et al., 1990; Sahni et al., 1994).

Further, the nesting sites, in as much as they are associated with pedogenic calcrete, fringed small lakes. Desiccation and subsequent sheetwash activity occurred leading to rapid matrix cementation and preservation of large dinosaur nests (Jolly et al., 1990). In this context extensive field work at Bara Simla Hill, Chui Hill and Lametaghat suggest a single stratigraphic level of sauropod nests associated with pedogenic calcretes in the Lower Limestone layer (Sahni & Khosla, 1994). Evidence of multiple layers of nesting is absent; the different topographic levels can be explained by the undulatory character of the palaeogeomorphic surface (Tandon et al., 1990). As such there is a strong evidence for 'site selectivity' on the part of the dinosaurs, rather than site fidelity. Moreover, the pedomorphic surface along the entire stretch of terrain from Jabalpur in the east towards Gujarat in west was selected by the sauropods for nesting sites (Jolly et al., 1990).

An alluvial-limnic environment under semi-arid conditions was suggested for various subenvironments of the Lametas exposed in Dongargaon Hill and Dhamni-Pavna sections by Mohabey et al. (1993). The eggshell-bearing horizons, especially near Pavna, are associated with overbank facies. Pink and red clays suggest the leaching action of reducing waters with occasional ponding of water, as shown by freshwater charophytes and ostracodes. However, at Pisdura and Dongargaon, a channel facies with immature pebbly and gritty sandstones with calcrete layers was delineated, with cross-stratification, convoluted bedding and channel fill structures. The lacustrine facies is characterised by finely laminated silty clays and contains *Lepisosteus, Lepidotes* and ostracodes (*Candionella* and *Mongolianella*).

The palaeophysiologic conditions of the Indian Cretaceous eggshells have been characterised mainly on shell thickness, pore distribution, density, pathologic thickening or thinning and resorption of mammillae (Sahni et al., 1994). The porosity values, which reflect nest humidity, for the eggshells are substantially less; these values are measured by water vapour conductance which vary from $2.65\,\mathrm{mg/(day.tor)}$ to $3.49\,\mathrm{mg/(day.tor)}$; such low values are probably due to the semi-arid environment.

The O^{18} and C^{13} values of the Lameta eggshells indicate that dinosaurs drank water from rivers and evaporating pools and consumed C-3 type plants, such as palms, dicot shrubs and conifers (Sarker et al., 1991).

PALAEOBIOGEOGRAPHY

Until recently, the main arguments supporting the hypothesis of Gondwanaland were derived from glaciation and distinctive floras. In recent years geophysics and oceanography have contributed suggestive new data, but it is the information from Gondwanan vertebrates that has

proved to be of inestimable value in providing a clearer palaeobiogeographic analysis in the scenario of drifting plates.

A look into the affinities of the Indian Gondwana tetrapods clearly provides sufficient evidence of Laurasian influence in these palaeocommunities, with no endemism. The Triassic Maleri dinosaur *Alwalkeria* is more or less similar to *Coelophysis* of North America and *Procompsognathus* of Germany. The lower Jurassic Kota dinosaur, *Barapasaurus tagorei* bears affinities to the European *Ohmdenosaurus liasicus*, Patagonian *Patagosaurus fariasi* and Chinese *Shunosaurus lii*.

Significant evidence, however, is the discovery of Maastrichtian mammal *Deccanolestes hislopi* in the Intertrappeans of Naskal, Andhra Pradesh (Prasad & Sahni, 1988). This genus shows morphological similarity to the North American *Cimolestes* and Mongolian *Kennalestes*.

Palaeorycted mammals are also known from the Paleocene of Morocco (Cappetta et al., 1978). In addition to palaeoryctids, molar teeth belonging to Docodontidae are known from the Late Jurassic of India (Prasad & Khajuria, 1990). Besides, pelobatid frogs, lizards and turtles, known from the Intertrappean beds of Nagpur, are also known from North American and Russian localities.

Amongst the invertebrates, the Intertrappean of Nagpur has yielded *Cypris, Candona, Altanicypris*, which are similar to Mongolian-Chinese form. Charophytes, such as *Platychara perlata* known from the Intertrappeans, are closely similar to *P. compressa* of North America. The aforementioned picture of lack of endemism and the cosmopolitan distribution of Indian dinosaurs, has been utilised and interpreted by some stabilists, who have invoked static models of Indian-Eurasian plates and their contiguity in the past (Chatterjee, 1984; 1987; Chatterjee & Hotton, 1986). These workers are of the view that India was never an island continent during its convergence towards Eurasia, and believed in a narrower Tethys with India occupying a position between Somalia and Eurasia in its pre-drift position (Chatterjee & Hotton, 1986). Also, the presence of Laurasian biotas in India and migrations, may be a consequence of land corridors between India and Eurasia that were maintained during Cretaceous (Chatterjee, 1992).

However the work of ardent mobilists, notably Sahni (1984), Sahni & Bajpai (1991) and Loyal (1984, 1985), have seriously questioned the validity of Chatterjee's (1984, 1987) conclusions.

Sahni (1984), while analyzing and admitting the Eurasiatic faunal presence in the Indian Gondwanas, concluded that migration of land faunas took place during the Cretaceous-Palaeocene from the eastern part of Africa, as India was then close to Madagascar. Later, Sahni et al. (1987) and Sahni & Bajpai (1991) suggested that the necessary land passage might have been provided by the island arcs of Dras Volcanics (Fig. 4); this activity might have been initiated earlier, in Late Jurassic (Sharma, 1987). In this context, an early Cretaceous India-Eurasia collision was suggested by Jaeger et al. (1989).

Further, to account for the cosmopolitan distribution, one of us (RSL) is of the opinion that two dispersal corridor routes existed for Gondwanaland-Laurasia intermigrations, viz. India-South Tibet-Afghanistan-Iran-Turkey and India-Africa-Siberia (Loyal, 1985). The fragmented portion of northernmost Gondwanaland (Tibet, Iran, Iraq, Afghanistan) formed a migrating festoon of island arcs, establishing links with Eurasia throughout Late Permian-Cretaceous. Therefore, these paths of migration (in Laurasia and Gondwanaland) were extremely significant in as much as they help explain the lack of faunal endemism of the Indian biotas during its time of geographic isolation and rapid northward journey.

Finally, though there exists now (as aforementioned) a growing body of vertebrate and invertebrate faunal data from the Indian Plate, pointing to strong India-Laurasia links similar palaeobiogeographic data from other Gondwanic areas (Africa, S. America, Antarctica, Australia) is almost meagre. Therefore, in this context, Laurasia-Gondwanaland faunal comparisons remain poorly understood: hence urgent and extensive fieldwork in the Mesozoic terrain of Gondwanic regions is necessary.

ACKNOWLEDGEMENTS

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OBSERVATIONS ON THE AUSTRALIAN ORNITHOPOD DINOSAUR, *MUTTABURRASAURUS*

RALPH E. MOLNAR

New material and a restudy of old suggests that *Muttaburrasaurus* is not an iguanodontid ornithopod, but probably diverged from the iguanodontian-hadrosaur lineage prior to the divergence of taxa such as *Dryosaurus* and *Tenontosaurus*. The type skull differs from a second, older skull from the Allaru Mudstone in ways that suggest a trend toward the evolution of a continuous more-or-less planar sheet of enamel along the labial face of the maxillary dentition. Teeth from Lightning Ridge (Griman Creek Fm.) may pertain to a more plesiomorphic species of *Muttaburrasaurus*. ☐ *Muttaburrasaurus, Ornithopoda, Australia.*

Ralph E. Molnar, Queensland Museum, P.O. Box 3300, South Brisbane, Queensland, 4101, Australia; 15 August 1996.

The discovery of a new skull of *Muttaburrasaurus* (from 'Dunluce', north-central Queensland) and further preparation of the holotype skull has yielded interesting new information bearing on its evolution and systematic position. Because preparation of both skulls proved more difficult and hence slower than expected, it is worthwhile presenting interim results that substantially alter the phylogenetic interpretation of Bartholomai & Molnar (1981) and Molnar (1984). New information on cranial features, especially those relevant to understanding the phylogenetic position of *Muttaburrasaurus* in relation to the classification presented by Sereno (1986), are given here. Some remarks on postcranial features are also included.

Collection designations. AM, Australian Museum, Sydney; NMV, Museum of Victoria, Melbourne; QM, Queensland Museum, Brisbane.

DESCRIPTION

HOLOTYPE SKULL (QM F6140). The original description of the skull of *Muttaburrasaurus langdoni* included no description of palatal or braincase structure and these are described here, insofar as feasible with the still incomplete state of preparation. Comments on the maxilla, the postorbital bar and the general form of the skull follow.

Quadrate. The quadrate is a robust columnar element, similar to those of other advanced ornithopods. The articular end remains in articulation with the mandible, and so cannot be examined in detail. The body is straight in lateral view as in *Iguanodon bernissartensis*, not curved as in *I. atherfieldensis*. The posterior surface, inclined to face slightly medially, tapers upwards to become a sharp ridge formed by the meeting of the lateral and medial surfaces of the element. A broad pterygoid wing projects anteromedially to meet the pterygoid in a smooth curve (Fig. 1). Posteriorly this process bears a marked concavity, adjacent to a vertical sulcus on the upper part of the body of the bone. The lateral face (jugal wing) projects anteriorly beneath the quadratojugal and is embayed by the round margin of the quadrate foramen.

Exoccipital. Presumably the exoccipitals and opisthotics are fused, but only the exoccipital portion of the compound element is easily visible, to best advantage on the left side. A dorsoventrally deep paroccipital process extends posterolaterally from the condyar region. Although the distal end is lacking, there is no indication that the process was declined distally as in *Iguanodon* and hadrosaurids (Fig. 2).

Medially a stout pillar descends from the paroccipital process to abut on the basioccipital and form the dorsolateral part of the occipital condyle. Part of the condyle, separated by a shallow groove from the ventral moiety, may be made up by the exoccpital. Because the contacts are fused it isn't clear that this is actually part of the exoccipital, as there is another possible contact — a discontinuity in the surface grain of the bone — at the junction of the pillar and the base of the paroccipital process. Just anterior to the presumed junction, there is an anteroposteriorly-directed concavity. This has yet to be fully cleaned but is likely to accommodate foramina for cranial nerves X, XI and XII.

Basioccipital. Only two points may be added to the original description. The articular surface of the condyle extends forward to form a lip
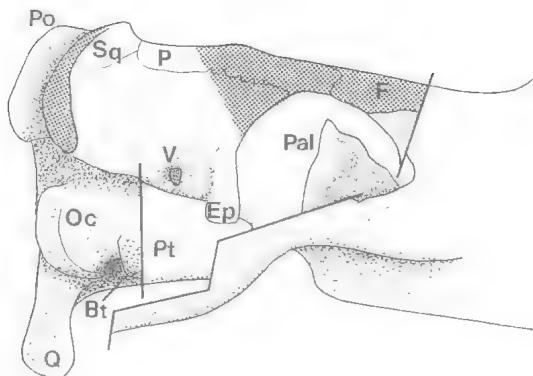
FIG. 1. Cutaway interpretation of braincase and posterior palatal structures of *Muttaburrasaurus langdoni*, QM F6140. Bars indicate cuts through the jugal arch, prefrontal region and quadrate wing of pterygoid. Dots indicate broken bone surfaces. Bt=basal tubera (basisphenoid), Ep=epipterygoid, F=frontal, Oc=occipital condyle, P=parietal, Pal=palatine, Po=paroccipital process, Pt=pterygoid (quadrate wing), Q=quadrate, Sq=squamosal, V=presumed trigeminal foramen.

FIG. 2. Skulls of A, *Iguanodon bernissartensis*; and B, *Muttaburrasaurus langdoni* in occipital view, to show the difference in forms of the paroccipital processes. To scale. (A redrawn from Norman, 1980, and B from Bartholomai & Molnar, 1980.)

'overhanging' the neck of the condyle, so the surface describes an arc in excess of 180° as in *I. atherfieldensis* (Norman, 1986, fig. 18). This lip connects with the basal tubera by a low, blunt keel on the ventral face of the condylar neck.

Basisphenoid. Only the inferior, and some of the lateral, surface of the basisphenoid is clearly visible and it carries large basal tubera, confluent medially to form a rugose transverse ridge. The left tuber is deflected sharply posteriorly and the right is incomplete. A large foramen on each side penetrates the tubera at the junction with the keel connecting to the occipital condyle. On the midline the ventral face of the confluent tubera has a larger foramen (Fig. 3). This foramen is in the same relative position as that of the median eustachian foramen (f. intertympanicum) of modern crocodilians, but whether or not it represents that structure cannot be determined at present.

About 2cm in front of the tubera, two robust 4cm-long basipterygoid processes extend ventrolaterally and somewhat anteriorly to contact the pterygoids. Just anterior to the tuber on the left side, a sheet of bone curls out from the basisphenoid (or prootic?) joining it to the quadrate process of the pterygoid. Although so far only partly prepared this seems to be very similar to a character state used to diagnose the Pachycephalosauria: Prootic-basisphenoid plate

present which extends laterally from the braincase, contacting the pterygoquadrate wing and effectively separating subtemporal and occipital regions (Sereno, 1986). In *Muttaburrasaurus* this contact also separates the subtemporal (adductor) chamber from the occipital region.

Pterygoid. Both right and left pterygoids are preserved, but that of the right is visible only in the basipterygoid-quadrate region, and that of the left is fragmentary. The quadrate process is a vertical sheet, with an acutely angled posterior margin, projecting posteriorly from the basipterygoid contact and laying ventral to the pterygoid wing of the quadrate ('Pt' in Fig. 1, where the entire extent is not shown). It bears a broad, blunt median longitudinal ridge. Anteroventrally it contacts another sheet laying in a plane inclined at about 45° to the horizontal. The extent of this portion cannot be determined without further preparation. The basipterygoid joint, which seems to have been immobile, is just anterior to the contact between these two sheets. In front of the joint a tapered process of the pterygoid extends medially and curves through 180° to form a (more or less) horizontal hook-like structure (Fig. 3, 'mp').

Epipterygoid. A few fragmentary sheets of much abraded bone between the laterosphenoid and the pterygoid on the right side probably represent the epipterygoid. They show little other than that one was present in the usual position (Fig. 1, 'Ep').

Palatine. The right palatine is visible and somewhat worn. It seems to be a thick, triangular plate rising sharply from the maxilla, with its dorsal margin just below or contacting the prefrontal (Fig. 1).

Maxilla. In QM F6140 the maxillae are orientated so that their toothrows have been brought
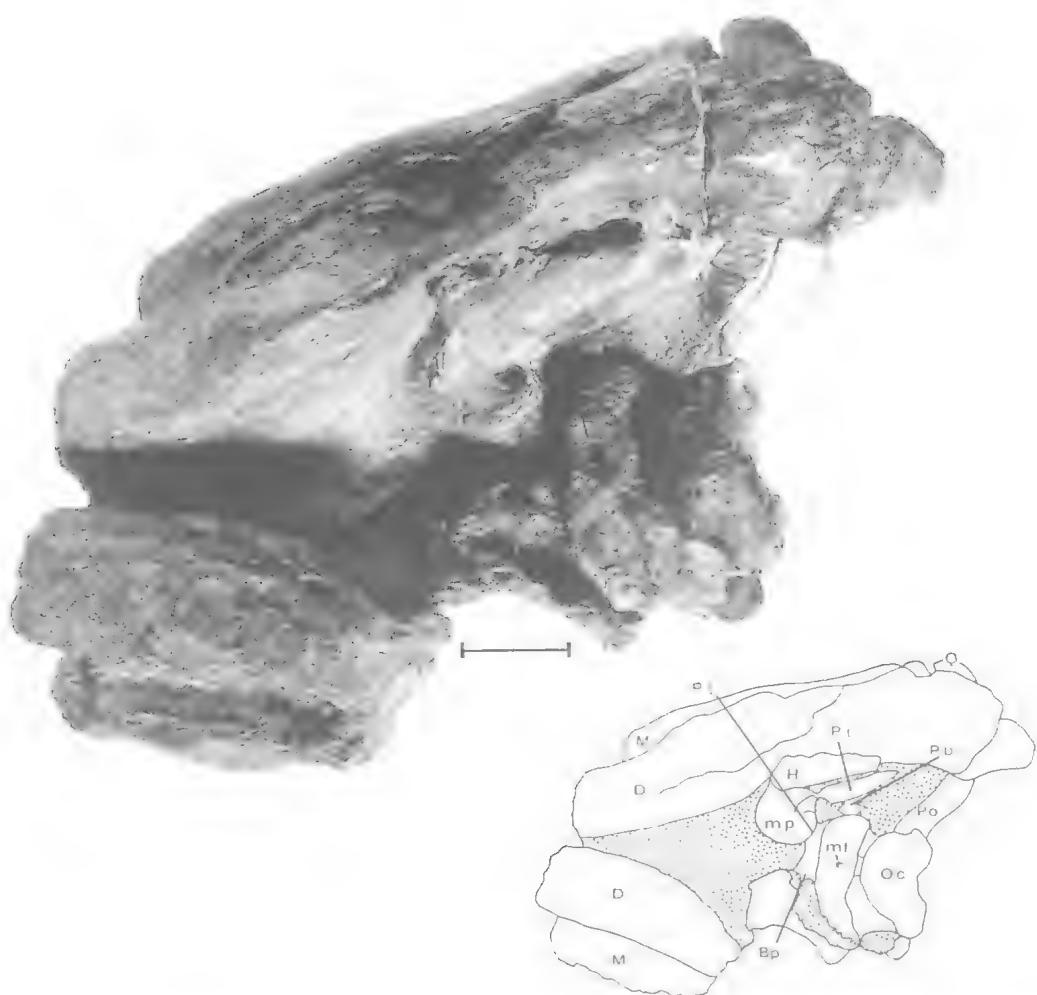
FIG. 3. The skull of *Muttaburrasaurus langdoni*, QM F6140, in ventral view. Bj=basipterygoid joint, Bp=basipterygoid process (basisphenoid), D=dentary, H=hyoid piece, M=maxilla, mf=median ventral foramen of basisphenoid, mp=medial hooked process of pterygoid, Pb=pterygoid-braincase contact. Other abbreviations as in Fig. 1. Scale = 50mm.

together, with the crowns only 5cm apart, directed toward one another with the labial faces of the teeth facing ventrally. The maxillary toothrows of the 'Dunluce' skull (QM F14921) have also been brought together, about 3cm apart, by crushing. The orientation of the maxillae in this specimen suggests that those of the holotype have been folded underneath the skull, so that their lateral surfaces have come to face ventrally. In fact this has also happened to a lesser extent in the 'Dunluce' skull, as shown by fracturing of the posterior part of the right maxilla. Such fractures are not apparent in the type skull, which has either suffered plastic deformation or rotation of

the maxillae about their dorsal margins. Since such rotation has been proposed as a masticatory device in the iguanodontian-hadrosaurian lineage (e.g., Weishampel, 1984; Norman & Weishampel, 1985), it is interesting to see if it was present in *Muttaburrasaurus*. The lateral surface of the posterior part of the left maxilla of the type skull curves through a 90° arc (in the frontal plane) beneath the orbit, from the nearly horizontal surface adjoining the jugal to the nearly vertical surface at the alveoli. But just forward of this the alveolar region has been flexed so that the teeth become directed medially, as described above. This suggests that this maxilla at least is

deformed, and provides no evidence for (or against) flexure at the maxillary-nasal junction. The reconstruction of the type skull (Fig. 4) corrects for this distortion.

Postorbital bar. Unlike the condition of most other ornithopods the postorbital bar of *M. langdoni* is more extensive transversely than anteroposteriorly (Fig. 5). In other words, it is broad. The descending process of the postorbital is 4cm wide (transversely) but only 1.75cm in the longitudinal dimension. The ascending process of the jugal is similarly formed, so the postorbital bar partly divides the orbital cavity from the adductor chamber. A similar state, postorbital bar transversely broadened with an interdigitating postorbital-jugal suture, is used by Sereno (1986) to partly define the Goyocephalia, the node just distal to the Pachycephalosauria. The contact between the jugal and postorbital in *M. langdoni* is tight, but only actually interdigitates at the tip of the ascending process of the jugal.

Skull form. Molnar (1995) presented an argument, based on the type skull, that the pos-

FIG. 4. Reconstruction of skulls of A, *Muttaburrasaurus langdoni* (QM F6140); and B, *Muttaburrasaurus* sp. (QM F14921). Restored portions in dashed lines. The region of the jugal and of the junction between the nasal bulla and body of the maxilla in QM F14921 is worn and hence the structures shown (form of jugal-maxillary contact and clefts beneath bulla) may represent structures just below the surface of the skull. The last maxillary tooth is very poorly preserved, so it is not certain if the last alveolus as drawn represents a single alveolus or two.

torbital region was enlarged relative to those of other ornithopods. This may be seen in Fig. 6, and has directed the orbits very slightly to the front. Although dorsoventrally deep, the snout was seemingly relatively narrow. The 'Dunluce' skull, in spite of its crushing, confirms that the postorbital region was approximately twice as broad as the snout.

'DUNLUCE' SKULL (QM F14921). The second skull was collected by Dr Mary Wade in 1987 from the Allaru Mudstone (not the Toolebuc Fm., as reported by Molnar, 1995) on Dunluce station, about halfway between Hughenden and Richmond in north-central Queensland. The Allaru Mudstone, a gray calcareous marine argillite, underlays the Mackunda Fm. from which the holotype derives. Thus this second specimen derives from an older population (although still

Albian) than the type. The skull is probably more complete that the holotype skull but has been laterally sheared and crushed, so that the the nasal bulla has been flattened and the skull roof has come to lie almost coplanar with the right side (Fig. 7). The postorbital region is severely damaged on the left, so that the quadrate now rests in the position of the posterior orbital margin (Fig. 7A). The postorbital is missing entirely on this side, and the (empty) impression for its reception may be seen on the ascending process of the jugal. Because of the damage, and because preparation is still in a preliminary stage, a full description of this skull will not be given here. Instead selected relevant features are reported. This skull is identified as *Muttaburrasaurus* on the basis of its general form, as well as the apomorphic nasal bulla and tooth form. Because of the damage and incomplete preparation, as
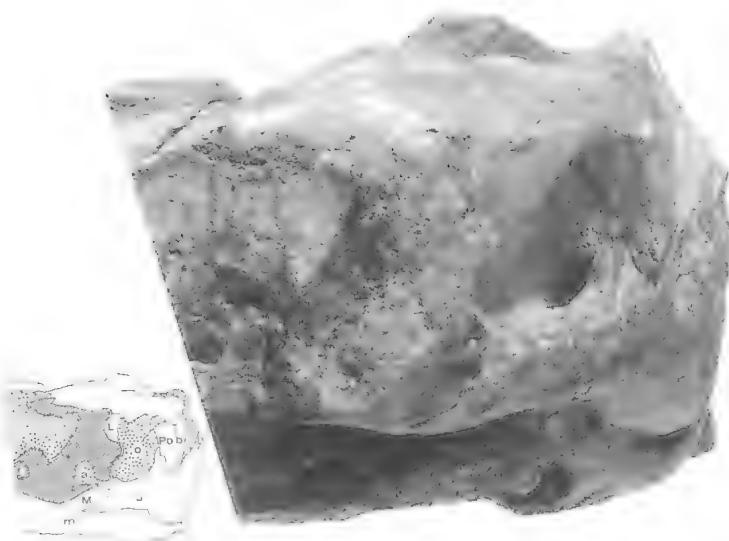
FIG. 5. The skull of *Muttaburrasaurus langdoni* (QM F6140) in anterolateral view, showing the breadth of the postorbital bar (Pob). Dots indicate broken bone surface; open dots indicate matrix. m=mandible, J=jugal, o=orbit, a=antorbital fossa, r=root of maxillary tooth, L=lachrymal. Other abbreviations as in Fig. 3.

well as the possession of partly erupted maxillary crowns anteriorly in the toothrow (those of *M. langdoni* are completely erupted along the entire visible maxillary toothrow) and differences in form, it is premature to assign it to *M. langdoni*, and it is referred to *Muttaburrasaurus* sp.

Nasal bulla. The anterior termination of nasal bulla is not preserved on the type skull, but on QM F14921 it seems to be present. Although much of the bony surface of this specimen has been lost surface bone is present at the front margin of the nasal bulla. Here the surface forms an anteriorly-directed vertical face, which then presumably bends through a right angle — the flexure itself is still embedded in carbonate — to give an adjacent horizontal bone surface extending anteriorly to the break at the front of the specimen. Although the nasal bulla has been flattened during preservation, it seems unlikely such transverse compression could create an illusory anterior termination to the bulla. This observation has been incorporated into the new reconstruction of the skull in Fig. 4B.

Although the nasal bulla of QM F4921 is badly crushed and incompletely prepared, some features can be better seen than in the holotype. On the right side, a crescentic element makes up the anterodorsal part of the lateral wall of the bulla (Fig. 7B). The left is worn and incompletely

prepared and so difficult to interpret, but gives no reason to doubt or modify the interpretation here given. This element contacts that, presumably the nasal, making up the dorsal roof of the bulla posteriorly, and what seem to be slit-like nares anteriorly. The concave inferior margin of the bone is unbroken, so that the posteroventral part of the lateral wall must have been formed by another element, not preserved. Thus the cresecentic element may be, or be part of, the premaxilla. This element cannot be seen on the bulla of the type skull, where instead the lateral wall seems to be made up of a single element. There is no clear indication of narial openings on such of the maxillae as is preserved anterior to the bulla.

Ventrally the bulla seems to have been separated from the underlying maxilla by two clefts, separated from each other by a thin sheet of bone (Fig. 7A). This sheet is continuous with the maxilla anteriorly, so the lower of the clefts seems to be part of the maxilla. These structures are also apparent on the left side, but cannot be seen in the type skull, presumably because they are internal structures exposed by wear on the 'Dunluce' skull. A thin median septum is apparent within the bulla, as in the type skull (which also has a second vertical sheet, described in Molnar [1984] more laterally placed at the left edge of the left narial opening). The bulla of the type skull also shows on its badly worn left side one, or perhaps two, thin, seemingly horizontal internal sheets of bone.

Antorbital fossa. The apparent antorbital fenestra on the left side of the 'Dunluce' skull (Fig. 7) is entirely surrounded by abraded bone that had been exposed prior to discovery. This has exposed a triangular antorbital fossa of respectable size, approximately 5 x 7cm.

Tooth replacement. The holotype skull is unusual among ornithopods, as well as other reptiles, in that there is no indication of the sequence of tooth replacement in the maxillary dentition. In fact, replacement teeth can be seen only where the skull has been broken transversely behind the nasal bulla. (The dentary crowns now visible
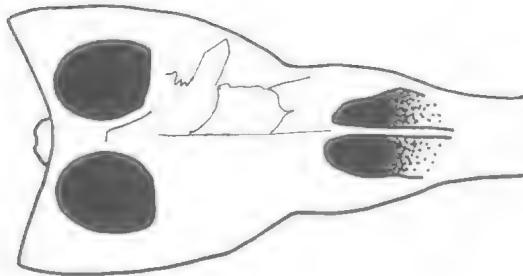
FIG. 6. Reconstructed skull of *Muttaburrasaurus langdoni* (QM F6140) in dorsal view. (From Molnar, 1995.)

seem to show an alternating pattern of replacement.) The 'Dunluce' skull has a complete, or almost complete but bady weathered, right maxillary toothrow. There are 22 tooth positions, with what seem to be replacement crowns in positions 4 and 6 (from the front). Only 15 positions are visible in the type skull, probably 6 to 21 assuming that it, too, had 22 maxillary teeth, and the anterior-most teeth are not well preserved. Thus some replacement in the type skull cannot completely be ruled out, but there is no indication of it.

TEETH

Maxillary teeth. Only the maxillary teeth of *M. langdoni* were described by Bartholomai & Molnar (1981). Although 17 maxillary crowns are exposed on the left side of the type skull, only three preserve substantial portions of the lateral face. These crowns differ from those of all other ornithischians in that they show an almost flat (slightly convex) lateral face marked by a series of parallel ridges and grooves, all of which are equally developed (Fig. 8). The ridges extend to the base of the crown anteriorly (mesially) but become progressively shorter posteriorly. They — with one possible exception — do not converge. None of the crowns shows clear indication of a primary ridge. On two, however, a primary ridge adjacent to the posterior (distal) margin of the crown is evident. This presumed ridge is only marked as such by an adjacent sulcus along the posterior margin (this sulcus is the 'deep groove' of Bartholomai & Molnar, 1981). Each crown slightly overlaps that posterior to it.

Maxillary crowns are also known in the 'Dunluce' skull, QM F14921, and probably — as isolated teeth — from Lightning Ridge. The latter were held in the private collection of Ms Elizabeth Smith but have been donated to the Australian Museum, and represented by casts in the Queensland Museum. As mentioned pre-

viously, most of the exposed maxillary crowns of the 'Dunluce' skull are poorly preserved, with their lateral faces badly weathered, but a fortuitous break on the left side exposed a well-preserved crown near the posterior end of the toothrow (Fig. 8B, E), probably number 19 or 20. The ornament of this crown is like that of the the type skull, but differs in some notable ways. The lateral face is almost flat, slightly concave, and bears 11 low ridges. These ridges are relatively larger than those of the holotype skull and broader, with flat — in some cases slightly grooved — tops. Most apparent, however, is the clear primary ridge near the distal margin with 8 of the low ridges mesial to it and 3 distal. In some ways this crown more closely resembles those of *Atlascopcosaurus loadsi* (NMV P157390) than those of the holotype skull. However, the maxillary crowns of QM F14921 do resemble those of the holotype in: outline of the crown; almost flat lateral face; large number of low, parallel grooves and ridges; and a low primary ridge near the distal margin.

The teeth from Lightning Ridge (New South Wales) from the Smith collection include one worn specimen preserving the root and base of the crown (QM F14420 [cast]), and a second that is almost complete (QM F14421 [cast]). (A third tooth, AM F81865, may also pertain to *Muttaburrasaurus*). They derive from the Griman Creek Fm. at McNamara's Three-Mile Field and were collected in, or just before, 1986. These were previously noted, but not described, by Molnar & Galton (1986). The first is too incomplete for consideration here — and may derive from the dentary — but the second shows a crown basically similar to that of the 'Dunluce' skull (Fig. 8F). It has a series of 6 low, parallel ridges mesial to a primary ridge, fewer than in QM F14921, and 1-2 distal to it in a shallow sulcus. It is also smaller than the 'Dunluce' tooth, about 69% as wide. The crown is referred to *Muttaburrasaurus*, rather than *Atlascopcosaurus*, on two character states: a curved (not angulate) proximal margin to the crown; and the extension of the primary ridge to the base of the lateral face. In *A. loadsi* the primary ridge extends to the distal margin of the crown rather than the proximal, and there is no real proximal margin, rather the mesial and distal margins converge (Fig. 8G).

Unlike any of the crowns in either the type or 'Dunluce' skulls, this crown (QM F14421) shows the lingual surface, which bears a series of at least four parallel, shallow grooves. Unfortunately, due to the silicification of the specimen it is not possible to determine if the surface bore enamel
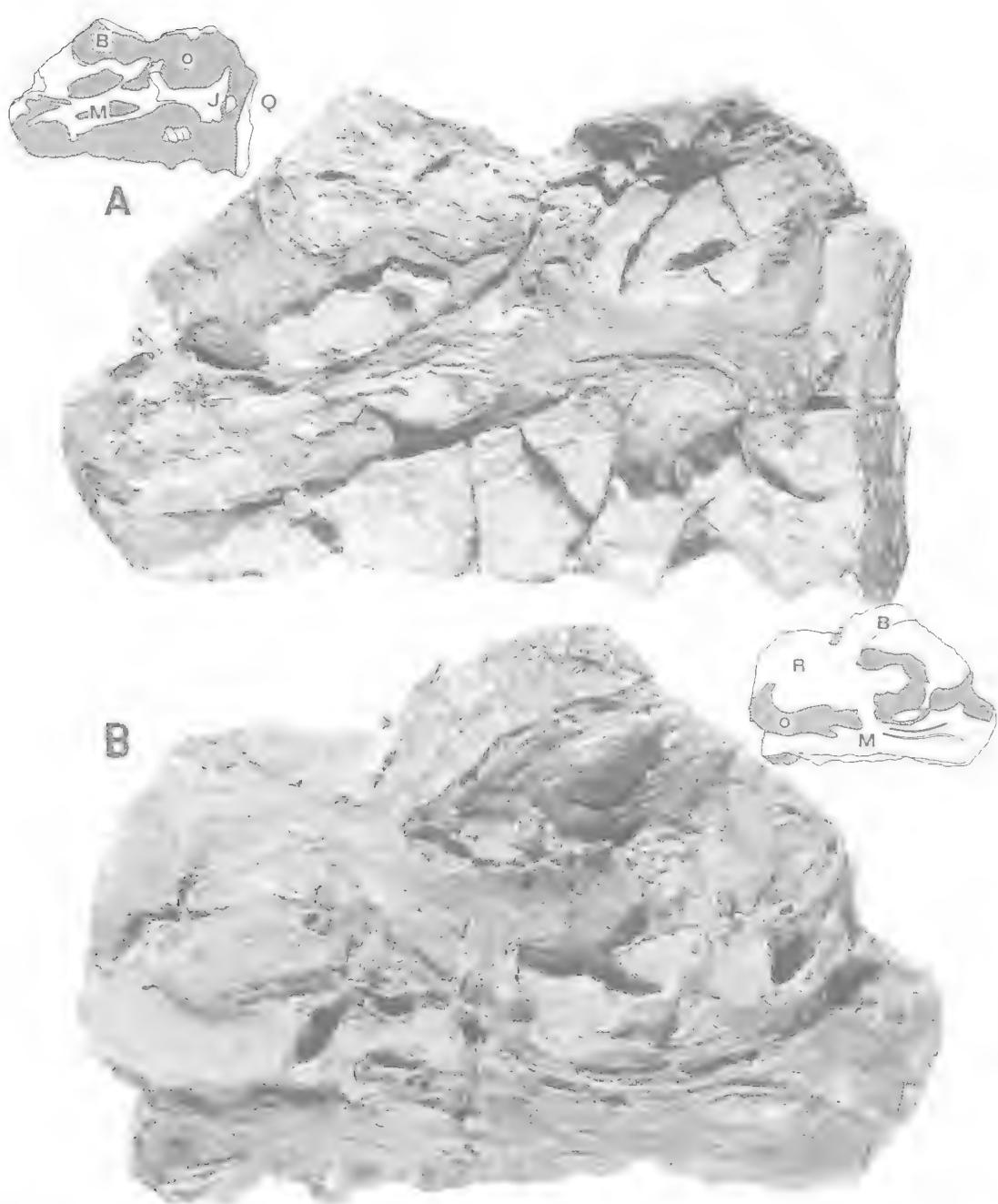
FIG. 7. The partially prepared skull of *Muttaburrasaurus* sp. (QM F14921), from the left A, and right B. The skull has been crushed, and the apparent antorbital fenestra and opening in the lower part of the nasal bulla are artefacts of erosion on the left side. The left quadrate has been displaced anteriorly to the region of the anterior margin of the laterotemporal fenestra. B=nasal bulla; R=skull roof.

and, if so, how much. The maxillary crowns of *A. loadsi* also have a series of shallow, parallel grooves on their lingual faces as does an incom-plete crown referred to *Muttaburrasaurus* sp. from near Hughenden (QM F12541) (Fig. 8C).
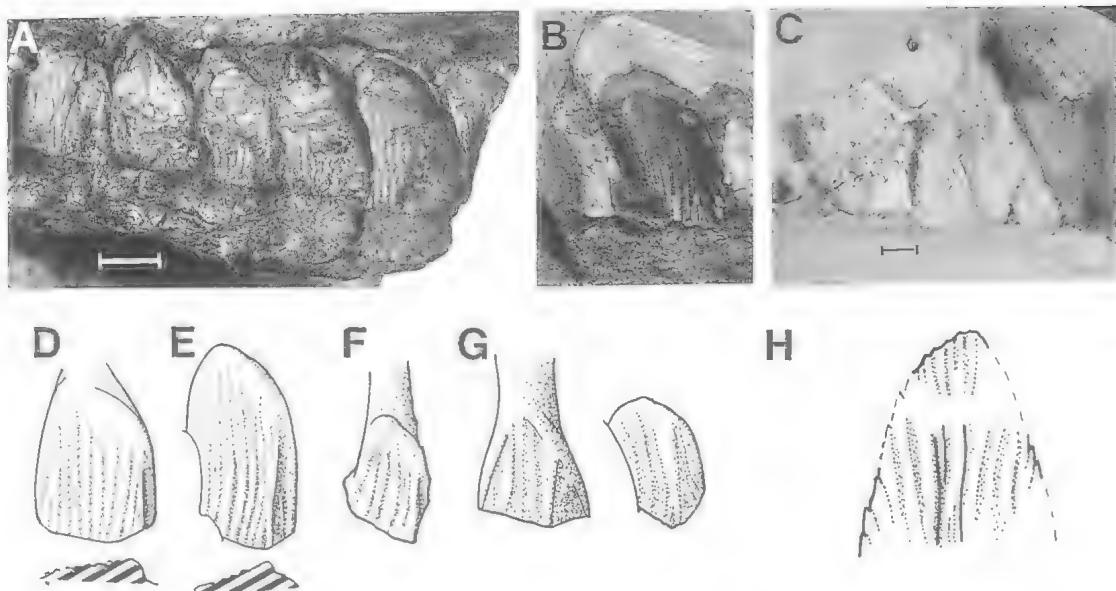
FIG. 8. Teeth of *Muttaburrasaurus*. A, Anterior maxillary teeth of *M. langdoni* (QM F6140). B, Posterior maxillary crown of *M.* sp. (QM F14921). C, Dentary crowns of *M.* sp. (QM F12541). D,, Right 11th or 12th maxillary crown of *M. langdoni* (QM F6140). Section through crown at bottom, showing position of presumed primary ridge. E, Left posterior maxillary crown of *M.* sp. (QM F14921). Section through crown, as in E, at bottom. F, Maxillary crown of *M.* sp. (QM F14421). G, Two maxillary crowns of *Atlascopcosaurus loadsi* (NMV 157390).H, Reconstructed dentary crown of *Muttaburrasaurus*, based on QM F12541 and QM F6140.

Dentary teeth. Dentary crowns have been exposed on the type skull, and also occur in a very fragmentary specimen (QM F12541) from the Allaru Mudstone from 'Iona', southeast of Hughenden. This was tentatively referred by Molnar (1984) to 'an unusually large hypsilophodont' on the basis of what are now recognised as plesiomorphic ornithopod or even euornithopod character states. This specimen is part of an associated partial skeleton, which has remained in Hughenden. It consists of parts of two dentary crowns found in a small block of carbonate, together with natural molds of parts of four other teeth. One of these represents the lingual face of the maxillary tooth mentioned above.

No dentary crown is completely exposed in either specimen, so only the upper half (or a little more) toward the tip may be described. The crown seems to be rounded, perhaps leaf-shaped, in form. A prominent carina occupies the middle, with a series of lower, parallel ridges, varying in size, occupying the face mesial and distal to it (Fig. 8C, H). These ridges are inclined to the carina and terminate at the margin in small, tapering denticles. The denticles are featureless, except that some divide distally, so that one ridge

may bear two denticles. In at least one specimen (QM F12541) the carina itself bears four or five low, parallel ridges basally. In all discernible features the dentary crowns of the type skull match that of QM F12541. A single displaced dentary tooth of the 'Dunluce' skull is also indistinguishable from these.

POSTCRANIUM (HOLOTYPE)

Manus. Initially *Muttaburrasaurus* was believed to be an iguanodontian, closely related to *Camptosaurus* (Bartholomai & Molnar, 1981): this work was carried out before the influence of phylogenetic systematics was felt in ornithischian taxonomy. At that time an incomplete flattened, tapering element was thought perhaps to represent a thumb-spike. If *Muttaburrasaurus* is indeed an ankylopollexian, this is a plausible interpretation. However, the bone is poorly preserved, abraded and broken. Therefore — in the absence of any assurance that *Muttaburrasaurus* is in this lineage and is as or more advanced than *Camptosaurus* — the piece cannot be reliably identified as a thumb-spike and so does not constitute evidence that *Muttaburrasaurus* is an ankylopollexian.

FIG. 9. Reconstruction of the skeleton of *Muttaburrasaurus langdoni* showing what parts are actually preserved. Scale = 1m.

Pes. During the reconstruction (Fig. 9) of *M. langdoni*, the pedal elements were re-examined. Further cleaning of the pieces revealed a contact between the proximal and distal parts of metatarsal III. This shows that the metatarsus is shorter than originally believed (Fig. 10), and reduces the anomalous disparity in length between metatarsal III and the others.

SYSTEMATIC POSITION

Since the original description of *Muttaburrasaurus* much new work on advanced ornithopods has appeared. The original interpretation of its systematic position was based significantly on Dodson (1980), but the re-interpretation of ornithischian phylogeny by Sereno (1986) suggests that a review of the position of *Muttaburrasaurus* is in order. Consideration of the original and new character states suggests that *Muttaburrasaurus* is not an iguanodontid (or camptosaurid), but a basal ornithopod whose lineage diverged early from the iguanodont-hadrosaur lineage.

Because of the incompleteness of the *Muttaburrasaurus* material (Fig. 9) many of the character states used by Sereno (1986) are not observable. The remaining states are assessed for *Muttaburrasaurus*, based on the type specimen but with some observations from the 'Dunluce' specimen. Three (mandibular dentition offset medially; moderate coronoid process; pubic peduncle of ilium less robust than ischial peduncle) of the seven states used by Sereno to diagnose the Genasauria are present in *Muttaburrasaurus*, so its inclusion in that group is reasonable.

States are considered in order of the nodes they define.

ORNITHOPODA

External opening of the antorbital fossa of moderate size or smaller: Present. The antorbital opening is present but small in the type skull. Unfortunately shedding of the surficial bone makes it impossible to tell just how small the opening was. The 'Dunluce' skull seems to have a relatively large antorbital opening for an ornithischian, however as mentioned previously this is an artefact arising from the loss of surficial bone. The type skull is fortuitously broken at the antorbital fenestra and shows that a relatively thin plate of bone laterally walls the antorbital fossa around the small antorbital opening.

The remaining three character states are not presently determinable, but the single state known gives no reason to doubt that *Muttaburrasaurus* is an ornithopod.

HYPSILOPHODONTIA

Prepubic process rod-shaped; wider transversely than tall dorsoventrally: Absent. The prepubic process in *Muttaburrasaurus* is mediolaterally compressed, taller than wide and not rod-shaped.

The other three character states are not determinable for *Muttaburrasaurus*, but the state here assessed gives no evidence for its being a hypsilophodontian.

IGUANODONTIA

Leaf-shaped denticles: Absent. Although denticles are present on the dentary teeth they are tapered in form, not leaf-shaped (Fig. 8C, D). The maxillary crowns do not (observably) have denticles.

Strong primary ridge on medial surface of dentary crowns: Present (Fig. 8C, D). Strong primary ridges are present on the dentary crowns in the type and 'Dunluce' skulls, and QM F12541.

External opening of the antorbital fossa is relatively small or entirely absent: Present, as mentioned above, in the type skull.

Quadratojugal reduced in size relative to the quadrate: Absent. As may be seen from Fig. 4A (and fig. 2, Bartholomai & Molnar, 1981) the quadratojugal is about as large (in its lateral extent) as the quadrate, maybe larger. It is not reduced relative to the quadrate.

Femur with weak anterior intercondylar groove and deep posterior intercondylar groove: Absent. The femur does indeed have a deep posterior intercondylar groove (Fig. 11A), but the anterior intercondylar groove is deep as well (Fig. 11B).

The other nine character states are not presently determinable, but as only two of the five determined agree with Sereno's states for iguanodon-
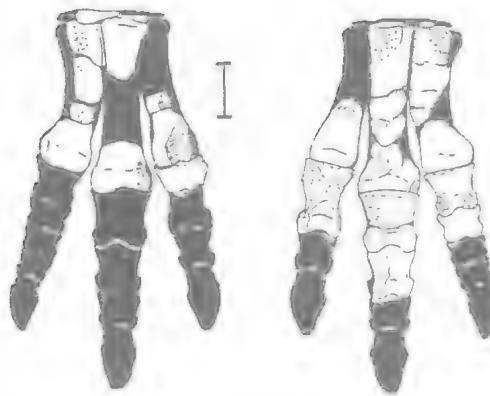
FIG. 10. Pes of *M. langdoni* (QM F6140) in dorsal (right) and plantal (left) views. Scale = 150mm.

tians, *Muttaburrasaurus* is probably not an iguanodontian.

DRYOMORPHA

Maxillary crown narrower anteroposteriorly than the opposing dentary crown: Present. The preservation of maxillary and dentary teeth in juxtaposition in the snout region of the type skull, shows that the maxillary crowns are indeed narrower than the dentary crowns, which overlap in their medial exposure. Overlap is less in the maxillary toothrow (Fig. 8A).

Lateral maxillary primary ridge stronger than the medial dentary primary ridge: Absent. Although there is a primary ridge on the maxillary crowns (not mentioned in Bartholomai & Molnar, 1981), this ridge is placed adjacent to the anterior (mesial) edge of the lateral face of the crown, and is less prominent than the corresponding ridge of the dentary crowns (Fig. 8A, B, E, F vs. C, D).

Diamond-shaped maxillary and dentary crowns; crowns with rounded anterior and posterior corners: Absent. As may be seen from Fig. 8, neither maxillary nor dentary crowns have diamond-shaped lateral faces, although in section they do exhibit rounded anterior and posterior margins (which is what I believe to be meant by 'anterior and posterior corners').

Space separating ventral margin of quadratojugal from jaw articulation: Present, in the type skull (Fig. 4A).

Ischial shaft round in cross section; transversely compressed distally: Absent. Only the proximal portions of both ischia are preserved so the presence of distal compression cannot be verified. However, the proximal parts of the shaft are compressed not round in section.

Two (or two and a half) of the five determinable character states (out of a total of eight) for dryomorphs can be found in *Muttaburrasaurus*. In view of the lack of match with the character states for more basal nodes it seems likely that *Muttaburrasaurus* is not a dryomorph, but the states that can be assessed are equivocal.

ANKYLOPOLLEXIA

Close packing along the toothrow and in the replacement series eliminating spaces between the bases of the crowns of adjacent functional teeth: Absent. The maxillary teeth are closely packed, but present an almost rectangular form in lateral view which eliminates the spaces between the crowns of adjacent functional teeth without leaving any space left over for the replacement crowns (Fig. 8A). No replacement crowns are visible in the maxillary series in either specimen, although only a small part of the series is visible in the 'Dunluce' skull. The dentary toothrows do show replacement crowns filling in the gaps between the bases of adjacent crowns, and have much more the standard appearance of ornithopod toothrows.

Prominent primary ridge on the lateral side of the maxillary crown: Absent. Although, as mentioned above, there are primary ridges on the lateral faces of the maxillary crowns, they are not prominent. And, due to their placement, they are almost impossible to discern in lateral view in the type, and can most easily be made out in cross section where the maxillary teeth have been broken.

Ornamentation of apical margin of individual denticles: Absent, no denticles show any indication of ornament.

Cervical neural spines very weak or absent: Absent. The cervical series has yet to be completely prepared, but the neural spines seem to be well-developed.

Robust, arching cervical postzygapophyses posterior to axis: Present. Such postzygapophyses are present at least in the anterior postaxial cervical series.

Moderate opisthocoely in cervical vertebrae 4-9; slight opisthocoely in dorsal vertebrae 1-2: Absent. The dorsals, having been found disarticulated and rather broken, have so far resisted efforts at determining their position. The anterior cervicals show moderate opisthocoely, but a posterior centrum is only slightly opisthocoelous.

Only one of these character states (or one and a half, being liberal about the first state) of six determinable (out of a total of nine) match those
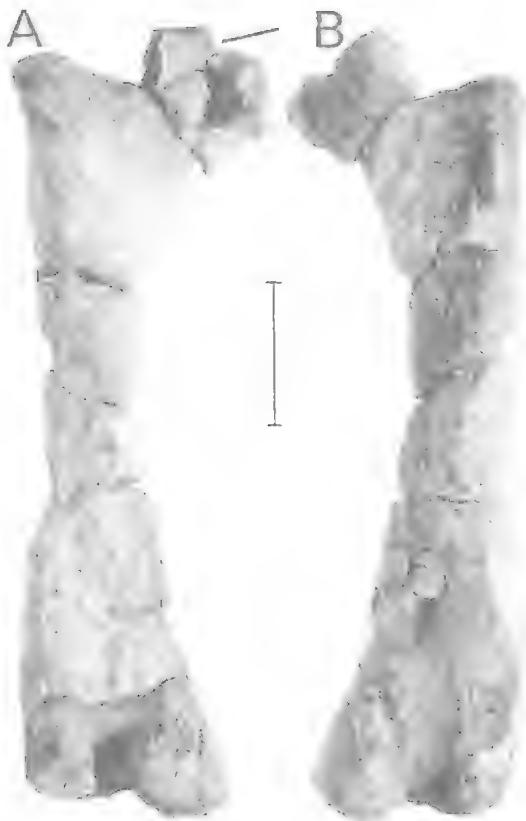
FIG. 11. Left femur of *M. langdoni* (QM F6140) in A, posterior; and B, anterior views. A block of matrix (bar) still adheres to the proximal surface of the neck. Scale = 200mm.

of ankylopellecians, thus *Muttaburrasaurus* seems not to be an ankylopellecian, contrary to the view of Bartholomai & Molnar (1981).

STYRACOSTERNA

At least 25 vertical columns in maxillary and dentary tooth rows: Absent. Eighteen columns are visible in place in the type skull. If the portion of the maxilla anterior to the anteriormost preserved tooth also held teeth there is space to accomodate at most only three additional columns. The back of the maxilla could accommodate one, or at most two, teeth, making the maximum estimate of maxillary columns 23. There are 22 on the right side in the 'Dunluce' skull.

Lanceolate-shaped maxillary crowns: Absent (Fig. 8A, B, E, F).

Strong opisthocoely in cervical vertebrae, beginning with the third cervical: Absent. The cervicals are opisthocoelous, but only weakly.

Humerus with proximally and posteriorly prominent head: Present. The right humerus of the type has a prominent, posteriorly-projected head. *Distal end of prepubic process moderately expanded dorsoventrally:* Present? This was believed to have been present by Bartholomai & Molnar (1981), and cannot presently be re-assessed.

Pubis with distinct, stout iliac peduncle: Absent. The proximal piece of pubis is abraded, but the form and orientation of the acetabular region suggests that a distinct iliac peduncle was not present (Fig. 12).

Femur with deep anterior intercondylar groove: Present, as discussed above (Fig. 11B).

Two or three of the determinable seven character states (out of 12 total) are present, which suggests that *Muttaburrasaurus* is not a styracosternan.

IGUANODONTOIDEA

External nares enlarged: Absent. Although the rostrum is missing from both skulls, the portions of the narial regions preserved give no indication that the nares were enlarged. The 'Dunluce' skull, although crushed in this region, suggests that the nares were slit-like and restricted to the anterior and dorsal faces of the nasal bulla. The type skull is less forthcoming, but shows no evidence contradicting this. In *Iguanodon* and hadrosaurs the naris is noticeably enlarged. There is no indication of similar enlargement in *Muttaburrasaurus*.

At least slight transverse narrowing of cranium from postorbital region, dorsal view: Absent. Molnar (1995) showed this is clearly not the case. *Paroccipital process relatively broader proximally and narrower distally:* Absent. This is also not the case in *Muttaburrasaurus*, with the paroccipital process being broad (dorsoventrally) distally. The distal extremity of the process is missing, but the posterior face of the quadrate is nearly complete. It indicates that the distal end of the paroccipital process was not declined as in *Iguanodon*.

Manual digit V with at least three phalanges: Present. If the manual digits were correctly interpreted by Bartholomai & Molnar (1981), then manual digit V has at least three phalanges.

The one out of four determinable states (from a total of 12) indicates that *Muttaburrasaurus* is not an iguanodontoid.

On the basis of what is known about *Muttaburrasaurus* it cannot be accommodated in any node distal to that of Ornithopoda, and even that is not as secure as might be wished. Presumably it is a genasaur, but may represent a lineage that
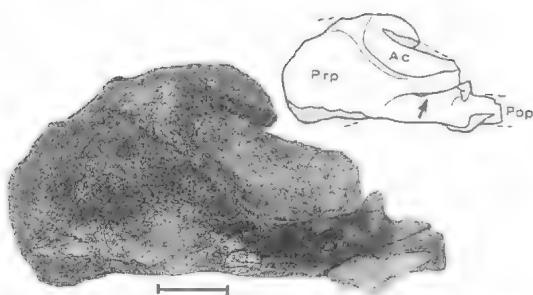
FIG. 12. Left (incomplete) pubis of *M. langdoni* (QM F6140). Arrow indicates pubic notch. Ac= acetabulum, Pop=postpubic process, Prp=prepubic process. Scale = 50mm.

diverged from the iguanodont-hadrosaur line prior to the divergence of *Tenontosaurus*.

PALAEOBIOLOGICAL SPECULATIONS

The type skull and that from 'Dunluce' differ in unexpected ways, specifically in maxillary tooth form and, apparently, the structure of the nasal bulla. There may be other differences, regarding the form of the jugal-maxillary contact (Fig. 7) and absence of replacement crowns in the maxillary series, but the state of preservation and preparation makes these uncertain. Therefore the question naturally arises as to the significance of the differences. This is also linked to the differences of the isolated maxillary teeth from Lightning Ridge. The differences may be interpreted in several fashions, as: stages in evolution; samples of population variation; examples of sexual dimorphism; stages of growth. I see no reason to regard them as pathological variants.

The two skulls may simply represent variant individuals, but if so the differences in the nasal bulla imply considerable variation in this structure. Because of this, skulls discovered in the future would be expected to also vary in structure from those now known. Although admittedly not calculable, the likelihood of finding by chance two extreme variants in bullar, and dental, structure would seem small. The uniformity of maxillary tooth form in the type skull argues against the difference from the 'Dunluce' specimen being due to variation in form along the toothrow. Growth seems an inappropriate explanation for differences between two skulls of almost equal size. It may, nonetheless, be relevant to the teeth from Lightning Ridge, which are smaller than those in the Queensland skulls. However, those teeth also differ in form from those of both skulls.

Changes in tooth form with ontogeny have never been systematically described in ornithischians, despite having good ontogenetic series of ceratopians (Brown & Schlaikjer, 1940; Dodson, 1976) and hadrosaurs (Dodson, 1975). Some of the recently discovered embryonic or hatchling dinosaur material have no teeth suitable for comparison with mature teeth (Carpenter, 1994; Chure et al., 1994) but some do. In the absence of systematic studies, the differences will be summarised here. Jacobs et al. (1994) figure a juvenile ankylosaur tooth that seems not to differ significantly from adult teeth. Since the specimen was not referred to a known taxon appropriate adult teeth for comparison are not available, so this is a tentative conclusion. Carpenter (1982) and Hatcher et al. (1907) reported that teeth of juvenile ceratopians lack the bifurcated root of adult teeth. Horner and Currie (1994) describe and figure teeth of embryonic and neonatal specimens of *Hypacrosaurus stebingeri*. Unless the adult teeth, so far undescribed, are very different from all other adult hadrosaur teeth the neonatal teeth are more plesiomorphic in appearance (Horner & Currie, 1994, figs 21.4A, 21.22, 21.23). The crowns are broader, leaf-shaped, and in the maxillary teeth have a more prominent primary ridge and marginal denticles. Superficially they have more resemble iguanodontian than hadrosaurian teeth. The tooth from Lightning Ridge does not show these kinds of differences from those of the Queensland *Muttaburrasaurus*, which suggests that it is not from a juvenile.

The nasal bulla is a large, prominent, cranial structure. Such structures in hadrosaurs may well have been associated with sexual selection and sexual dimorphism (Molnar, 1977; Dodson, 1975), so this is not unlikely in *Muttaburrasaurus* as well. Even the difference in tooth form may be related. Shine (1989) points out that females, particularly during the reproductive season, may have different nutritional requirements than males. In some ducks, for example, this is reflected in the lamellar form of the bills (Shine, 1989). Although the specific differences in *Muttaburrasaurus* food requirements obviously remain unknown — as does its food in general — this is a possible explanation for the difference in tooth form.

That the differences in form may represent evolutionary changes is suggested by the differences in age of the material. The type specimen derives from the Mackunda Fm. of Late Albian age, the 'Dunluce' specimen from the underlying Allaru Mudstone also Late Albian, and the Lightning Ridge teeth from the Griman Creek

Fm., from the Middle Albian (Exon & Senior, 1976; Burger, 1986). Thus the differences may define a temporal sequence. This notion fits the changes in form of the maxillary teeth, with a progressive reduction in the prominence of the primary ridge and its progressive shift to distal edge of the lateral face. The Lightning Ridge teeth suggest a third trend, toward an increased number of secondary ridges. The presence of two possible replacement teeth in the 'Dunluce' skull and none in the type skull is consistent with a trend toward the replacement of the maxillary toothrow en masse. The adaptive — or otherwise — nature of these changes cannot now be assessed. However, the result of the trends provides an almost unbroken strip of enamel along the maxillary toothrow for the dentary dentition to operate against. (This remains true even if there is some individual replacement of the anterior maxillary teeth.) This strip would presumably be only minimally impaired during the en masse replacement of the maxillary teeth. This is consistent with an adaptive change in the toothrow to give, or improve, a shearing function.

Thus of the five potential explanations for the differences considered here two, pathology and ontogentic development, are rejected. The remaining three, variation, sexual dimorphism and phylogenetic trends, remain viable alternatives. If the evolutionary trends are real — and they are based on only a few specimens — it should be possible to find an ancestral form that is consistent with them. As I (Molnar, 1991, 1992) have argued that the Australian dinosaur fauna was partially isolated from those elsewhere, such a form should be available in Australia. The only other Australian ornithopods are those from Lightning Ridge (New South Wales) described by Molnar & Galton (1986) and those from southern Victoria described by Rich & Rich (1989). A tooth from Lightning Ridge (QM F9505, a cast), mentioned by Molnar (1984), shows no particular resemblance to those of *Muttaburrasaurus*, nor do the maxillary teeth of *Leaellynasaura amicagraphica* (Rich & Rich, 1989, fig. 3A). Those of *Atlascopcosaurus loadsi* (NMV P157390, referred) from the Eumeralla Fm. (deposited near the Aptian-Albian boundary) do show a prominent primary ridge, arising from the base of distal margin of the crown. A literature survey of the teeth of other small or plesiomorphic ornithopods (*Camptosaurus, Dryosaurus, fabrosaurs, Hypsilophodon, Kangnasaurus, Parksosaurus, Tenontosaurus, Thescelosaurus, Yandusaurus, Zephyrosaurus*) shows nothing

matching the maxillary teeth of *Atlascopcosaurus*, althougsome of those of *Yandusaurus hongheensis* (He, 1979) show a primary ridge displaced toward the distal margin.

The maxillary teeth of *Atlascopcosaurus* provide a possible plesiomorphic form of the teeth of the *Muttaburrasaurus* lineage, and a link to the form of teeth in overseas ornithopods, such as *Yandusaurus*. This is consistent with the greater age of *Atlascopcosaurus*, and provides some evidence that the differences do represent evolutionary trends rather than sexual dimorphism or simple variation. Nonetheless the sample size of specimens is so small that these other potential explanations should not be completely ruled out.

CONCLUSIONS

Examination of the holotype (QM F6140) and a second specimen (QM F14921) of *Muttaburrasaurus* indicates that it cannot be referred to the Hypsilophodontia, Iguanodontia, Ankylopollexia or more distal nodes of the iguanodontian lineage as defined by Sereno (1986). It may represent a lineage that diverged from this line before the divergence of *Tenontosaurus*.

Differences in bullar structure and dental form suggest that QM F14921, from the Allaru Mudstone, is slightly more primitive than the type specimen of *Muttaburrasaurus langdoni*, from the younger, Late Albian Mackunda Fm. Variation and sexual dimorphism are deemed possible, but less likely, explanations. This material, together with a tooth from the Griman Creek Fm. at Lightning Ridge, suggests that the teeth in this lineage evolved to progressively reduce the size of the primary ridge on the maxillary teeth, progressively displace it towards the posterior (distal) edge of the lateral face and increase the number of secondary ridges. This provided a continuous, lightly corrugated strip of enamel along the lateral side of the upper dentition. This condition is consistent with the earlier (Bartholomai & Molnar, 1980) suggestion of a shearing dentition in *Muttaburrasaurus*. The maxillary teeth of *Atlascopcosaurus* (NMV P157390) are close to the expected ancestral state of those of *Muttaburrasaurus*.

Kohout and Ms Hatch. Peter Arnold provided welcome assistance during the study. Tom Rich and Laurie Bierne contributed helpful comments and the latter provided Figs 9 and 10. The Lightning Ridge material was discovered by Lars and Bea Tape, and they, together with Ms Elizabeth Smith, arranged for its donation to the Australian Museum. The photos are by Geoff Wright and Bruce Cowell, QM photography section.

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PRELIMINARY REPORT ON A NEW ANKYLOSAUR FROM THE EARLY CRETACEOUS OF QUEENSLAND, AUSTRALIA

RALPH E. MOLNAR

The skeleton of a small ankylosaur, referred to the genus *Minmi* (Molnar 1980), was recovered from the Albian Allaru Mudstone of north-central Queensland. The specimen shows most of the contacts between the cranial bones and preserves most of the dorsal armor in place. Unusual features include an apparently very large inferior process of the premaxilla, thin ventral sheets of the nasals, an apparently rod-like, vertical lachrymal, and a pronounced coronoid process on the mandible. The ilium is joined to two sacrals by a broad 'bridge' of bone. The skeleton is thought to derive from a mature or almost mature individual, and may have been mummified before burial. ☐ *Early Cretaceous, ankylosaur, Australia, taphonomy.*

Ralph E. Molnar, Queensland Museum, P.O. Box 3300, South Brisbane, Queensland, Australia; 15 August 1996.

The most complete dinosaurian specimen yet found in Australia was discovered by Mr Ian Ievers in north-central Queensland in November 1989. While resting on an outcrop of limestone concretions, he noticed fossil bone in them. He then contacted the Queensland Museum and the specimen was collected in January 1990. Mr Ievers subsequently located further blocks, with parts of the neck and shoulder girdle, which he kindly forwarded to the museum.

This specimen represents the most complete dinosaurian material yet found in eastern Gondwanaland (Australia and Antarctica) and one of the most complete Early Cretaceous ankylosaurs. In addition it is one of the few ankylosaurs to clearly show the contacts between the cranial bones and the disposition of the dorsal dermal armor, almost all of which seemingly remains in place.

Because both preparation and study have yet to be completed, this account will necessarily emphasise the features that have been studied, especially the dermal armor and cranial morphology. More cursory comments on postcranial elements are also included. A complete description, together with an analysis of the phylogenetic relationships and description of another recently-discovered thyreophore skeleton (probably conspecific), is contemplated for the near future. Popular discussions of the specimen have been published in Japan (Molnar, 1994) and Australia (Molnar, 1991a, 1991b), and color photos of the reassembled specimen have been published in popular books (Lambert, 1993; Lambert & Bunting, 1995; Tomida & Sato, 1995).

Collection designations. AM, Australian Museum, Sydney; QM, Queensland Museum, Brisbane.

Abbreviations. b, sheet of bone linking scarum and ilia; Bo, basioccipital; D, ossification of dermal armor; Dy, dentary; Eo, exoccipital (paroccipital process); F, frontals; fm, foramen magnum; J, jugal; L, (presumed) lachrymal; lf, left femur; lh, left humerus; li, left ilium; lu, left antebrachium; m, unremoved matrix; Mx, maxilla; N, nasals; n, neural spines; o, orbit; P, parietals; Pf, prefrontal; Pm, premaxilla; Po, postorbital; Pof, postfrontal; Pt, pterygoid; Q, quadrate; Qj, quadratojugal; R, nasal passage; ri, right ilium; S, presumed sinus chamber; s, skull; So, supraorbital; Soc, (presumed) suraoccipital; Sq, squamosal; 'Sq', squamosal, postfrontal & postorbital; sr, sacral ribs; stf, supratemporal fenestra; t, transverse processes.

OCCURRENCE AND STRATIGRAPHY

The specimen (QM F18101) was found on a low ridge in open country south of the Flinders River on Marathon Station, east of Richmond, north-central Queensland. The bones were partially enclosed in silty buff-grey micrite concretions. These concretions derive from weathering of the Albian Allaru Mudstone, which consists of mudstones and siltstones, often calcareous, deposited in the inland sea.

The carbonate was deposited immediately around the skeleton, with no large masses free from bone. This suggests that the nodule may originally (prior to its weathering in the soil) have roughly preserved the body outline of the carcass.
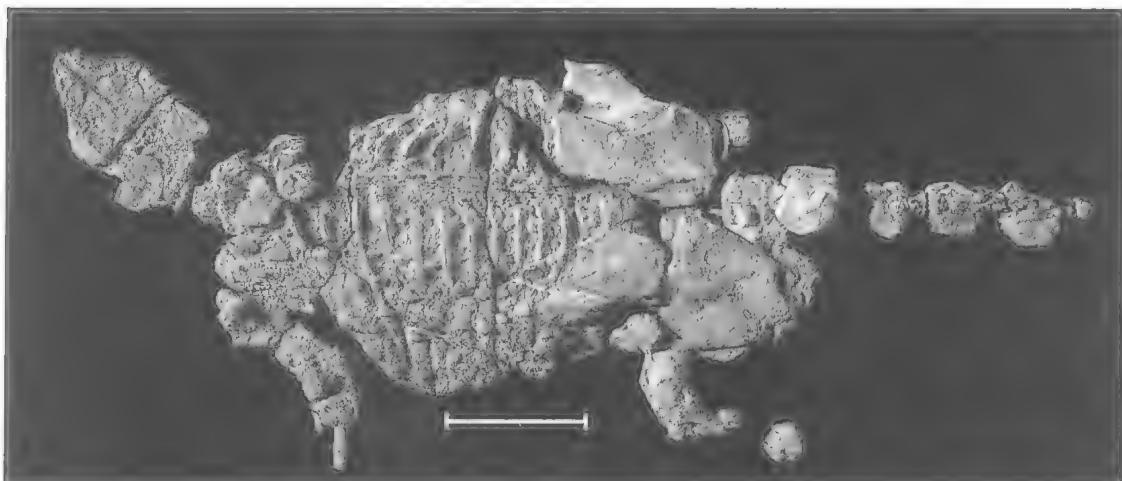
FIG. 1. Reassembled skeleton of the ankylosaur, *Minmi* sp. (QM F18101), from north-central Queensland. This photo was taken prior to beginning preparation. Scale = 250mm.

The ribs, dorsal armor and tips of the neural spines were exposed on the lower surfaces of the blocks almost as though artificially prepared, but the ilia were almost completely covered by carbonate. The remaining elements, especially the distal limb pieces, were found either in small blocks of carbonate or as isolated bones in the soil.

The skeleton was intimately associated with abundant plates of *Inoceramus* shell, a few *Echinorhinus* teeth and part of one small, incomplete — and unfortunately indeterminate — ammonite. The Allaru on 'Marathon' has also yielded large teleosts, ichthyosaurs (Etheridge, 1888) and a nearly complete small sauropterygian, as well as marine invertebrates, but no other terrestrial forms. Nonmarine tetrapods from the Allaru elsewhere in central Queensland include *Muttaburrasaurus* sp. (Molnar, this volume) and a pterosaur. Six other specimens represent armored dinosaurs, probably ankylosaurs, all but one of which are fragmentary: they will not be described here.

IDENTIFICATION

Only a single armored dinosaur, *Minmi paravertebra* (Molnar, 1980), is known from Austrtalia. This specimen matches the holotype *M. paravertebra* in the possession of paravertebrae, ossified aponeuroses and tendons along the dorsal vertebral column. However the type of *M. paravertebra* derives from the Aptian Bungil Fm. whereas this specimen is from the Albian. Since study of the new material is not yet com-

plete, and there may be differences of form in the ribs, the question of its specific allocation remains open. Furthermore the type material was too incomplete for a phylogenetic analysis, although the possession of paravertebrae is an autapomorphy for the genus (cf. Molnar, 1980). Hence the 'Marathon' specimen is herein designated *Minmi* sp. Pending the planned phylogenetic analysis the genus *Minmi* is presumed to belong to the Ankylosauria, but is not allocated to a family.

Only five Cretaceous thyreophores are known from the southern hemisphere outside Australia (cf. Molnar & Frey, 1987). Ankylosaurian material has recently been described from Upper Cretaceous beds in Antarctica (Gasparini et al., 1987; Olivero et al., 1991; Gasparini et al., this volume), New Zealand (Molnar & Wiffen, 1994), Argentina (Salgado & Coria, in press) and India (Chatterjee & Rudra, this volume). A stegosaur, *Dravidosaurus blanfordi*, has been reported from the Coniacian of India (Yadagiri & Ayyasami, 1979), the only stegosaur described from the Late Cretaceous. All of these are represented by substantially less complete specimens than that from 'Marathon'. Isolated ankylosaur elements have also been found in the Lower Cretaceous sediments of Victoria (Rich & V.- Rich, 1994).

DISPOSITION OF SKELETON

Since this is only a preliminary description of the skeleton, the completeness and condition of the specimen when collected are presented here separately from the description. The specimen
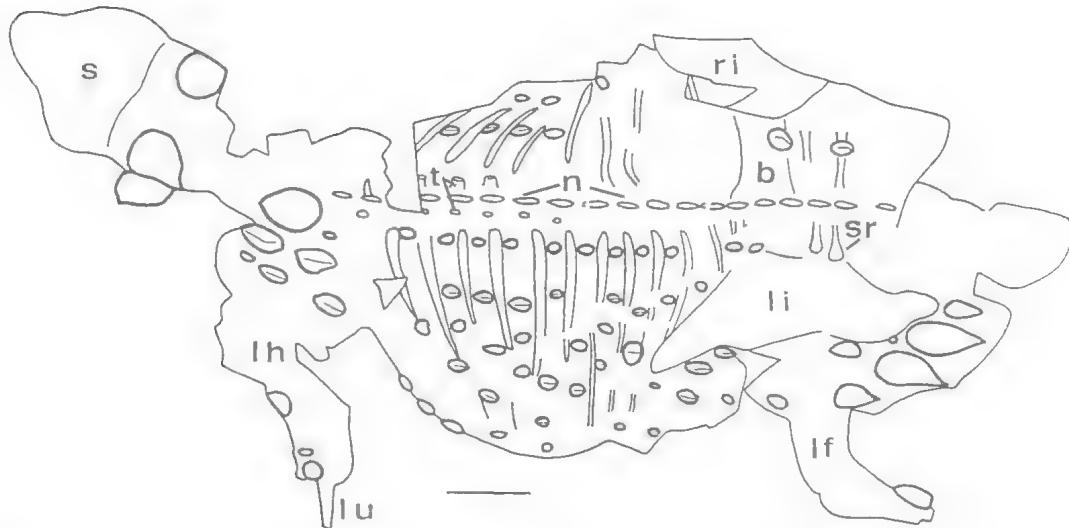
FIG. 2. The pattern of dorsal armor of *Minmi* sp. (QM F18101). Elements of the armor are shown in heavy outline, and endoskeletal elements (skull roof, tips of neural spines & transverse processes, dorsal & sacral ribs and ilia) are in light outline. Scale = 100mm.

includes most of the skull and the articulated axial skeleton back to the proximal tail, to probably the ninth caudal (Figs 1, 2). The arches of some vertebrae have been crushed. The neural arch of the axis was found isolated in the soil about a metre away from the block enclosing the skull and anterior cervicals. The more distal part of the tail was not found and the distal parts of both left limbs are also missing. The left shoulder girdle seems complete. The coracoids are not fused to the scapulae, and were displaced. The left humerus is almost complete and the proximal parts of both left radius and ulna are present. The left ilium is nearly complete, and the proximal halves of both ischium and pubis are also present on that side. Much of the right pelvis, however, has been lost. Both femora are essentially complete, but weathered, as are the crural elements. Only a few disarticulated manual and pedal elements were found, although the right manus may be embedded beneath the rib cage.

The specimen was upside down when excavated, except perhaps for the block containing the skull which had been uncovered before our arrival. The neural canal of one vertebra (enclosed in a small block of carbonate) contains sediment (with embedded dermal ossicles) at the top and white calcite crystals below clearly indicating the inverted position of the trunk in the ground.

When reassembled, the vertebral column is straight, except for the cervical column near the skull which inclines to the right at about 20° (Fig. 1). The base of the tail extends straight out posteriorly from the trunk and the pieces of the more distal part of the tail fit together to also give a straight column. The ribs on the left side have been flattened and so have lost their natural curvature, but the ribs on the right — except for those just in front of the pelvis — have been rotated backwards. The right ilium has apparently become separated from the sacrum and displaced forward and laterally. Both left fore and hind limbs extend laterally horizontally from the trunk, but both right limbs are folded across the belly. Both forelimbs are flexed at the elbow and both hindlimbs at the knee. The left femur is in situ in the acetabulum but projects horizontally, parallel to the top of the ilium. The trunk gives the impression of having collapsed to lay flat on the substrate.

MATURITY

Recently there has been much emphasis (e.g., Rowe & Gauthier, 1990) on using adult characters (in the sense of skeletal maturity) in phylogenetic classification and the unusual features of this specimen raise the question of whether or not it was mature, or nearly so. This skeleton was probably 2.5-3.5m long when com-

plete. This is a small ankylosaur (cf. Coombs & Maryanska, 1990): does it represent a small adult or an immature individual? All known early ankylosaurs (*Dracopelta, Priodontognathus, Sarcolestes* and *Tianchiasaurus*) are small, as are later, insular ankylosaurs such as *Struthiosaurus*. *Minmi* is a relatively early ankylosaur and, in addition, may have evolved on the east Queensland island of the Aptian (Dettmann et al., 1992). The holotype specimen of *Minmi paravertebra* was found in Aptian marine sediments (Bungil Fm.) near this island (Molnar, 1980) and probably derived from there (Fig. 3). If the lineage evolved there a small adult body size is plausible. Late Cretaceous European insular ankylosaurs (*Struthiosaurus*) are of about the same size as the holotype and the 'Marathon' animal, and notably smaller than those from western North America and central Asia.

Some features — absence of fusion of the cranial elements, absence of fusion of the scapulae and coracoids, absence of fusion of the pelvic elements — in addition to its small size, suggest that it was immature at death. But there are also reasons to suggest that was mature or nearly so. There are five other specimens from Queensland certainly or plausibly referred to the genus *Minmi*: QM F33565 and F33566 (probably deriving from a single individual and so considered here), AM F35259, QM F33286, QM F10329 (the holotype) and an unregistered specimen that will probably be housed at the Australian Museum. All of these, except the first which is also the most different morphologically and hence possibly represents a distinct taxon, are within 10% of the linear dimensions of the 'Marathon' skeleton. Ignoring the first specimen would suggest that all known specimens of Queensland ankylosaurs are mature but small, but including it indicates that five of six are immature, if the 'Marathon' skeleton is from an immature individual. It seems prima facie unlikely that of six specimens that were, judging from their geographical distribution, probably drawn from different populations, all but one would represent immature individuals at the same stage of growth. Nonetheless this is not impossible, especially as Horner (1979) pointed out that most occurrences of dinosaurs in marine beds are of immature individuals.

Although the junctions between the cranial bones generally are not fused both frontals and parietals are fused along the midline, and the contacts in braincase are fused. Fusion of the cranial elements is thought to be a marker of
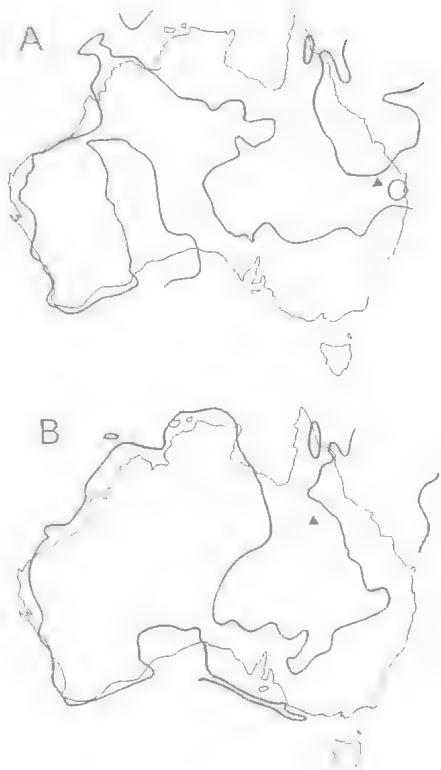
FIG. 3. Shorelines of Australia during the ages when *Minmi* lived, A, Aptian, B, Albian. Heavy lines mark contemporaneous shorelines, light lines modern shorelines. The triangles indicate the localities of *Minmi paravertebra* (A) and *Minmi* sp. (B). Both specimens probably drifted from the eastern Queensland landmass, which in the Aptian was a set of islands and in the Albian a peninsula. (Redrawn from Dettmann et al., 1992)

adulthood in ankylosaurs (Coombs & Maryanska, 1990), but lack of fusion is also the plesiomorphic state and cranial fusion may have developed only in later ankylosaurs. The maxilla of *Priodontognathus*, probably early Late Jurassic in age, shows no indication of having been fused to the other cranial bones (Galton, 1980). In the 'Marathon' specimen the coracoids are not fused to the scapulae. This lack of fusion is not considered a juvenile character by Coombs & Maryanska (1990) and some ankylosaurs lack fused scapulocoracoids as adults (Carpenter, 1990; Pereda-S., 1994).

Currie (pers. comm., 1991) observed that clearly juvenile *Pinacosaurus* have only ossicles making up the armor of the trunk. In the 'Marathon' *Minmi* the trunk armor comprises
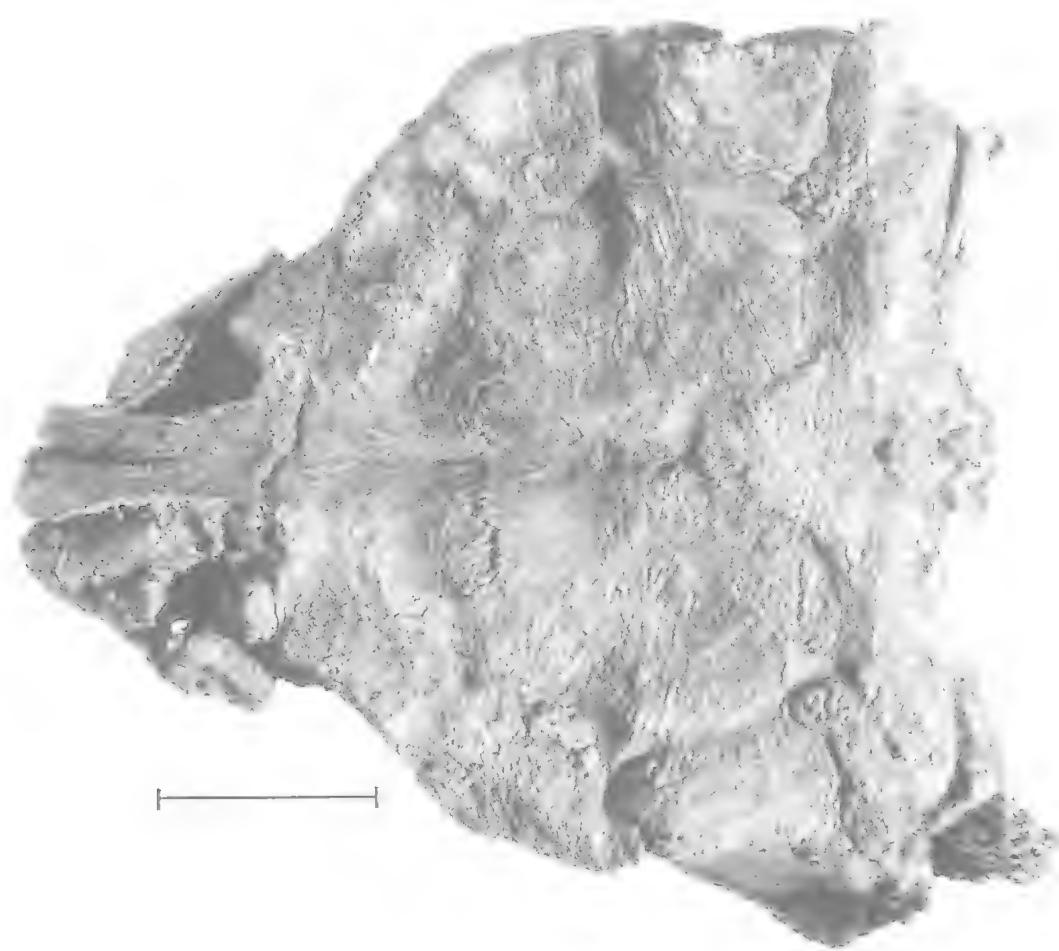
FIG. 4. Skull, in dorsal view, of *Minmi* sp. (QM F18101). Anterior is to the left. Elements of the dermal armor remain in the narial region and behind the quadrate. Scale = 50mm.

both ossicles and scutes, suggesting it was adult, or nearly so.

Thus although there are some grounds (contra Molnar, 1994) to think this specimen is a juvenile, these are not entirely compelling and it may simply be plesiomorphic. Tentatively the 'Marathon' specimen is best regarded as representing an almost mature, or newly mature, individual.

DISPOSITION OF ARMOR

Armor is present across the dorsum of the neck and trunk, as well as on the tail and limbs (Fig. 2). Several kinds of dermal elements are present: large nuchal, scapular, pelvic, appendicular and caudal scutes; small dorsal scutes; ossicles; and (probably) triangular caudal plates.

The broadly oval nuchal scutes are larger (to 13cm wide x 9cm long) than any of the dorsal scutes, and comparable in size to the pelvic scutes and caudal plates. Four (three of which are preserved) form an incomplete transverse band just behind the skull. The pair on either side are in contact (preserved on the left), but the medial of each pair are separated by a gap of 5.5cm. Behind this is a suite of one large (9.5 x 75cm) three medium (c. 5.5 x 3cm) and two small scutes (c. 2 x 1.5cm) arranged with the large one medially placed and the others spread laterally over the shoulder region. These shoulder scutes, like those of the back, are roughly oval with a low longitudinal keel and aligned parasagittally. They are preserved only on the left side.

The smaller scutes of the back are arranged linearly, at least towards the midline. A row of at
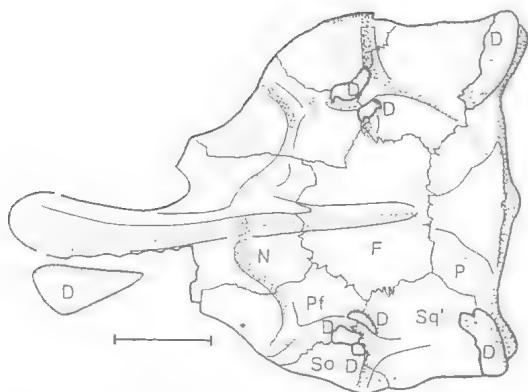
FIG. 5. Skull, in dorsal view, of *Minmi* sp. (QM F18101). Anterior is to the left. Occipital face not shown. The element on the left side of the nasals is a large piece of dermal armor placed in what is thought to be its proper position. Abbreviations given in text. Scale = 50mm.

least ten lay to either side of the vertebral column, extending from the base of the neck at least to the pelvic region. Further laterally, the arrangement is more haphazard, although this may arise from post-mortem disturbance. In all cases the scutes are placed between the ribs. The arrangement at the shoulder may be an extension of that of the back, but this is not clear. Unlike the shoulder scutes, on the back the lateral scutes are slightly larger than the medial.

Along the lateral side of the left ilium is a row of three large flat plates (to 10.5 x 7cm). Basically oval in form, they come to a sharp point posteriorly, and so look like tear-drops. Three of these are preserved, arranged sequentially along the posterior portion of the lateral margin of the ilium and curving around behind it. All except the last are displaced from the ilium, with but a few

medium or small scutes in the intervening region. Unfortunately, because this part of the specimen is almost completely flattened it is not clear whether these plates lay flush with the skin, or if the posterior points projected outwards above the hind limb.

The neck, back and limbs were probably completely covered by small ossicles embedded in the skin. Layers of ossicles are also found ventral to the vertebrae and ribs, in what was the body cavity. This suggests that like the holotype of *M. paravertebra*, the belly was also covered by a chain-mail of these ossicles. Some of the scutes, particularly those of the shoulder region, have the appearance of having been formed from — or at least augmented by — the accretion of ossicles.

The ossicles are rectangular to trapezoidal in outline and seem have two forms. One is convex with faint concentric ridges or striae, and the other an almost stellate form of sharp interconnecting ridges surrounding distinct pockets. Examination of ossicles freed during preparation, however suggests that there is only a single form. Presumably the 'stellate' face was directed externally and the convex, pillow-like face internally. The appearance of both forms in the armor preserved in place suggests that some have become inverted without having been displaced. Unbroken ossicles measure about 4 x 6mm.

The tail bore at least two kinds of armor. A row of two or three large, smooth triangular plates are preserved along one side of the tail. Their orientation is unclear. As preserved, they project ventrolaterally, but all are broken at their bases, as if they had been forced downwards into this position during preservation. In addition, there are keeled, pitted, roughly rectangular scutes, each slightly less than half as long as the triangular plates. Again their arrangement is not
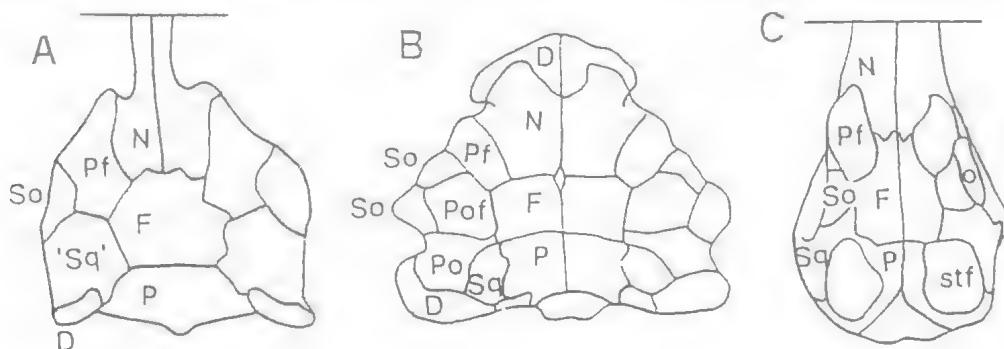

FIG. 6. Pattern of cranial elements in dorsal view for A, *Minmi* sp. B, *Pinacosaurus grangeri*; and C, *Scelidosaurus harrisonii*. Not to scale (*Pinacosaurus* after Maryanska (1977), *Scelidosaurus* after Coombs, et al. (1990)).
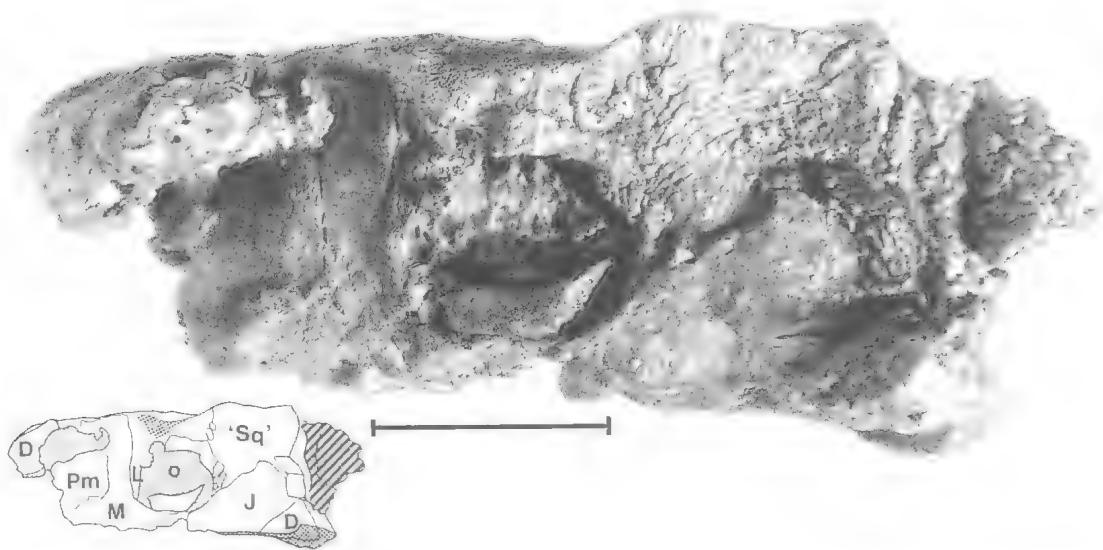
FIG. 7. Skull, in lateral view, of *Minmi* sp. (QM F18101). Anterior is the left. Part of the integumentary dermal armor remains intact behind the skull at right. Inset shows matrix (open dots), broken bone (dots) and still adherent nuchal ossicles (hatching). Scale = 50mm.

known, as all seem to be out of place, some having come to rest inserted between the bases of the large plates and the caudal vertebrae. They may have formed a row along the bottom of the tail, two to every triangular plate.

The appendicular armor is not as completely preserved, however both sets of limbs carried large scutes, as well as small ossicles. The forelimb had a subrounded, keeled scute midway along the humerus and a low, round, pitted scute at the lateral side of the elbow, along the ulna. The hind limb bore a large keeled scute along the back of the calf.

CRANIAL MORPHOLOGY

Although the form of the ankylosaurian skull as a whole is well known, the form of the individual cranial bones is not. Only a single skull (of *Pinacosaurus*) is known showing the contacts between the cranial bones, and those only for the skull roof (Maryanska, 1977). For the rest of the taxa only an isolated maxilla has been described in Galton's (1980) study of *Priodontognathus*. The 'Marathon' specimen, however, shows all of these contacts, except in the braincase where they are fused.

The skull looks like a pentagonal box, because all of the sides (and occipital face) meet the skull roof at approximately right angles. It is slightly longer (240mm as preserved) than wide (195mm). The skull roof is almost flat, but the nasals arch slightly (c. 3mm) above the level of the skull roof. Unfortunately, the skull has been broken and slightly crushed in places, fortunately, little seems to be missing and the crushing has not done much damage.
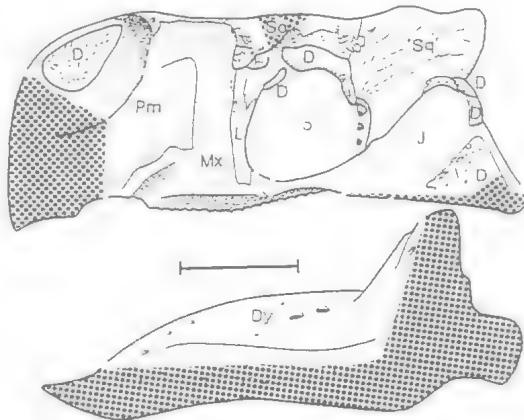
FIG. 8. Reconstruction of skull and left mandible, in lateral view, of *Minmi* sp. (QM F18101). Anterior is to the left. Hatching represents missing parts or broken surfaces. Abbeviations given in text. Scale = 50mm.
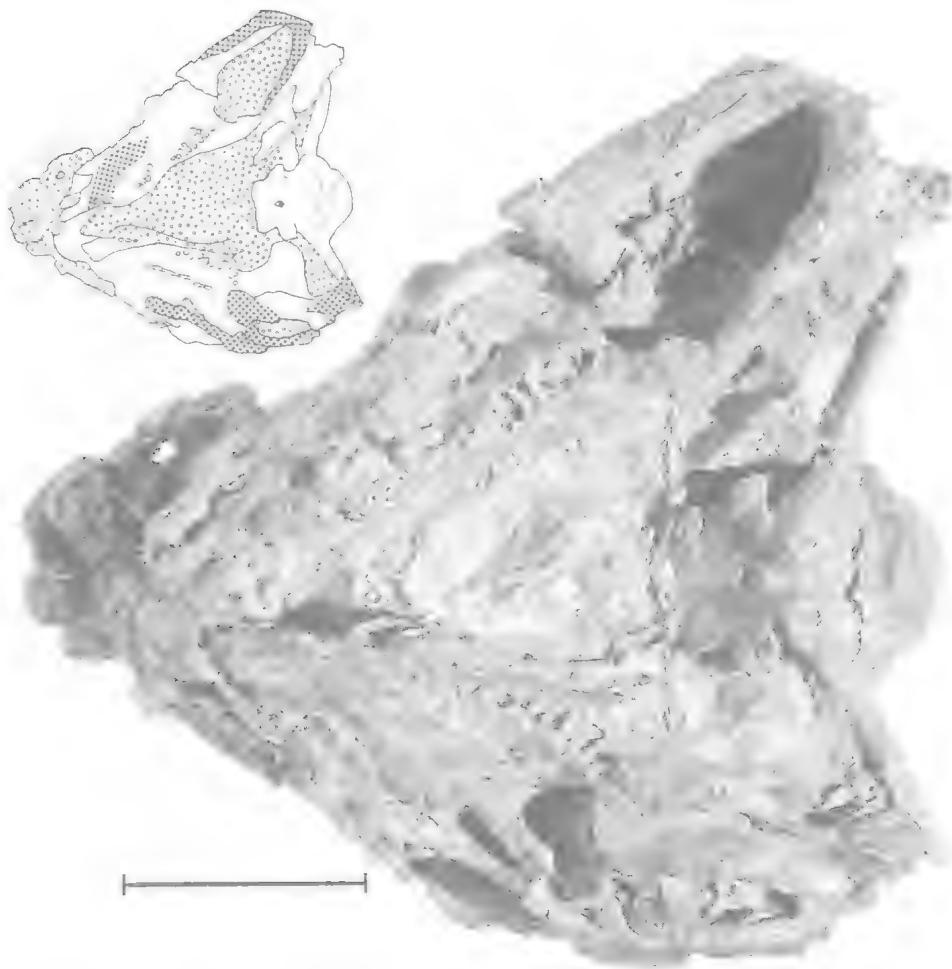
FIG. 9. Skull, in ventral view, of *Minmi* sp. (QM F18101). Anterior is to the left. Inset shows areas still covered by matrix (open dots) and broken bone surfaces (dots). Scale = 50mm.

On the top of the skull both the grooves presumably demarcating the boundaries of the dermal plates and the sutures are clearly preserved (Figs 4, 5). There are also a few dermal ossicles. The skull roof elements are fewer and simpler than in *Pinacosaurus*, basically similar in pattern to those of *Scelidosaurus* (Coombs, Weishampel & Witmer, 1990, fig. 20.1) (Fig. 6). The nasals, prefrontals, frontals, parietals and 'squamosals' and supraorbitals contribute to the dorsal face. The supratemporal fenestrae are entirely obscured by the 'squamosals', parietals and maybe the frontals.

The side of the skull is made up by the premaxilla, maxilla, lachrymal, a little of the supraorbital, and the 'squamosal' and jugal (Figs 7, 8). The orbit is large, laterally directed, and roughly hexagonal in shape. Just in front of it, the sides of the skull converge towards the narial region, forming the abbreviate snout. In the nodosaurid *Edmontonia* the snout (from tip of premaxilla to center of the orbit) comprises about 70% of the total cranial length, but in the ankylosaurid *Euoplocephalus*, and the 'Marathon' skull (as preserved), it is about 60%. The antorbital fenestra has been closed, possibly by a backwards extension of the maxilla. Nor is there any laterotemporal fenestra, which was seemingly covered by the jugal and, maybe, the 'squamosal'. The palate is still largely unprepared, but there is so far no indication of the median vomerine septum, and if it were present
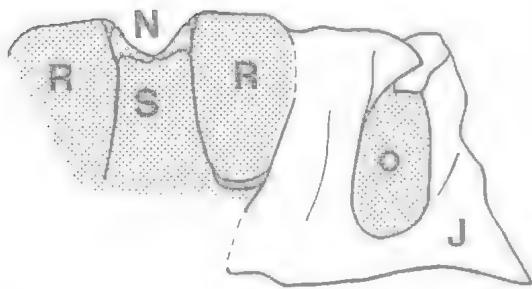
FIG. 10. Diagram of skull, in anterior view, of *Minmi* sp. (QM F18101) showing the the ventral sheets of the nasals. Abbreviations given in text.

and in place, it would expected to have been exposed by now.

A transverse fracture, most obvious on the palatal surface (Fig. 9), crosses the skull through the front of the subtemporal fenestrae. On the left the back of the maxilla and the overlying anterior process of the jugal, have been displaced into the orbital cavity: on the right the subtemporal fenestra seems undamaged, but is occupied by a piece of bone, perhaps part of the coronoid process. Both pterygoids have been broken from their contacts with the basipterygoid processes and displaced dorsally, more so on the left side. The postorbital region on the left may have been slightly crushed and the right maxilla has been broken and pushed into the palatal vacuity. The left maxillary teeth have all either fallen from their sockets, or been snapped off at the neck, so that a few (four) crowns lie adjacent and lateral to their respective alveoli. The snout is incomplete, but the inferior processes of the premaxillae still associated with the maxillae, suggest that only a little is actually missing, and this is corroborated by the left mandible which is too short to have fitted a much longer skull.

Premaxilla. The premaxilla is represented by a large, smooth plate forming at least 50% of the length of the snout (Fig. 8). This plate seems to be a greatly expanded inferior process of the premaxilla. It overlaps the vertical plate of the maxilla behind, and seemingly rests in a groove in the dorsal margin of the anterior part of the body of the maxilla. The plate is basically flat, but is slightly convex posteriorly and slightly concave dorsally. Its oblique anterodorsal edge presumably forms the posterior margin of the external naris.

Maxilla. The maxilla is a low, broad, elongate element, that forms the ventral margin of the snout and underlies the orbital cavity (Fig. 8). The

body is massive and broad anteriorly becoming thinner but broader posteriorly. A vertical plate rises behind and adjacent to the inferior process of the premaxilla. This plate ascends to the dorsal face of the skull to contact the prefrontal above. In palatal view, the maxillary toothrow is curved, slightly concave laterally. At least 21 alveoli are present, increasing in size posteriorly. The posterior alveoli are transversely broad, but constricted centrally to look like the figure '8'. The medial lobe of the alveolus was (and still is in some) occupied by the root of the replacement tooth, almost as large as that of the functional tooth.

Nasal. The nasals are elongate elements, longitudinally arched (and incomplete) anteriorly but concave transversely, forming a central longitudinal groove. Posteriorly they expand markedly in the transverse plane, giving them a roughly 'T' shape in dorsal view. They meet the frontals in an almost transverse very slightly interdigitating contact, and laterally they are smoothly overlapped by the prefrontals. The anterior moiety medially and posteriorly bounds the external nares. Medial to the nares thin sheets of bone project ventrally at least 35mm from the margins of the nasals, giving the bone an M-shaped form in section (Fig. 10). It is not known how, or if, the passage situated between these sheets contacted the laterally placed chambers.

Prefrontal. The prefrontals are elongate elements, extending anteriorly from the posterior sutural contacts with the frontal and 'squamosal' to the edge of the skull in front of the orbits (Fig. 5). Each joins the supraorbital posterolaterally in a suture, and the vertical plate of the maxilla in front of that in a smooth contact. They are exposed only on the dorsum of the skull.

Lachrymal. The anterior margin of the orbit is composed of a set of unfamiliar, rodlike elements (Fig. 8). The presumed lachrymal is a vertical rodlike element, that extends along this margin. It gradually tapers ventrally, to abut on the maxilla. In addition there are two other rod-like elements, or processes, extending ventrally along the front edge of the orbit, one in anterior to and the other behind the presumed lachrymal. The anterior may be a descending process of the prefrontal or supraorbital, but the possible junction is obscured.

Supraorbital. The subtriangular supraorbital roofs the orbital cavity between the prefrontals and 'squamosals' (Fig. 5). Beneath it posteriorly (on the right side) is an elongate lightly ornamented element (Fig. 8), that appears to be part
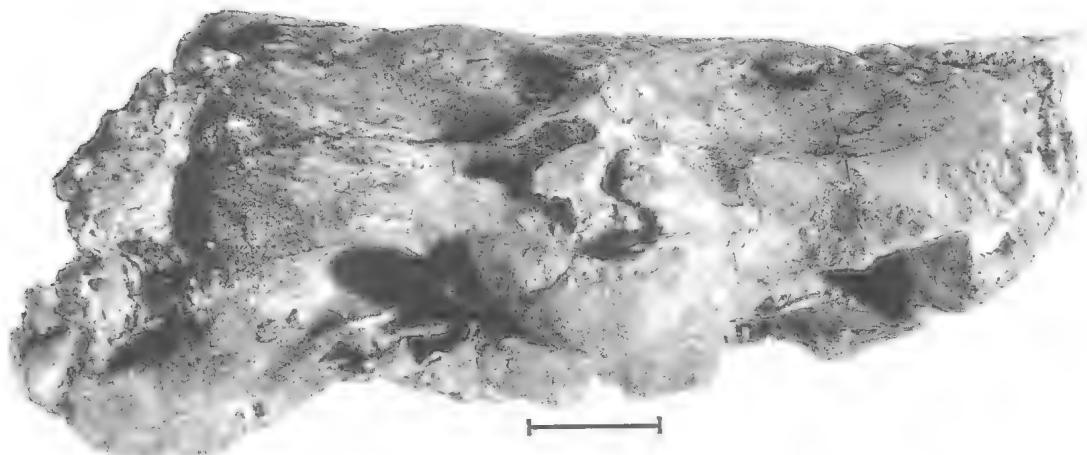
FIG. 11. Skull, in posterior view, of *Minmi* sp. (QM F18101). The upper part of the foramen magnum is occluded, especially on the left, by matrix containing parts of the atlas-axis complex. Also on the left is part of the integumentary dermal armor of the neck, just lateral to the distal end of the left paroccipital process. Scale = 25mm.

of the dermal armor, or perhaps a second supra-orbital.

Frontal. The frontals are fused and basically hexagonal in form, joining the nasals anteriorly, the parietals posteriorly, the prefrontals antero-laterally, and the 'squamosals' posterolaterally (Fig. 5). The dorsal sulcus of the nasals continues posteriorly across the frontals to terminate just anterior to the parietal contact.

Jugal. Behind the maxilla and posteroventral to the orbit is the large, flat, smooth, triangular jugal (Fig. 8). It has the form of two plates, the vertical triangular one behind forming the side of the cheek region of the skull, and a horizontal one in front that floors the orbital cavity. It overlaps the quadratojugal posteriorly — which is thereby obscured from lateral view — and in turn is overlapped by a small, triangular dermal element at its posteroventral extremity.

Squamosal, Postfrontal and Postorbital. The bone here called the 'squamosal' is probably the fused squamosal, postfrontal and postorbital. It is a hexagonal bone, situated at the posterolateral corner of the skull, that forms the upper part of the cheek region (Figs 5, 8). It is overlapped by the jugal below, and sutures to the supraorbital in front and the frontal medially. Unlike the smooth jugal, its lateral face is ornamented by subparallel curved grooves directed posterodorsally, becoming horizontal posteriorly.

Quadratojugal. The quadratojugal is medial to the posterior part of the jugal and lateral to the lower part of the quadrate. It contributed little if anything to the lateral side of the skull, but is visible along the ventral margin of the jugal arch. In posterior aspect it is revealed as a thin element rising vertically probably to contact the 'squamosal'. A large foramen separates it from the quadrate just above their ventral contact.

Pterygoid. Only the broad, thin horizontal quadrate processes of the pterygoids are so far revealed (Fig. 9). They project laterally from the basisphenoid region where the junctions are broken, to elongate contacts with the quadrates.

Quadrate. Both quadrates are present, but that on the right is obscured. The articular condyles are missing from both. The left is broken at midshaft, but not displaced. The quadrate seems to form a vertical pillar. The lateral inclination of almost 45° of the ventral portion is due to the crushing of the back part of the skull on the left side. The strong, medial vertical plate-like process projects anteromedially, to reach the pterygoids.
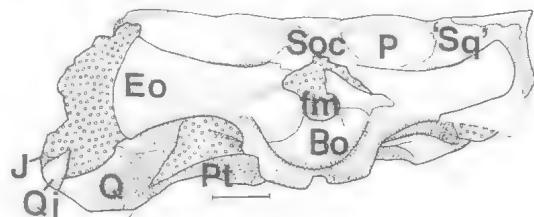

FIG. 12. Skull in posterior view. Abbreviations given in text. Open dots indicates matrix. Scale = 25mm.
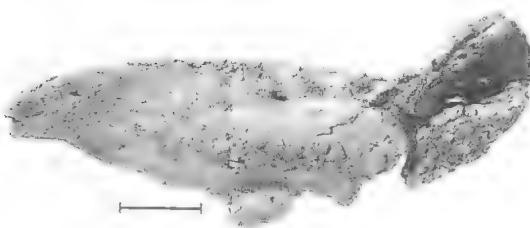
FIG. 13. Mandible (dentary), in lateral view, of *Minmi* sp. (QM F18101). Anterior is to the left. Only the dorsal margin of the body and anterodorsal margin of the coronoid process are preserved, the rest of the edges are breaks. Scale = 25mm.

Parietal. The parietals are transversely elongate elements, fused at the midline, and located along the posterior margin of the skull (Figs 5, 12). Their posterior face seems to extend ventrally for 3cm to contact the paroccipital processes, and overlap the occipital faces of the 'squamosals'.

Exoccipital. The paroccipital processes extend directly laterally and flare at their distal ends, to make up the ventral half of the occipital face of the skull (Fig. 12). From each side a stout pedicle projects ventromedially and a little posteriorly to abut on the basioccipal below the foramen magnum. These exoccipital processes and the basioccipital each contribute about 1/3 to the ventral margin of the foramen magnum.

Supraoccipital. A large supraoccipital in the form of a capital lambda, or inverted 'V', may be present above the foramen magnum (Fig. 12) but further cleaning is necessary to confirm this.

Basioccipital. The occipital condyle, on the basioccipital, sits at the end of a stout, tapering 'neck' that is broader than the condyle itself. In posterior aspect the condyle is reniform and it is directed posteriorly (Fig. 12), rather than posteroventrally.

Basisphenoid. Only the ventral surface of the basisphenoid is yet exposed. Between the basipterygoid processes the ventral face of the basisphenoid is nearly flat, with a small median foramen or depression (Fig. 9). Posteriorly the basisphenoid tubera lie close together near the midline. There is no excavation between and behind them as in certain taxa (*Struthiosaurus*, Pereda-S. & Galton, 1994), but only a smooth surface, facing almost directly backwards, extending to the base of the neck of the occipital condyle. The basioccipital-basisphenoid junction is fused.

Cranial dermal armor. On each side of the skull, roof, three small dermal ossicles sit at the 'apex' of the supraorbital-prefrontal-'squamosal' con-

tact, and a large one sits just lateral to them (Fig. 5). An elongate ossicle sits atop the posterior rim of each 'squamosal'. Dermal ossicles are also found at several places on the sides of the skull, along the posterior margin to the jugal, and the postreior margin of the orbit. A large, elongate ossicle just below the lateral margin of supraorbital, forms the dorsal margin of the orbit. A smaller, triangular ossicle overlies the junction of the lachrymal with the supraorbital. These two may be the second and third supraorbitals, characteristic of thyreophores (Sereno, 1986), although if so they differ from those of the others in that neither is exposed on the top of the skull. A thin, flat, triangular ossicle overlying the posteroventral 'corner' of the jugal (and quadratojugal) is presumably the quadratojugal plate, also found in ankylosaurids.

Dentary. The left mandible is very incomplete as everything medial to the lateral sides of the alveoli has been lost. Only the dentary remains (Fig. 13). But much of its length is preserved, from the down-curved anterior region to well back into the coronoid process. This strong coronoid process arises abruptly lateral to the back of the toothrow, and is clearly more exten-

FIG. 14. Three teeth of *Minmi* sp. (QM 18101) as preserved after having fallen from their alveoli. A partially prepared tooth is at the left, two completely prepared teeth at center, and a block of matrix and consolidant at right. Scale = 5mm.

sive than in any other described thyreophore. The distance from the declined anterior part of the toothrow near the front end of the mandible to the coronoid suggests that the mandible was relatively short.
Teeth. Two sets of isolated teeth are available, one a crown from the anterior part of the skull (presumably the anterior maxilla), and the other a set of three adherent teeth (Fig. 14) from the mid-maxillary (or dentary?) region. The anterior crown has a cingulum 2-3mm deep, with the fluted part of the crown 2-3mm high. The cingulum is broad and bulbous, 3mm wide, and the crown above it only 1mm wide. Seven denticles, and the furrows between them, are present on one side of the crown, whilst the other is almost smooth, with only the lateralmost furrows present. The mid-maxillary teeth are 18-26mm long. The roots are straight and cylindrical, constricted at the neck and open, although perhaps broken, at the tip. The best crown is 7mm high, including a 3mm cingulum. One crown has seven denticles and the remaining two have nine. The enamel is covered with very fine protuberances, giving a finely pebbled appearance under a magnifier. The crowns are 6mm long and 3mm broad at their cingula and 2mm broad just above the cingula. The upper margin of the cingulum is distinct on both faces. Furrows extend all the way from edge to cingulum, unlike the anterior tooth, where they extend only a short distance from the denticles.

FIG. 15. A, Left humerus, in anterior view, of *Minmi* sp. (QM F18101). Some ossicles adhere to it distally, and the matrix visible along both medial and lateral margins holds a sheet of ossicles in place on its reverse (cf. Fig. 1). B, Proximal segments of left radius and ulna of *Minmi* sp. (QM F18101) in medial view. The block of matrix joining both bones proximally holds dermal armor in place on its reverse (cf. Fig. 1). Scale = 50mm.

VERTEBRAE

So far only the sacrals and middle caudals have been prepared. The sacrals are partially obscured by ossicles that presumably fell onto them from the ventral body wall, so little can be said of them. However it is clear that although the last centrum of the presacral rod was ventrally flattened the synsacral centra lack a ventral sulcus, at least posteriorly.

The more distal of these have a centrum that is hexagonal in section, with a ventral sulcus. The most distal preserved have a broad, flat dorsal surface, with the neural arch restricted to the middle third. Proximally the centra remain hexagonal, but become deeper, and then become quadrangular in section. The ventral sulcus becomes progressively shallower anteriorly, until the ventral face is simply flat. The caudals are slightly amphicoelous.

Although the prezygapophyses are relatively long, they are not as elongate as in ankylosaurids. There is no indication of a tail club, or that the distal part of the tail was modified into a rigid rod. All parts of the tail preserved suggest that some flexibility was possible.

Several series of ossified tendons extend along the tail, mostly above the transverse processes. So they probably were part of the epaxial muscula-
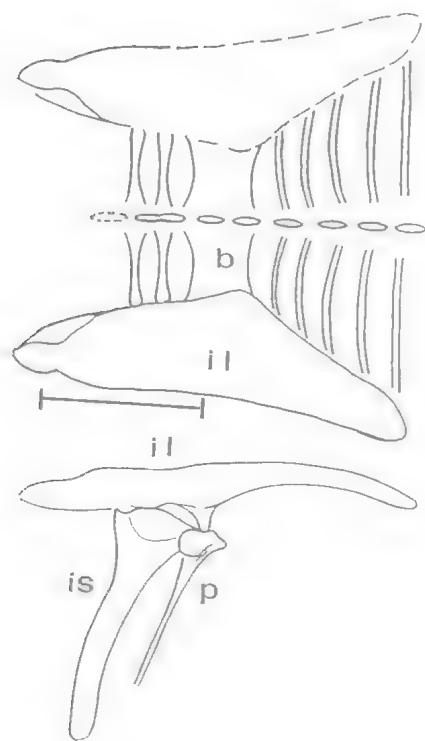
FIG. 16. Reconstructed pelvis of *Minmi* sp.; A, in dorsal view; and B, lateral. In A the dashed line indicates the approximate margin of the left ilium, and the posterior portion of the ilium has been completed from a second specimen, QM F33286. The right side of the reconstructed pelvis is a reflection of the left of the specimen. The broad 'bridge'(b) linking sacrum and ilium may be seen. Scale = 200mm.

ture, although there are one or two that were in the muscles below the transverse processes.

FORELIMB

Scapula. The left scapula is preserved just below the dermal armor. Although preparation is not complete, it shows to have a (mediolaterally) thin blade c. 27cm long, and a well-developed pseudacromial process 3.3cm high. (A complete, but fractured, left coracoid is also present but not yet studied.)

Humerus. The left humerus (26.5cm long) is nearly complete with only the proximolateral 'corner' of the deltopectoral crest missing (Fig. 15A). The shaft is constricted near its midlength and the ends enlarged, but not nearly as strongly as in other thyreophores. The head is anteroposteriorly broadened and set about a third

of the way out from the proximal trochanter. It is supported behind by a buttress extending about a third of the way down the shaft. There is also a ridge along the back of the deltopectoral crest, so forming a shallow fossa between this and the buttress supporting the head. The deltopectoral crest extends about a third of the way down the shaft and lacks the distal expansion described in ankylosaurids (Coombs & Maryanska, 1990).

The distal articular surface, at the elbow, subtends an angle of almost 180° anteroposteriorly. The elbow was probably a hinge joints as in most tetrapods.

Antebrachial elements. The proximal end of the ulna (Fig. 15B) is still incompletely prepared, but it seemingly lacks an olecranal process, so prominent in other thryeophores. Instead there is a flattened, expanded, mushroom-like proximal articular surface that makes an angle of about 45° with the long axis of the shaft. The radial sulcus is well-developed. The shaft is slender and distinctly flattened, with shallow grooves in the broad faces giving an almost figure-8 form to the cross-section.

Little is preserved of the radius (Fig. 15B), although the shaft is slender and oval in cross-section. Both radius and ulna are noticably more slender than in other thyreophores.

HINDLIMB

Ilium. The ilium is well-preserved on the left side. It is a flat, moderately broad element, with the antacetabular processes inclined laterally at about 35° (Fig. 16A). It is unique among ankylosaurs in that the postacetabular process is elongate. In *Euoplocephalus* the postacetabular process makes up about 27% of the iliac length, while in *Stegosaurus* this is 33%. In the 'Marathon' specimen it is at least 38%. The ilium is connected to the sacrum by a broad 'bridge' of bone. This structure joins the medial margin of the ilium to the dorsal portions of the neural spines of at least three, maybe five, sacrals. These are probably in the middle of the series, although precisely which sacrals cannot be determined until further preparation. The sheet-like 'bridge' seems to overlie the sacral ribs and no trace of it can be seen ventrally although the sacral ribs are prominent. It is well preserved on the right side in QM F18101, but indistinct on the left. It is also present in QM F33286. To my knowledge nothing like this has been reported in other ankylosaurs, but it seems very similar to the sheet
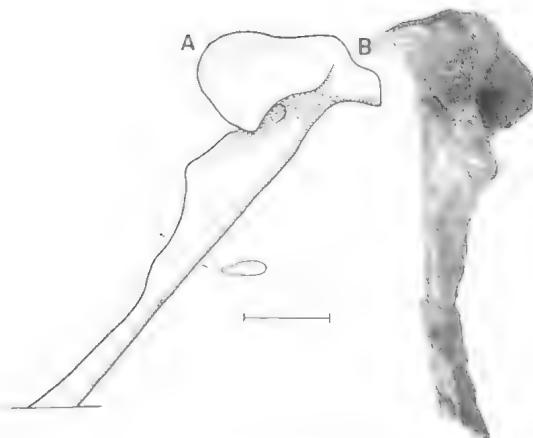
FIG. 17. A, Pubis in lateral; and B, anterior view. Scale = 25mm.


FIG. 18. Lower face of left pelvic block of QM F18101 showing left(?) ischium (Isc) at center. Inset shows matrix indicated by open dots, and blocks of ossciles by dots. Scale = 50mm.

of bone that covers the sacral ribs in *Stegosaurus* (Gilmore, 1914).

Pubis. The left pubis is nicely preserved, although incomplete distally (Figs 16, 17). It has a block-like body, of 'standard' form and a long slender postpubis, that is mildly blade-like in form proximally.

Ischium. The ischium (Figs 16, 18) looks much like those of other ankylosaurs, broad subtriangular proximally and rodlike distally.

Femur. The femur is a robust, straight element, still incompletely prepared. The head is set off medially, as in nodosaurids and the lesser trochanter is not fused to the greater along its length, but is set off by a shallow groove.

Crural & pedal elements. The tibia and fibula are present, the latter at least in part, but have yet to be studied, and no fibulae have been found. Two isolated claw-like unguals resemble those of *Acanthopholis*.

TAPHONOMY

The skeleton was found upside down in a marine deposit. There being no reason to believe this was an amphibious dinosaur, presumably the body washed out to sea. The skeleton was completely articulated — except perhaps for the feet, the distal end of the tail and the axis — and the small dermal ossicles of the back are still largely (or entirely) in place. This suggests that the skin was present and intact on the back right up to the time of burial. No evidence, such as tooth marks, that the carcass was scavenged before it came to lie on the sea floor has been seen, although a few

teeth of the small shark *Echinorhinus* were found in association with the skeleton and may indicate that a little scavenging occurred after it sank.

Since the skin of the back seems to have been present, the skeleton may have been held together by it, at least in part. If the skin remainined intact, some of the ligaments and capsular tissue might have done so, too. However, the preservation of the left femur still in contact with the acetabulum but directed horizontally outwards, suggests that the ligaments and capsular tissue had relaxed or decayed enough to permit what was presumably a very un-life-like attitude. Furthermore, the discovery of the neural arch of the axis some distance from the skull and neck suggests that this element had become freed of its ligamentous (and bony) attachments. The remaining cervical vertebrae were all found associated or articulated and enclosed within the calacreous nodules, which in turn suggests that the axial neural arch became freed before the nodule started to form.

Either the carcass was more or less complete when it washed out to sea, or it had dried out and mummified. As it was found some distance from the reconstructed shorelines, it had presumably floated for a while before sinking to the bottom. If intact the carcass may have decayed, formed gas bubbles (which would help it float) and eventually ruptured the belly wall, allowing it to sink. Or it may have floated as a dry mummy until it became waterlogged. The ventral sheet of os-

sicles seems to have been disrupted and fallen into the body cavity, consistent with rupture by decay gasses. But the dorsal sheet of ossicles has 'sunk' in between the ribs, which is consistent with mummification, and difficult to explain if that did not occur. Furthermore, the anomalous position of the neural arch of the axis is consistent with this explanation: the carcass had dried out to the extent of allowing it to come free of its attachment to soft tissues and the rest of the skeleton. While the carcass was sinking the arch fell away to come to rest on the seafloor some distance from the remainder of the skeleton. This is not, however, the only possible explanation, it may have been carried off and then dropped by one of the small scavenging sharks.

The evidence seems in favor of the interpretation of mummification prior to being swept out to sea by one point, the 'sinking in' of the dorsal armor and hence the dorsal hide between the ribs. Perhaps this is also consistent with the interpretation of having bloated and burst, but it isn't obvious how. Further work on this aspect is planned as, if true, the mummification interpretation has some interesting implications. First the carcass would have had to have been exposed long enough to dry out, without being noticibly scavenged, and then washed into a river or the sea. This implies an extended, perhaps seasonal, dry period followed by rains heavy enough to remove the carcass, and a surprising lack of scavengers. The seasonality is not inconsistent with what is known about Albian palaeoclimates in Queensland (Dettmann et al., 1992), but perhaps suggests that the seasons were more marked than generally thought.

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AN ANTARCTIC CRETACEOUS THEROPOD

R.E. MOLNAR, ALEJANDRO LOPEZ ANGRIMAN & ZULMA GASPARINI

The distal part of a theropod tibia has been recovered from the Coniacian-Santonian Hidden Lake Fm. near Cape Lachmann, James Ross Island. The piece closely resembles the corresponding region in *Megalosaurus* and, more closely, in *Piatnitzkysaurus*. This suggests that a persistently plesiomorphic tetanuran lineage inhabited the Antarctic. The relatively small size of the animal argues against a mean annual temperature below 15°C in its environment. □ *Antarctica, theropod, Late Cretaceous, biogeography, tetanuran.*

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During the summer of 1988 one of the authors (A.L.A.) discovered a small bone in the Cretaceous deposits 4km north of Col Crame, in the Cape Lachman region, northwestern James Ross Island (Fig. 1). In a basin in the northwestern sector of the Weddell Sea, the origin of the island is related to the opening of that sea during the breakup of Gondwanaland (Medína et al., 1992). The specimen derives from the middle section of the Hidden Lake Fm., Gustav Gr. (Ineson et al., 1986), referred to the Coniacian-Santonian (Buatois & López Angríman, 1992a). It is the first Cretaceous Antarctic theropod and the oldest Cretaceous tetrapod from Antarcica.

Prior to Angríman's discovery, ornithischians were the only Cretaceous dinosaurs known from Antarctica (Gasparini et al., 1987; Olivero et al., 1991; Hooker et al., 1991). The Late Cretaceous theropods from New Zealand (Molnar & Wiffen, 1994) imply that theropods also lived in Antarctica at that time (cf. Molnar, 1989) but this discovery verifies their occurrence and helps fill out our knowledge of Antarctic faunal evolution. A theropod is known from the Early Jurassic of Antarctica (Hammer & Hickerson, 1994).

Collection designations. ANSP, Academy of Natural Sciences, Philadelphia; MLP, Departamento de Paleontología Vertebrados, Museo de La Plata, La Plata.

DESCRIPTION

The specimen (MLP: 89-XII-1-1) is the distal end — representing probably 10-15% of the total length — of a left tibia. The piece is complete save for very small portions of the extremities of the medial malleolus and the flange that backs the fibula. In general form it is (Fig. 2) is similar to the corresponding part of the tibia in *Megalosaurus bucklandi, Piatnitzkysaurus floresi* and *Poekilopleuron bucklandii*. Seen from the front, the shaft is expanded laterally to form a broadly rounded post-fibular flange, and medially into an angularly truncate medial malleolus. A broad, flat-surfaced prominence proximomedially bounds the ascending process and dorsal face of the astragalus, extending proximolaterally across the anterior face from the medial malleolus. Its edges are marked by sharp angulations. This is termed the medial buttress. The posterior face is almost flat but with a slight longitudinal concavity laterally. Above the post-fibular flange the surface of this concavity abruptly slopes anteriorly to meet the anterior surface of the shaft at a sharp edge.

The broken end reveals a central cavity surrounded by relatively thin-walled bone (Fig. 2D). The shaft is tear-shaped in section at the break. Fragments of bone in the calcite fill of the central cavity suggest that the shaft was crushed just above the broken end before or shortly after burial. The distal end is slightly concave from the front and triangular when viewed distally, with the anterior surface forming the longest edge and the inclined lateral edge the shortest. The distal surface is shallowly concave in the middle, becoming mildly convex both medially and laterally.

The form of the anterior surface of the distal tibia (Fig. 2C) indicates that the ascending process of the astragalus was moderately low, relatively narrow and restricted to the lateral half of the tibial shaft. Thus the astragalus would have been unlike those of ornithomimosaurs or tyrannosaurs in form, but probably much like that of *Poekilopleuron bucklandii*.
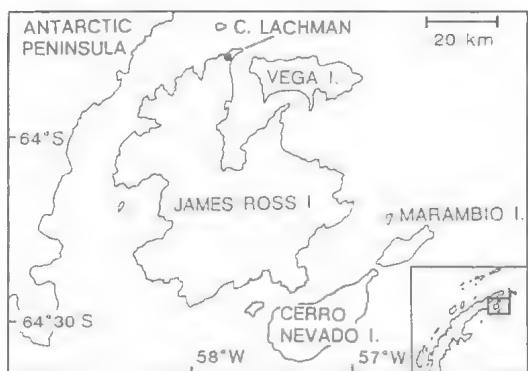
FIG. 1. Map of James Ross Island, showing where the theropod tibia was found (dot). C=Cape, I=Island.

IDENTIFICATION. The general form and relatively thin-walled hollow shaft indicate that this tibia derives from a theropod. Dryosaurs have also been reported with thin-walled limb elements (Chinsamy, 1995) and dryosaurs or similar forms are known from Late Cretaceous New Zealand (Wiffen & Molnar, 1989), hence probably inhabited Antarctica at this time. However no other dinosaurs have the astragalar ascending process set into a depression of the anterior face of the distal tibia, dorsomedially bounded by an abrupt step or offset in the anterior face. This feature is characteristic of neotheropods (Sereno et al., 1994), and isn't found in herrerasaurs (Fig. 3). The truncate medial malleolus also occurs in a restricted group of theropods (Table 1), but this probably represents a stage in the evolution of distal tibial form (Fig. 3).

The work on theropod astragali of Welles & Long, 1974, (with the correction of Carpenter, 1992) accords well with recent phylogenetic analyses of theropods (Holtz, 1994; Russell & Dong, 1993; Sereno et al., 1994). A general tendency toward increased height and breadth of the ascending process can be seen in the lineage leading to arctometatarsalians (Fig. 3). Furthermore, a survey of figured tibiae indicates that distal tibial form is reasonably distinctive for the recognised theropod groups (Table 1).

The distal tibia of ceratosaurs is variable because of the evolution of the ankle in this group. In distal view the tibia is not anteroposteriorly compressed in the Triassic and Early Jurassic forms, as it is in later ceratosaurs and tetanurans. The ascending process is absent or low and narrow, the medial buttress is absent in *Coelophysis* and *Syntarsus* but present in *Dilophosaurus*, and the medial malleolus is quite subdued or absent in

Coelophysis and *Dilophosaurus* but present and angular in *Syntarsus* (Raath, 1969; Welles, 1984; Colbert, 1989). Early ceratosaurs, e.g., *Coelophysis*, (and herrerasaurs) lack an ascending process and the astragalus interlocks with an offset distal surface of the tibia, the offset being visible anteriorly (Padian, 1986, fig. 5.5).

The neoceratosaur distal tibia is known only in *Ceratosaurus* and *Xenotarsosaurus*, where the distal expansion is approximately symmetrical and the fossa for the ascending process low. In *Ceratosaurus* the medial buttress is broad with the 'step' extending nearly horizontally at least 2/3 of the way across the shaft (about halfway in the Hidden Lake specimen) and the medial malleolus does not extend as far proximally along the shaft, so is more pointed in anterior view (Gilmore, 1920); the distal tibia of *Xenotarsosaurus* is similar but with a broadly rounded malleolus (Martinez et al., 1987). Dromaeosaurs (i.e., *Deinonychus antirrhopus*) have a broad, high, ascending process, lack the medial buttress — probably correlated with the broadening of the ascending process — and have a broadly rounded medial malleolus (Ostrom, 1969). Arctometatarsalian theropods also have a broad, high ascending process and lack the medial buttress, and have a nearly symmetrical distal end (in anterior or posterior view) with no distinctive form to the medial malleolus (Welles & Long, 1974). Other coelurosaurs (e.g., *Calamosaurus*) similarly have a high, broad ascending process and no medial buttress but the medial malleolus is similar in silhouette, from in front, to that of the Hidden Lake tibia (Lydekker, 1891). There is little data available on oviraptorosaurs, but judging from *Chirostenotes* and *Microvenator*, the form is similar to that in arctometatarsalians, with the exception that the fibular flange seems truncate in the former genus (Ostrom, 1970; Currie & Russell, 1988). The segnosaur distal tibia remains unknown or undescribed. That of *Yangchuanosaurus* shows a low ascending process, a medial buttress different in form and an angular medial malleolus (Dong et al., 1983). In *Sinraptor* the ascending process is low and narrow, the medial buttress essentially similar to that of *Ceratosaurus*, and with an angular medial malleolus (Currie & Zhao, 1993). In distal view the tibia is more anteroposteriorly compressed. *Allosaurus* has a broader, higher ascending process, a narrower medial buttress, and a generally similar medial malleolus that is, however, more medially projecting and more rounded in outline (Gilmore, 1920; Madsen, 1976).
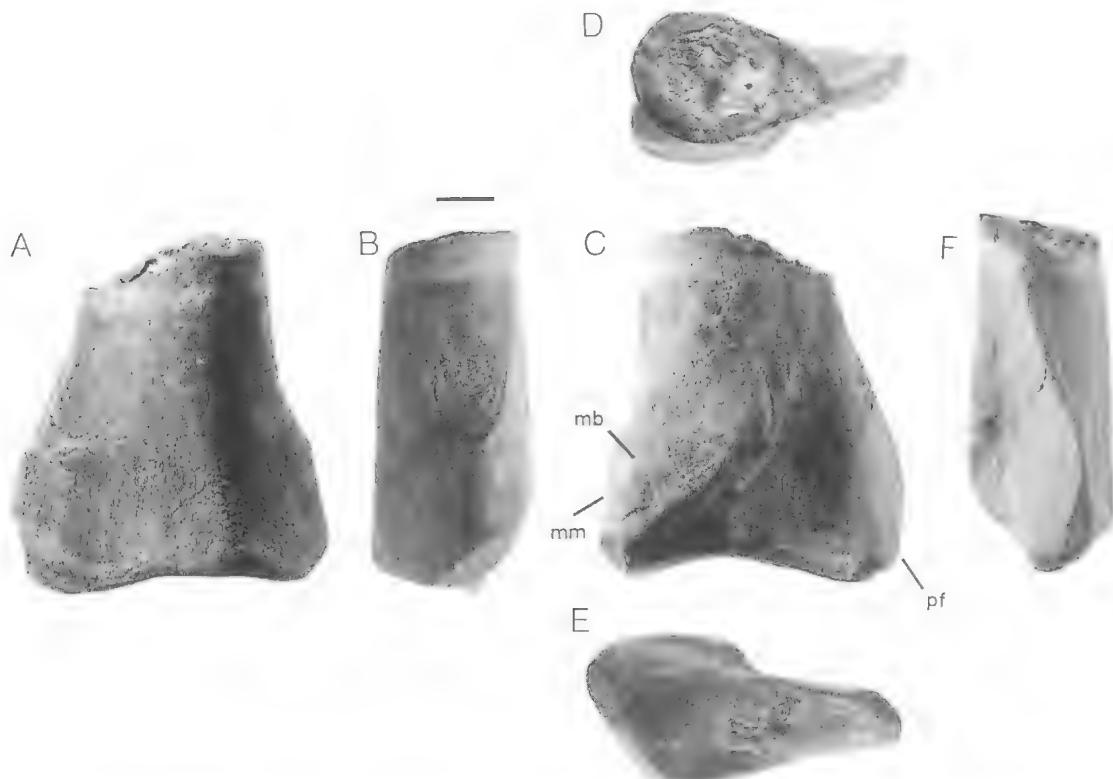
FIG. 2. The theropod distal tibia (MLP: 89-XII-1-1) from the Hidden Lake Fm., James Ross Island, in: A, posterior; B, medial; C, anterior; D, proximal; E, distal; and F, lateral views. mb=medial buttress, mm=medial malleolus, pf=flange behind fibula, scale = 1cm.

The distal tibiae of *Megalosaurus bucklandi* (Huxley, 1870; Hulke, 1879) and *Poekilopleuron bucklandii* (Eudes-Deslongchamps, 1837) — possibly related forms — *Erectopus superbus* (Sauvage, 1882) — of uncertain affinities — and *Piatnitzkysaurus floresi* (Bonaparte, 1986) — a plesiomorphic allosauroid — are the most similar. However, the tibiae of torvosaurids (specifically *Afrovenator abakensis*, *Eustreptospondylus oxoniensis* and *Torvosaurus tanneri*), animals similar in other ways to megalosaurs, differ in having an angular medial malleolus (e.g., Britt, 1991). Of those with similar distal tibiae, the most similar is that of *P. floresi*, which matches that of the Hidden Lake theropod in the forms of the medial malleolus and buttress — particularly the curve of the step adjacent to the facet for the astragalar ascending process — and the fibular flange. The distal tibiae of the previously noted megalosaurs, and of *Erectopus*, differ in that the fibular flange projects distally, forming the distalmost part of the tibia. This does not occur in *Piatnitzkysaurus* or the Hidden Lake tibia. There are slight differences: the Hidden Lake tibia is less compressed distally, its fibular flange projects less and its medial buttress is slightly broader than in *P. floresi*. Nonetheless, had the Hidden Lake tibia been found instead in the Cañadon Asfalto Fm. (Callovian-Oxfordian) of Argentina, it would likely have been attributed to an immature *Piatnitzkysaurus*.

The similarity of the Hidden Lake tibia to those of megalosaurs and *Piatnitzkysaurus*, all Middle Jurassic forms, and *Erectopus*, an Albian form, implies that the Hidden Lake theropod represents a lineage probably derived from relatively plesiomorphic megalosaur or primitive allosauroid (but not sinraptorid) stock, unrelated to the lineages culminating in the more or less contemporaneous arctometatarsalians. Interestingly, the only other known Antarctic theropod, the Early Jurassic *Cryolophosaurus ellioti* (Hammer & Hickerson, 1994), is also now thought to be a plesiomorphic allosauroid (Hammer, pers.

comm., 1996). Generic identifica-
tion of the Hidden Lake specimen
is not possible, unless more is
recovered.

DISCUSSION

The Hidden Lake tibia is the
same size as the distal end of the
tibia of the ornithomimosaur
Coelosaurus antiquus (ANSP
9222) which is about 40cm long
overall. If the proportions were the
same, then the Hidden Lake
theropod would have been about
3-3.5m long. If, on the other hand
it was more robust, with the tibia
proportioned like those of *Piat-
nitzkysaurus floresi*, then it would
have been about 22-23cm long and
the whole animal about 2.5-3m
long. Assuming that it is from a
mature animal, and we have no
reason to think otherwise, in either
case it represents a moderately
small theropod about the size of a
large *Coelophysis*. This theropod
would have been too small to have
been ectothermic and to have lived
under a climate with a mean annual
temperature of less than 15°C (cf.
Molnar & Wiffen, 1994; Spotila et
al., 1991). This suggests that James
Ross Island enjoyed a rather mild
climate, at least in some places,
during the Coniacian-Santonian.
The specimen was found in the
middle section of the Hidden Lake
Fm., in the level of the calcareous
sand with abundant carbonised
material. Associated trace fossils
include *Planolites* sp. and
Palaeophycus sp., and remains of logs without
the borings of *Teredolites* that are often found in
the upper and lower levels of this formation
(Buatois & López Angríman, 1992b). The en-
vironment of deposition was a developing dis-
tributary plain in the central fan of a fan delta
depositional system (Buatois & López Angríman,
1992a) into which, we infer, the specimen had
been transported after death.

This tibia suggests a more primitive theropod,
or at least one with less advanced distal tibial
structure, than was common in the Late
Cretaceous Asiamerica or South America. Thus it
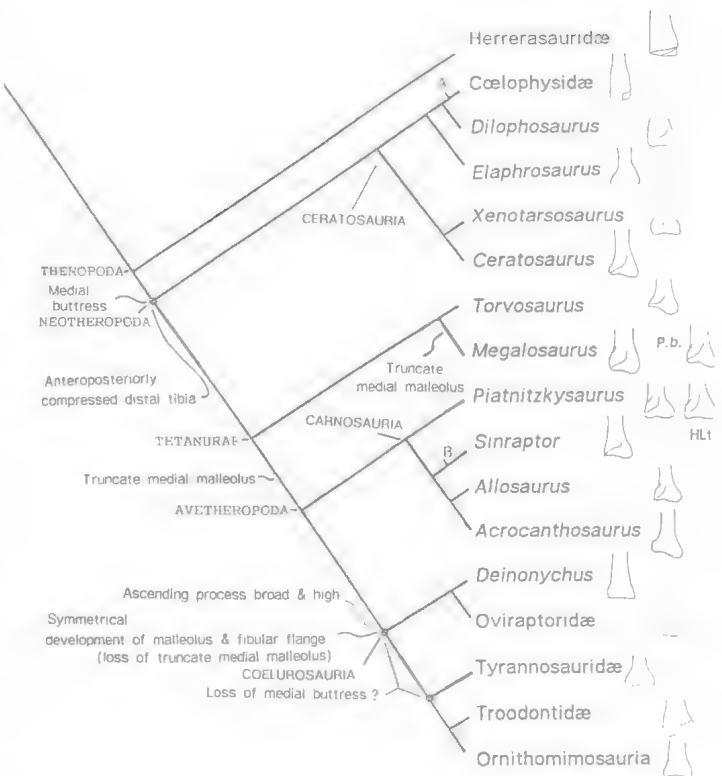
FIG. 3. Phylogenetic relationships among theropods, with astragalar and
distal tibial characters discussed in text assigned to nodes. A and B
indicate presumed reversals of character state: A, to uncompressed
distal tibia; B, to angular (rather than truncate) medial malleolus. Along
the right margin are diagrams of the distal tibiae of the genera included,
with that for *Poekilopleuron bucklandii* (P.b.) added next to that for
Megalosaurus, and that for the Hidden Lake theropod (HLt) next to
Piatnitzkysaurus. Cladogram after Holtz (1994), with the positions of
Sinraptor, following Sereno, et al. (1994), and *Piatnitzkysaurus*, fol-
lowing Molnar, et al. (1990), added. (Tibial diagrams redrawn from the
literature, except for the Hidden Lake theropod and *Piatnitzkysaurus*).

suggests that lineages deriving from Middle
Jurassic forms persisted in the Antarctic.

ACKNOWLEDGEMENTS

TABLE 1. Theropod distal tibial form. In the last column, 'lateral' indicates that the lateral flange is more strongly developed than the medial malleolus; 'symmetric' that flange and malleolus are about equally developed and symmetrical in anterior view; 'both' that flange and malleolus are equally developed but not symmetrical .

Taxa	Medial malleolar development	Medial buttress	Astragalar ascending process		Distal tibial development
			width	height	
Herrerasauridae	slight	absent	narrow	low	slight
Coelophysidae	slight	absent	narrow	lows	light
Dilophosaurus	slight	present	narrow	low	lateral
Elaphrosaurus	angular	?	?[1]	?	symmetric
Xenotarsosaurus	rounded	?	moderate	low	symmetric
Ceratosaurus	angular	present	moderate	low	both
Torvosaurus	angular	present	moderate	low	lateral
Megalosaurus	truncate	present	moderate	low	lateral
Piatnitzkysaurus	truncate	present	?	?	lateral
Sinraptor	angular	present	moderate	low	lateral
Allosaurus	truncate	present	moderate	low	lateral
Acrocanthosaurus	truncate	present	?	?	both
Deinonychus	rounded	absent	broad	high	symmetric
Oviraptoridae	slight	low or absent	broad	?	both
Avimimus	slight	absent	broad	high	symmetric
Tyrannosauridae	rounded	absent	broad	high	symmetric
Troodontidae	slight	absent	broad	high	symmetric
Ornithomimidae	slight	absent	broad	high	symmetric

[1] Welles & Long (1974) describe the astragalar ascending process of *Elaphrosaurus bambergi* as high and broad, citing Janensch (1925). However it is not clear from Janensch that the ascending process is actually preserved so this may be an inference. Hence the proportions are here considered to be unknown.

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ALVAREZSAURIDAE, CRETACEOUS BASAL BIRDS FROM PATAGONIA AND MONGOLIA

FERNANDO E. NOVAS

Alvarezsauridae represents a clade of bizarre birds with extremely reduced but powerful forelimbs. Twenty synapomorphic features shared by *Patagonykus*, *Alvarezsaurus* and *Mononykus* supports Alvarezsauridae as a monophyletic group of avialan theropods. Diagnostic characters, mainly referred to vertebral, forelimb, pelvic and hindlimb anatomy, emerge from a cladistic analysis of 74 derived features depicting Alvarezsauridae as the sister taxon of the avialian clade Ornithothoraces. Since the origin and early diversification of the Alvarezsauridae probably took place during, or prior to, the Early Cretaceous, their common presence in Patagonia and Mongolia reflects a wider geographical distribution over the world, prior to the development of major geographical barriers between Laurasia and Gondwana during Aptian to Cenomanian times. ☐ *Alvarezsauridae, Patagonykus, Mononykus, birds.*

Los Alvarezsauridae constituyen un clado de extrañas aves basales, caracterizados por sus miembros anteriores extremadamente reducidos, aunque proporcionalmente robustos. Veinte sinapomorfías compartidas por *Patagonykus*, *Alvarezsaurus* y *Mononykus* sustentan la hipótesis que Alvarezsauridae conforma un grupo monofilético de terópodos avialanos. Los caracteres diagnósticos de Alvarezsauridae se refieren principalmente a la columna vertebral, miembros anteriores y posteriores, y pélvis, y emergen de un análisis cladístico de 74 rasgos derivados muestran a Alvarezsauridae como el grupo hermano del clado avialiano Ornithothoraces. En base a las hipótesis filogenéticas propuestas, se estima que el origen y temprana radiación de los alvarezsáuridos habría ocurrido, al menos, durante el Cretácico temprano. Este dato permite suponer que estos terópodos se habrían dispersado en varios continentes (p.ej., América del Sur, América del Norte, y Asia) antes que se instalaran barreras geográficas de importancia entre Laurasia y Gondwana durante el Cretácico 'Medio'.

Fernando E. Novas, Museo Argentino de Ciencias Naturales, Av. Angel Gallardo 470, 1405 Buenos Aires, Argentina; 1 February 1995.

Alvarezsauridae (Bonaparte, 1991) is a clade of bizarre avialan theropods from Upper Cretaceous rocks of Mongolia and Patagonia. At present they are known by three different species: the Patagonian *Alvarezsaurus calvoi* (Bonaparte, 1991), *Patagonykus puertai* gen. et sp. nov. (Novas, in press a) and the Mongolian *Mononykus olecranus* (Perle et al., 1993, 1994; Chiappe et al., this volume). By far, the latter species is the best represented one, being known from complete cranial and postcranial skeletons (Perle et al, 1993; 1994; Chiappe et al., this volume). On the contrary, the South American taxa *Patagonykus* and *Alvarezsaurus* are not completely known and the most serious lack of information refers to the skull. Nevertheless, the available osteological material pertaining to the Patagonian forms is informative, allowing recognition of autapomorphic features diagnostic of each of the Patagonian species. Although incompletely represented, *Patagonykus* and *Alvarezsaurus* are significant phylogenetically since they retained the plesiomorphic state for several features that *Mononykus* shares with birds, more derived than *Archaeopteryx*.

Better documented now than they were five years ago (Bonaparte, 1991), some aspects of the phylogenetic relationships of the alvarezsaurids are now better understood. For example, it is now clear that Alvarezsauridae does not constitute a theropod branch of uncertain relationships, as originally interpreted by Bonaparte (1991); on the contrary, they are deeply internested within Tetanurae, Coelurosauria and Maniraptora because they exhibit hypapophyses on vertebrae from the cervicothoracic region, semilunate carpal, retroverted pubis, posterodorsal margin of ilium ventrally curved in lateral view and pubic foot cranially reduced (Gauthier, 1986).

There are, however, several features that make these theropods particularly interesting: first, they exhibit peculiar adaptations in the forelimbs and vertebral column, the functional significance of which is controversial (e.g., Perle et al., 1993,

1994; Ostrom, 1994); second, alvarezsaurids share with birds several apomorphic resemblances, more derived than *Archaeopteryx*, raising new questions about the early evolution of birds (Perle et al., 1993, 1994; Chiappe et al., this volume); third, alvarezsaurids are known from distant Upper Cretaceous localities of the world (e.g., Patagonia and Mongolia) and thus are interesting from a palaeobiogeographical point of view.

ABBREVIATIONS. AMNH, American Museum of Natural History, New York; BSP, Bayerische Staatssammlung für Paläontologie, Munich; CM, Carnegie Museum of Natural History, Pittsburgh; HMN MB, Humboldt Museum für Naturkunde, Berlin; GI, Geological Institute, Mongolian Academy of Sciences, Ulan Bator; MACN, Museo Argentino de Ciencias Naturales 'B. Rivadavia', Buenos Aires; MCZ, Museum of Comparative Zoology, Cambridge; MLP, Museo de La Plata, La Plata; MUCPV, Museo de Ciencias Naturales, Universidad Nacional del Comahue, Neuquén; PVL, Paleontología de Vertebrados, Fundación 'Miguel Lillo', San Miguel de Tucumán; PVPH, Paleontología Vertebrados, Museo Municipal 'Carmen Funes', Plaza Huincul, Neuquén; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan; USNM, United States National Museum, Washington, DC; YPM, Yale Peabody Museum, New Haven.

MATERIALS AND METHODS

MATERIAL EXAMINED. A comparative study of the holotypes of *Patagonykus puertai* (PVPH 37), *Alvarezsaurus calvoi* (MUCPV 54) and *Mononykus olecranus* (GI N107/6 cast) was conducted. The following specimens were also studied: *Albertosaurus libratus* (AMNH 5468), *Alectrosaurus olseni* (AMNH 6554), *Allosaurus fragilis* (AMNH 5767), *Archaeopteryx lithographica* (HMN MB 1880/81 and casts of London and Eichstätt specimens), *Archaeornithomimus asiaticus* (AMNH 6566, 6567, 6570), *Caiman latirostris* (pers. collection), *Compsognathus longipes* (BSP AS I 536), *Deinonychus antirrhopus* (AMNH 3015, MCZ 4371, YPM 5205, 5206, 5236), *Herrerasaurus ischigualastensis* (PVSJ 373), *Iberomesornis romerali* (MACN unnumbered cast), *Meleagris gallopavo* (pers. collection), *Mussaurus patagonicus* (MLP-68-III-27-1), *Ornitholestes hermani* (AMNH 619), *Ornithomimus velox* (AMNH 5355), *Ornithomimus sedens* (USNM 2164) and *Piatnitzkysaurus floresi* (MACN-CH 895).

ANATOMICAL TERMINOLOGY. I follow the terminology of Clark, 1993. 'Cranial' and 'caudal' are used here in place of 'anterior' and 'posterior', respectively.

SYSTEMATIC NOMENCLATURE. I ascribe to the notion of phylogenetic (node-based or stem-based) definitions for all taxa (de Queiroz & Gauthier, 1994). Aves is defined to encompass all the descendants of the most recent common ancestor of Ratitae, Tinami and Neognathae (Gauthier, 1986); Avialae includes *Archaeopteryx lithographica*, Aves and their most recent common ancestor; Maniraptora includes all those theropods more closely related to Aves than to the Ornithomimidae (Gauthier, 1986). With respect to Maniraptora, I am not following the synapomorphy-based definition given by Holtz (1994), who has also included ornithomimids and tyrannosaurids within Maniraptora on the assumption that the ancestors of these two taxa also possessed the diagnostic features of Maniraptora (e.g., raptorial manus, etc.). The node-based definition originally given by Gauthier (1986:30) perfectly fits to the clade formed by Dromaeosauridae plus Avialae, even accepting the monophyly of Arctometatarsalia (= Elmisauridae + *Avimimus* + Tyrannosauridae + (Troodontidae + Ornithomimosauria); sensu Holtz, 1994).

SYSTEMATIC PALAEONTOLOGY

Basic information on the new taxon *Patagonykus puertai* is provided here. A detailed anatomical description and discussion of the autamorphies diagnosing this species are given elsewhere (Novas, in press a).

COELUROSAURIA Huene, 1920
MANIRAPTORA Gauthier, 1986
AVIALAE Gauthier, 1986
METORNITHES Perle et al., 1993
ALVARESAURIDAE Bonaparte, 1991

Patagonykus gen. nov.

Patagonykus puertai gen. et sp. nov.

MATERIAL EXAMINED. HOLOTYPE PVPH 37, two incomplete dorsal vertabrae, incomplete sacrum, two proximal and two distal caudal vertabrae; incomplete left and right coracoids, proximal and distal ends of both humeri, right proximal portions of ulna and radius, and distal portion of left ulna, articulated carpometacarpus and first phalanx of digit I of the right manus; incomplete ungual phalanx probably corresponding to digit I; portions of ilia, proximal ends of ischia, and portions of pubes; proximal and distal por-
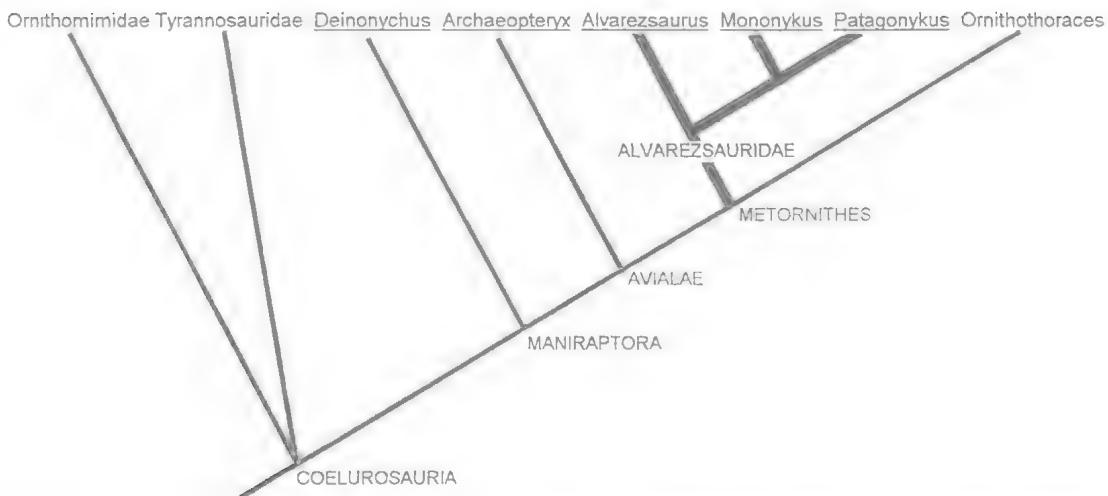
FIG. 1. Cladogram depicting the phylogenetic relationships among *Patagonykus, Alvarezsaurus* and *Mononykus*, and five immediate outgroups.

tions of right femur, and distal end of the left; proximal and distal ends of both tibiae, fused with proximal tarsals; metatarsals II and III fused to distal tarsals III; several pedal phalanges.

HORIZON AND AGE. Portezuelo Member of the Río Neuquén Formation (possibly Turonian, Late Cretaceous; Cruz et al., 1989), Sierra del Portezuelo, 22km west of Plaza Huincul City, Neuquén Province, NW Patagonia, Argentina. The quarry is situated 500m NW of National Route 22.

DIAGNOSIS. *Patagonykus puertai* is an alvarez-saurid avialian theropod diagnosed by the following: postzygapophyses in dorsal vertebrae with ventrally curved, tongue-shaped lateral margin; dorsal, sacral and caudal vertabrae with a bulge on the caudal base of the neural arch; humeral articular facet of coracoid transversely narrow; internal tuberosity of humerus subcylindrical, wider at its extremity rather than in its base; humeral entepicondyle conical and strongly projected medially; first phalanx of manual digit I with proximomedial hook-like processes; ecto-condylar tuber of femur rectangular in distal view.

PHYLOGENETIC RESULTS

Seventy four derived features were coded as binary and their distribution examined in three terminal taxa and five outgroups (see Appendix). The data matrix was subjected to parsimony analysis using the implicit enumeration (ie) com-mand in HENNIG 86 (version 1.5) by J.S. Farris (1988). A single most parsimonious tree was obtained (Fig. 1), with a length of 102 steps, a consistency index of 0.72 and a retention index of 0.74. This tree depicts Alvarezsauridae as the sister group of Ornithothoraces, but it must be emphasised that the tree supporting Alvarez-sauridae outside Avialae (namely as the sister taxon of *Deinonychus* plus Avialae) differs in five evolutionary steps (characters listed in the Appendix). Until more evidence becomes available, I will consider alvarezsaurids as birds (e.g., avialians more derived than *Archaeopteryx*), in agreement with Perle et al. (1993, 1994) and Chiappe et al. (this volume).

OUTGROUP RELATIONSHIPS. The following taxa have been chosen for outgroup comparisons: Ornithothoraces, *Archaeopteryx, Deinonychus*, Tyrannosauridae and Ornithomimidae. Although there is a diversity of opinion about the phylogenetic arrangement of the terminal taxa, there is agreement among authors (e.g., Bakker et al., 1988; Novas, 1991; 1992; Holtz, 1994) that the Tyrannosauridae are more closely related to Ornithomimidae, Dromaeosauridae, Aves and other coelurosaurs, than to *Allosaurus* (contra Gauthier, 1986; Molnar et al., 1990). Another point of consensus is that Dromaeosauridae and Avialae form a clade (e.g., Maniraptora; Gauthier, 1986; Novas, 1991; 1992; Holtz, 1994).

In reference to the Avialae, the available data supports Alvarezsauridae as the sister taxon of Ornithothoraces, with *Archaeopteryx* as the out-

group (Perle et al., 1993, 1994; Chiappe et al., this volume).

TERMINAL TAXA. *Patagonykus puertai, Alvarezsaurus calvoi* and *Mononykus olecranus* were chosen as operational taxonomic units (OTU's) for parsimony analysis. The latter two taxa are diagnosed below on the basis of apomorphic characters, which are numbered and preceded by a letter identifying their presence in the corresponding taxon (A, *Alvarezsaurus*; M, *Mononykus*).

Alvarezsaurus calvoi Bonaparte, 1991. This taxon was originally diagnosed by Bonaparte (1991) on the basis of several features, some of which are problematic. For example, presence of '*cervical pleurocoels ... 5 or 6 sacrals ... ilium low and long ... unfused metatarsals and tarsals ... astragalus with wide condyles ... metatarsal III narrower in caudal view respect to the remaining metatarsals ... metatarsal IV greater proximally than the other metatarsals*' are all characters widely distributed within Tetanurae (Gauthier, 1986), and clearly none of these features is autapomorphic for *Alvarezsaurus calvoi*. Other features (e.g., cranial sacrals with a slight axial depression on ventral surface; ilium with postacetabular blade greater than the preacetabular one) are widely — and unevenly — distributed among several non-avialian and avialian taxa and their status is difficult to verify. Other characters originally included in the diagnosis of this taxon (Bonaparte, 1991), such as '*neural spines vestigial in cervical and cranial dorsal vertebrae*' and '*caudal sacrals with narrow ventral margin*' are features also present in *Mononykus* and *Patagonykus* and are better interpreted as diagnostic of the Alvarezsauridae. Bonaparte has also listed the small size of the specimen as a diagnostic feature of *Alvarezsaurus*. However, the lack of fusion of the centra and respective neural arches of the cervical vertebrae, as well as the unfused centra of the sacrals, reveal that the holotype specimen of *Alvarezsaurus calvoi* was an immature individual that probably did not reach its maximum body size.

Restudy of the partial skeleton of *Alvarezsaurus calvoi* (MUCPV 54) allowed recognition of the following autapomorphies:

A1) Cervical centra amphicoelous (Fig. 2). Bonaparte (1991) originally recognised this character as diagnostic of *Alvarezsaurus*. This condition sharply contrasts with that present in the remaining Tetanurae (including *Mononykus*), in which the cranial articular surfaces of cervical
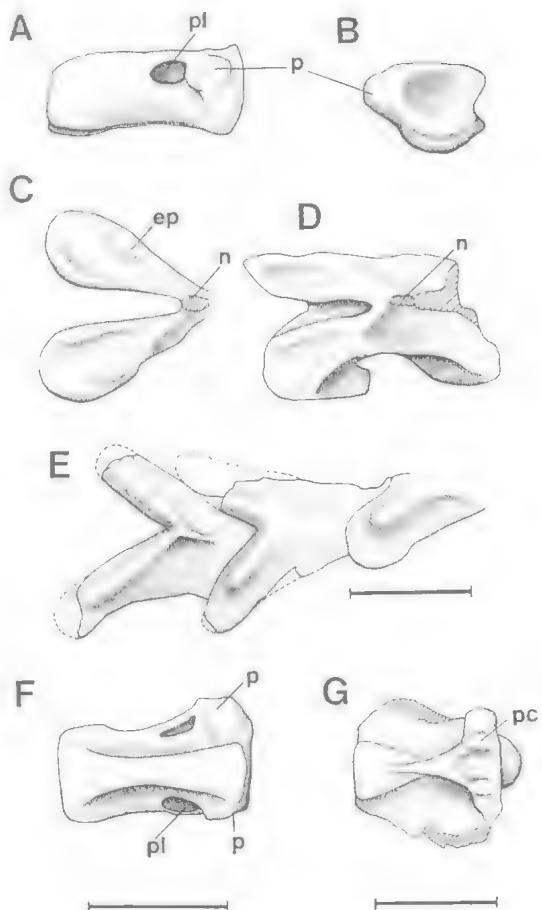

FIG. 2. Cervical vertebrae of Alvarezsauridae. A-D, F, *Alvarezsaurus calvoi* (MUCPC 54). A, B, F, cervical ?5th. D, 7th. C, 8th. E, G, *Mononykus olecranus* (GI N107/6 cast). E, ?6th to ?8th. G, 9th. (A, lateral; B, cranial; C, D, E, dorsal; F,G, ventral views). ep= epipophysis, n=neural spine, p=parapophysis, pc= processus caroticus, pl=pleurocoel; scale = 10mm.

centra are flat or convex. Procoelous cervical centra are also present in Ornithomimidae (e.g., *Archaeornithomimus* AMNH 6566, 6567, 6570).

A2) Cervical postzygapophyses dorsoventrally flattened, paddle-shaped in dorsal view, and with a pair of strong craniocaudal ridges (Fig. 2). *Alvarezsaurus* exhibits paddle-shaped, craniocaudally elongate postzygapophyses on cervical vertebrae (Bonaparte, 1991). This condition contrasts with other theropods (e.g., *Piatnitzkysaurus, Archaeornithomimus, Ornitholestes, Deinonychus*) in which the postzygapophyses are rectangular, not constricted at their bases, and with a convex dorsal surface bearing a prominent

epipophysis. In the caudal cervicals of *Alvarezsaurus* the postzygapophyses exhibit a strong, craniocaudally-oriented buttress running along the medial margin. This condition is seen in cervicals 7 to 9, but in cervicals 7 and 8 a lateral crest is also present, bounding a shallow basin over the dorsal surface of the postzygapophyses. This condition of the dorsal surface of the postzygapophyses contrasts with that present in other theropods, including *Mononykus* (GI N 107/6) in which the dorsal surface of the cervical postzygapophyses is smooth and transversely convex.

A3) Length of distal caudals more than 200% of the length of proximal caudals. In *Alvarezsaurus* (MUCPV 54) the centrum of the distalmost preserved caudal (presumably corresponding to the region of caudals 15 through 18), is 213% of the length of the most proximally preserved caudal. This condition resembles that of *Archaeopteryx* (Wellnhofer, 1974; 1988; 1993), in which the longest tail vertebrae (caudals 12 and 13) represents 185 to 287% of the length of the proximal caudal vertebrae (caudals 1 through 3). The elongation of the distal caudal segments in *Alvarezsaurus* sharply contrast with the proportions seen in non-avialian maniraptorans (e.g., *Ornitholestes, Sinornithoides, Deinonychus*; Osborn, 1917; Ostrom, 1969; Russell & Dong, 1993b) in which the length of the distal caudals represents no more than 175% the length of the proximal caudals. *Alvarezsaurus* also differs from other alvarezsaurids, in which the length of caudal vertebrae remains more or less similar along the tail (e.g., *Mononykus*; Perle et al., 1994), or they are considerably smaller than the proximal ones, as in *Patagonykus* (PVPH 37). As for the Ornithothoraces, the distal caudal vertebrae are uniformly short (e.g., *Baptornis, Hesperornis, Ichthyornis, Patagopteryx*; Marsh, 1880; Martin
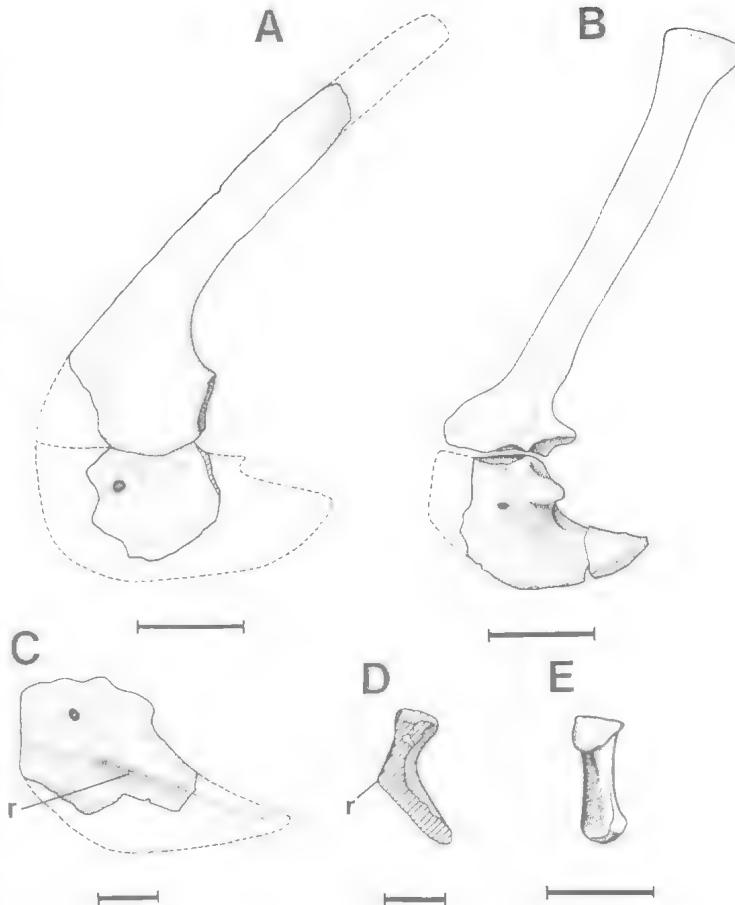

FIG. 3. Pectoral girdle of alvarezsaurids. A, *Alvarezsaurus calvoi* (modified from Bonaparte, 1991). B, E, *Mononykus olecranus* (GI N107/6 cast). C, D, *Patagonykus puertai* (composite reconstruction based on left and right coracoids of PVPH 37). (A, B, C, left lateral view of scapula and coracoid; D, E, caudal view of left coracoid). r=craniocaudal ridge, scale = 20mm.

& Tate, 1976; Alvarenga & Bonaparte, 1992), but this condition can not be easily considered ancestral for the clade, since in basal ornithothoracines (e.g., *Iberomesornis, Sinornis*; Sanz et al., 1988; Sereno & Rao, 1992) the distal caudals are strongly fused forming a pygostyle, preventing measurement of the length of each vertebral segment.

A4) Scapular blade slender and reduced (Fig. 3). Bonaparte (1991) included this feature in his original diagnosis. Although the distal end of the scapula of *Alvarezsaurus* is broken off, the cranial and caudal margins of the blade tend to converge distally, suggesting the lack of a distal expansion as present in other theropods (e.g., *Mononykus, Archaeopteryx, Tyrannosaurus, Allosaurus*;
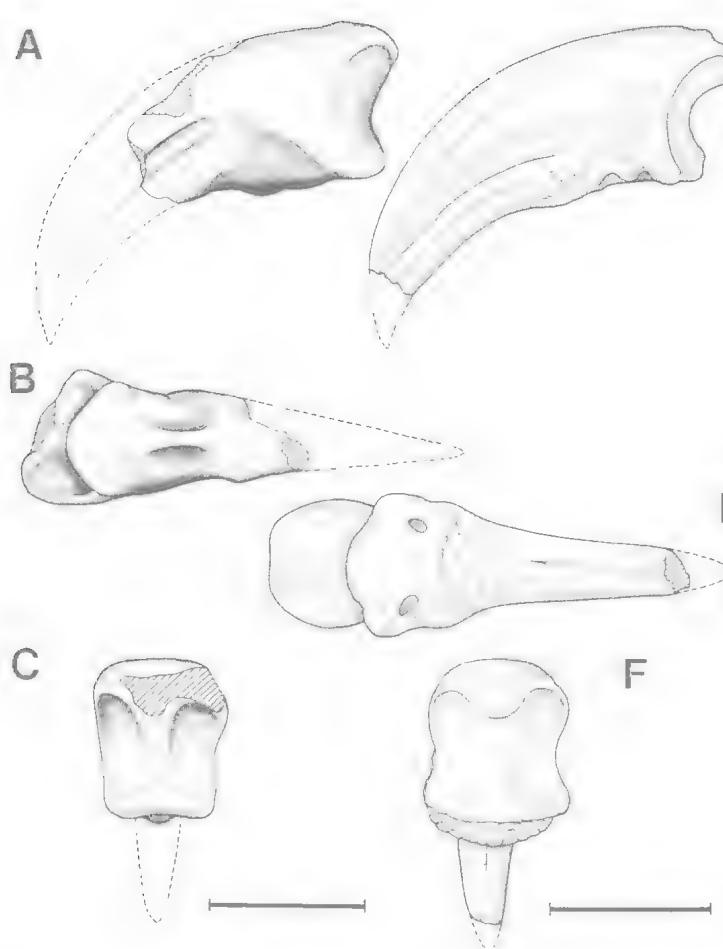
FIG. 4. Ungual phalanx of first manual digit of Alvarezsauridae. A, B, C, *Alvarezsaurus calvoi* (MUCPC 54). D, E, F, *Mononykus olecranus* (Gl N107/6). (A, D, lateral; B, E, ventral; C, F, proximal views). Scale = 10mm.

Osborn, 1905; Madsen, 1976; Ostrom, 1976a; Perle et al., 1994). The scapula of *Alvarezsaurus* seems to be more slender than that of *Mononykus* (Perle et al., 1994), a conclusion that emerges when the scapula is compared with other skeletal elements: for example, in *Alvarezsaurus* (Bonaparte, 1991) the scapula represents 47% of the craniocaudal length of the iliac blade, instead in *Mononykus* (Perle et al., 1994) the scapula represents 86% of the craniocaudal length of the ilium.

A5) Ungual phalanx of digit I ventrally keeled (Fig. 4). Revision of the holotype specimen of *Alvarezsaurus calvoi* (MUCPV 54) allowed identification of a manual ungual phalanx, originally undescribed by Bonaparte (1991). This phalanx is remarkably similar to that of *Mononykus* (see character 22), although in *Alvarezsaurus* the first manual ungual exhibits a strongly developed ventral keel on its proximoventral surface. By contrast, manual claws of most theropods (e.g., *Allosaurus, Ornithomimus, Deinonychus, Patagonykus, Mononykus*; Marsh, 1896; Ostrom, 1969; Madsen, 1976; Perle et al., 1994) this keel is absent and the ventral ungual surface is transversely rounded or flattened.

Mononykus olecranus Perle et al., 1993. The list of characters offered below differs from that originally given by Perle et al. (1993, 1994), not only because some features exhibit a wider distribution than previously thought, but also since new features have been recognised. *Mononykus* differs from other alvarezsaurids in the following autapomorphies:

M1) Absence of pleurocoels in cervical vertebrae (Fig. 2). Presence of pleurocoels in cervical vertebrae is a common feature among Theropoda (Gauthier, 1986). This condition seems to be ancestral for the Alvarezsauridae, because pleurocoel openings are present in neck vertebrae of *Alvarezsaurus* (Bonaparte, 1991). Contrarily, cervical vertebrae of *Mononykus* lack pleurocoels (Perle et al., 1994), a character convergently acquired in ornithurine birds (Chiappe, in press).

M2) Presence of sulcus caroticus in cervical vertebrae (Fig. 2). In *Mononykus* the cranioventral margin of the cervical centra is complex, due to the presence of a craniocaudal groove laterally bounded by a strongly developed ventral processes. This ventral process of *Mononykus* resembles the processus caroticus of modern birds, in which the major muscle mass of M. longus colli ventralis is attached (Baumel & Witmer, 1993). This character is present in other

Mesozoic birds (e.g., *Ichthyornis, Hesperornis* and presumably *Patagopteryx*; Marsh, 1880; Alvarenga & Bonaparte, 1992), although it is unknown in other avialans (e.g., *Iberomesornis, Neuquenornis*; Sanz et al.,1988; Chiappe & Calvo, 1994). The phylogenetic status of this character is uncertain (i.e., synapomorphic of Metornithes or autapomorphic of *Mononykus*), mainly because the sulcus and lateroventral processes are absent in the cervicals of *Alvarezsaurus calvoi* (MUCPV 54).

M3) Presacral vertebrae with diapophyses and parapophyses occupying the same level (Fig. 5). Perle et al. (1994) noted this peculiar condition for *Mononykus* which is unique among Theropoda. The preserved dorsal vertebrae of *Patagonykus* (PVPH 37) show the ancestral archosaur condition in which the parapophyses are cranioventrally placed with respect to the diapophyses. The few dorsal vertebrae known in *Alvarezsaurus* correspond to the cranial region (Bonaparte, 1991).

M4) Dorsal vertebrae lacking hyposphene-hypantrum, and postzygapophyses lateroventrally oriented (Fig. 5). As Perle et al. (1994) described, all of the presacral vertebrae of *Mononykus* lack hyposphene-hypantrum articulations. However, these authors did not include this feature in the diagnosis of *Mononykus*, but interpreted it as an equivocal synapomorphy of Metornithes (Chiappe et al., this volume). However, I do not agree with this interpretation. Although it is true that *Mononykus* lacks hyposphenes (viz., the postzygapophyses are elongate and separated from each other by a deep cleft), the same is not true for *Patagonykus*, because the postzygapophyses are ventrally confluent in a block-like hyposphene, the proportions of which do not significantly differ from those of other theropods such as *Deinonychus* and *Allosaurus* (Ostrom, 1969; Madsen, 1976).
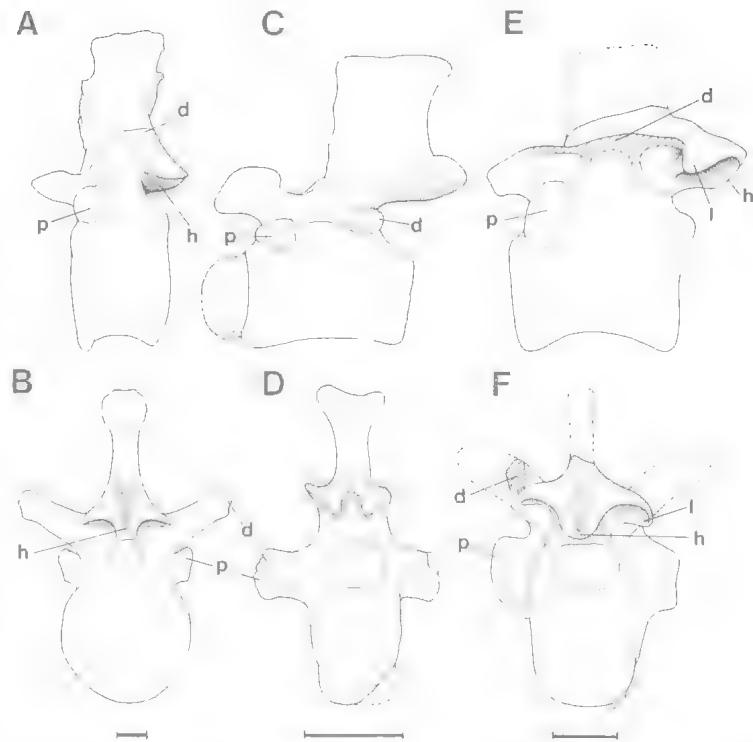

FIG. 5. Dorsal vertebrae of theropod taxa showing the morphology of the postzygapophiseal region. A, B, *Deinonychus antirrhopus* ('11th? dorsal vertebra'; from Ostrom, 1969). C, D, *Mononykus olecranus* ('middorsal'; modified from Perle et al., 1994). E, F, *Patagonykus puertai* (middorsal; PVPH 37). (A, C, E, left lateral; B, D, F caudal view). d=diapophysis, h=hyposphene, l=lateroventral margin of postzygapophysis, p=parapophysis; scale = 10mm.

Another curious aspect of *Mononykus* is that the articular surface of the postzygapophyses is flat and faces lateroventrally, a condition uniformly present along the dorsal series (Perle et al., 1994). On the contrary, the articular facet of the postzygapophyses in other theropods (e.g., *Allosaurus, Deinonychus, Patagonykus*) is ventrally concave and faces more ventrally than laterally.

M5) Cranial dorsal vertebrae transversally compressed. In *Mononykus* (Perle et al., 1994) the centra of the cranial dorsal vertebrae are strongly compressed transversely. As a result, a pronounced ventral keel is present in the cranial dorsal vertebrae. This condition is absent in the available dorsals of *Patagonykus* (PVPH 37), in which the centra are transversely wider and ventrally flat. Preserved cranial dorsal vertebrae of *Alvarezsaurus* (MUCPV 54) are transversely compressed and a slight ventral keel is present, but it is not so marked as in *Mononykus*.
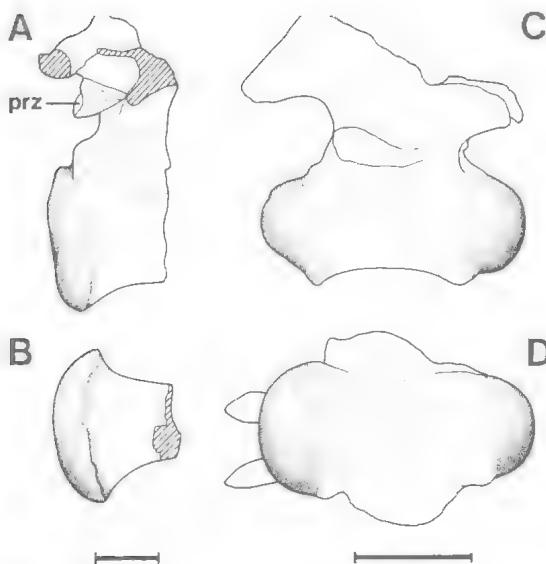
FIG. 6. Middorsal vertebrae of alvarezsaurids showing the morphology of central articular facets. A, B, caudal portion of dorsal vertebra of *Patagonykus puertai* (PVPH 37). C, D, *Mononykus olecranus* (from Perle et al., 1994). (A, C, right lateral view; B, D, ventral; broken bone surface indicated by dashed lines). prz=prezygapophysis of another dorsal vertebra, adjacent caudally; scale = 10mm.

FIG. 7. Last sacral vertebrae of alvarezsaurids. A, B, *Patagonykus puertai* (PVPH 37). C, D, *Mononykus olecranus* (GI N107/6 cast). (A, C, right lateral view; B, D, caudal). Scale = 10mm.

M6) Caudal dorsal vertebrae strongly procoelous. *Mononykus* is one of the few theropods in which caudal dorsal vertebrae are strongly procoelous. *Patagonykus* resembles *Mononykus* in that caudal dorsal vertebrae exhibit the procoelous condition, but they differ in that the convexity of the caudal articular surface of dorsal vertebrae is considerably more pronounced in *Mononykus* than in the Patagonian taxon (Fig. 6). In *Alvarezsaurus* the condition of the dorsal vertebrae is unknown. As Perle et al. (1993, 1994) pointed out, a strong procoelous condition for caudal dorsals is uncommon among theropods and the other case in which it was reported is the ornithothoracine bird *Patagopteryx* (Alvarenga & Bonaparte, 1992; Chiappe, 1992).

M7) Extreme transverse compression of the last sacral vertebra (Fig.7). The last sacral of *Mononykus* exhibits extreme transverse compression. This condition sharply differs from that present in *Patagonykus* and *Alvarezsaurus*, in which the sacral centra are considerably less compressed transversely. The transverse compression described for *Mononykus* is accompanied by a ventral projection of the centrum below the level of the caudal articular surface.

This modification is evident when the last sacral of both *Mononykus* and *Patagonykus* is compared in caudal aspect (Fig.7). In the first taxon the ventral keel nearly equals the dorsoventral depth of the caudal articular surface of the centrum, while in *Patagonykus* the ventral keel is considerably less developed with respect to the caudal articular surface. *Alvarezsaurus* shows the same condition as *Patagonykus*.

M8) Coracoidal shaft elliptical in lateral view (Fig. 3). The coracoid of *Mononykus* is elliptical, as seen in lateral aspect, being craniocaudally long and dorsoventrally low. This morphology is in sharp contrast to that of other maniraptorans (e.g., *Deinonychus, Sinornithoides, Archaeopteryx*, Ornithothoraces; Ostrom, 1969, 1974, 1976a; Russell & Dong, 1993; Walker 1981; Chiappe, 1996) in which the coracoid is dorsoventrally deeper than craniocaudally long with a rectangular to strut-like shape. The coracoid of *Mononykus* resembles the ancestral theropod condition (Gauthier, 1986), and is better interpreted as an evolutionary reversal that is diagnostic for this taxon. The actual shape of the coracoids of *Patagonykus* and *Alvarezsaurus* is not known (the reconstruction given in Fig. 3 is approximate). Hence, the distribution of this character may be wider than thought and its phylogenetic status different.

M9) Coracoid transversely flat (Fig.3). In *Mononykus* (GI N107/6) the lateral surface of the coracoid is slightly convex craniocaudally, but it is lateromedially flat. Instead, in *Patagonykus*, as well as other theropods (e.g., *Allosaurus, Deinonychus, Archaeopteryx*), the coracoid is strongly inflected medially, with the lateral surface proximodistally and craniocaudally convex. Also, *Patagonykus* has a sharp craniocaudal ridge along the lateral surface of the coracoid. Unfortunately, the coracoid of *Alvarezsaurus* is too poorly preserved to discern the condition of this feature.

M10) Sternum with thick carina. The presence of an ossified sternal keel is interpreted as a synapomorphy of Metornithes (Perle et al., 1993, 1994; Chiappe et al., this volume). *Mononykus*, however, is peculiar among avialians in that the sternal carina is transversely thick and V-shaped in cranial view, instead of being transversely narrow and T-shaped as in ornithothoracine birds (Perle et al., 1994, Chiappe et al., this volume). Unfortunately, the sternum is unknown in both *Alvarezsaurus* and *Patagonykus* and for this reason the condition described above for *Mononykus* constitutes an ambiguous autapomorphy of the later taxon.

M11) Radius with extensive articular surface for the ulna (Fig. 8). In *Mononykus* (Perle et al., 1994) the proximocaudal portion of the radius forms a single, extensive surface for articulation with the ulna. In *Patagonykus*, instead, two proximocaudal surfaces for the ulnar articulation are present. However, these surfaces are considerably smaller than those of the Mongolian taxon.

M12) Radius with carpal articular facet hypertrophied (Fig. 8). *Mononykus* is unique among theropods in the unusual development of the
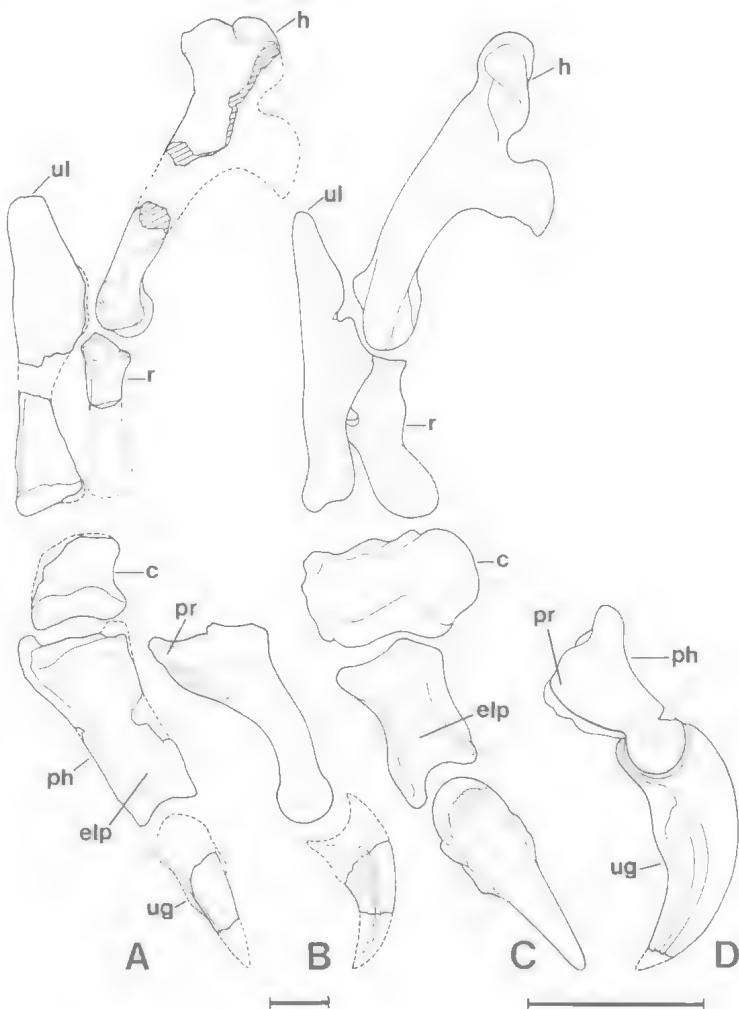

FIG. 8. Forelimbs of alvarezsaurids. A, B, composite reconstruction based on left and right forelimb bones of *Patagonykus puertai* (PVPH 37). C, D, *Mononykus olecranus* (from Perle et al., 1994). (A, C, lateral view; B, D, caudal view of first phalanx and ungual phalanx of digit I). c=carpometacarpus, elp=extensor ligamentary pit, h=humerus, ph=first phalanx, pr=proximomedial ridge, r=radius, ul=ulna, ug=ungual phalanx; scale = 20mm.

radiocarpal articular facet (Perle et al., 1994). This morphology is almost certainly absent in *Patagonykus*, because the shaft of the radius is rod-like and triangular in cross section, lacking indications of the presence of an hypertrophied radiocarpal articular facet.

M13) First phalanx of digit I with a very prominent proximocaudal process (Fig. 8). In *Mononykus* the proximocaudal corner of the first phalanx of digit I develops a prominence that wraps over the ginglymus of metacarpal I. This
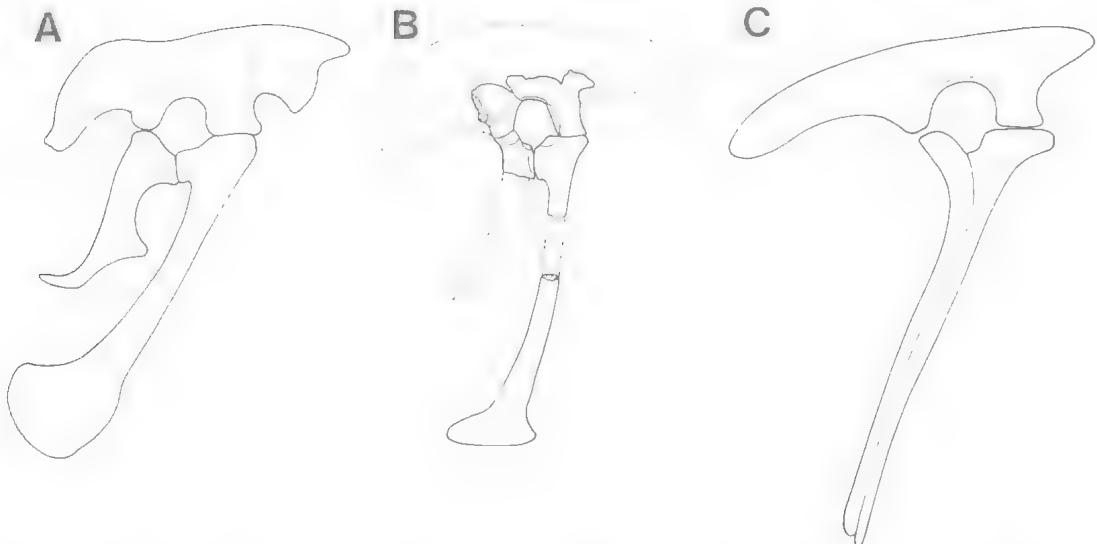
FIG. 9. Pelves of maniraptorans in lateral aspect. A, *Adasaurus mongoliensis* (from Barsbold, 1983). B, *Patagonykus puertai* (composite reconstruction based on left and right bones of the pelvis of PVPH 37). C, *Mononykus olecranus* (from Perle et al., 1994). Not to scale.

process, probably related to the insertion of strong extensor muscles, is absent in other theropods, including *Patagonykus*.

M14) Pubis caudoventrally oriented (Fig. 9). In *Mononykus* (Perle et al., 1994; Chiappe et al., this volume) the main axis of the pubic shaft describes an angle of nearly 70° with the proximal iliac surface of the pubis. In *Patagonykus*, instead, the proximal portion of the pubic shaft is oriented almost perpendicularly with respect to this surface of the pubis. The differences in pubic retroversion documented within Alvarezsauridae supports the interpretation that a strong caudoventral orientation of the pubis, becoming parallel to the ischium, evolved more than once within Metornithes: once in *Mononykus* and again in birds more derived than *Archaeopteryx* (Wellnhofer, 1974; 1988; 1993).

M15) Pubic foot absent (Fig. 9). *Mononykus* lacks a distal pubic foot (Perle et al., 1993, 1994; Chiappe et al., this volume). This feature was originally thought to be an ambiguous synapomorphy of Metornithes, because a distal foot was present in the basal ornithothoracine *Sinornis* (Sereno & Rao, 1992, Perle et al., 1993; Chiappe, 1995c). However, the absence of a distal foot in the pubis of *Mononykus* is interpreted as autapomorphic of this taxon, because a well developed distal expansion is documented in the pubis of *Patagonykus* and basal ornithothoracine birds. The pubes are not preserved in *Alvarez-*

saurus nor in the basal ornithothoracine bird *Iberomesornis* (Sanz et al., 1989). In the context of all the evidence, I interpret the lack of a pubic foot as independently evolved in *Mononykus* and ornithothoracines more derived than *Patagopteryx*.

M16) Ischium extremely reduced (Fig. 9). In *Mononykus* (Perle et al., 1993, 1994; Chiappe et al., this volume) the ischium is markedly reduced. In *Patagonykus* the ischium is also reduced with respect to other theropods (e.g., Ornithomimidae), but its proximal end, at least, is more massive than that of *Mononykus*. *Patagonykus* retained a well defined ischiac pedicle on the ilium, with the antitrochanter extending over both ilium and ischium. The articulation between pubis and ischium is dorsoventrally deep in the Patagonian taxon. In *Mononykus* the ilium and ischium are strongly fused, and the antitrochanter is formed by both pelvic bones (Perle et al., 1994).

M17) Femoral distal condyles transversely expanded, nearly confluent below popliteal fossa (Fig. 10). In *Mononykus* (Perle et al., 1994) the medial condyle of the femur is extremely expanded transversely, its transverse axis being nearly 75% of its craniocaudal extension. Perle et al. (1993, 1994) noted the distal enclosure of the popliteal fossa resembling the condition present in more derived birds (Chiappe & Calvo, 1994; Chiappe, 1992, 1995a). This enclosure of the popliteal fossa results from the transverse expan-

sion of both the medial distal condyle and the ectocondylar tuber, which are almost in contact with each other, distal to the popliteal fossa. On the contrary, in *Patagonykus*, as in other non-avialian theropods (e.g., *Deinonychus*, Ornithomimidae, Tyrannosauridae) this fossa is entirely open distally, because both the medial condyle and the ectocondylar tuber are less expanded transversely. The modification described above for the femur of *Mononykus* correlates with that present in the proximal tibia, in which the outer condyle greatly expands transversely, contacting with the inner condyle of the same bone. In regard to the tibia, *Patagonykus* exhibits the ancestral condition, with the outer condyle less expanded transversely.

M18) Tibia with accessory (medial) cnemial crest. As interpreted by Perle et al. (1993, 1994), the presence of a smooth crest on the medial face of the proximal tibia is convergent with Ornithurae, because a medial crest is absent in Maniraptora ancestrally (e.g., *Deinonychus*; Ostrom, 1969), as well as in *Patagonykus*.

M19) Outer malleolus of distal tibia craniocaudally thick (Fig. 11). In *Alvarezsaurus* and *Patagonykus* the outer malleolus of the distal tibia is craniocaudally narrow with respect to that portion of the calcaneum that is in front of it, representing nearly 36% of the craniocaudal diameter of the calcaneum. In *Mononykus*, instead, the outer malleolus is craniocaudally thicker, representing nearly 143% of the craniocaudal dimension of that portion of the calcaneum that is in front of it.

M20) Astragalocalcaneum with deep intercondylar groove (Fig. 11). In *Mononykus* the fusion between astragalus and calcaneum is stronger, and the intercondylar groove deeper, than in both *Patagonykus* and *Alvarezsaurus*. In the latter two taxa the astragalocalcaneal suture is still visible.

M21) Ascending process of astragalus laterally displaced (Fig. 11). In *Mononykus* the ascending astragalar process is deeply notched along its medial margin, resulting in an ascending process transversely narrow in cranial view (Perle et al., 1994). Also, the ascending process of the astragalus appears to be more laterally placed than in other maniraptorans (e.g., *Patagonykus, Alvarezsaurus, Deinonychus*), as suggested by the overlap of the lateral margin of this process with the lateral margin of the tibia. This condition contrasts with that present in other Coelurosauria (e.g., Tyrannosauridae, Ornithomimidae, Dromaeosauridae, *Patagonykus, Alvarezsaurus*) in which the ascending process of the astragalus
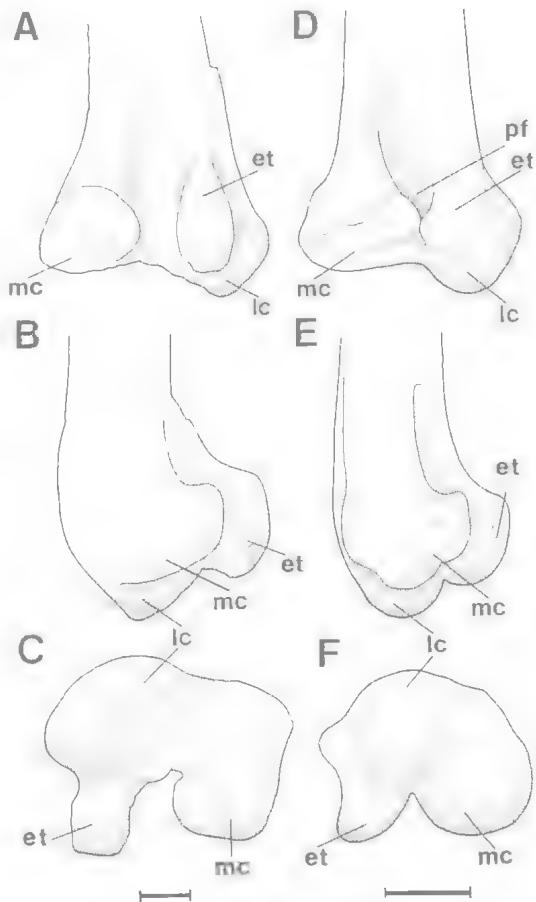

FIG. 10. Left distal femora of alvarezsaurids. A, B, C, *Patagonykus puertai* (PVPH 37). D, E, F, *Mononykus olecranus* (from Perle et al., 1994). (A, D, caudal view; B, E, medial; C, F, distal). et=ectocondylar tuber, lc=lateral condyle, mc=medial condyle, pf=popliteal fossa; scale = 20mm.

is transversely wide. Particularly the medial margin of this process is not notched as in *Mononykus*, but extends in a nearly straight line from the medial condyle of the astragalus to the proximal tip of the ascending process. The lateral margin of the ascending process does not reach the lateral border of the tibia. Interestingly, the condition of *Mononykus* resembles that of modern avians, in which the 'pretibial bone' (homologous to the ascending process of the astragalus; McGowan, 1985) is transversely narrow and laterally displaced.

M22) Femoral trochanteric crest present. In Coelurosauria ancestrally (e.g., Ornithomimidae, Tyrannosauridae), as well as in *Deinonychus* (MCZ 4371), *Patagonykus, Alvarezsaurus* and
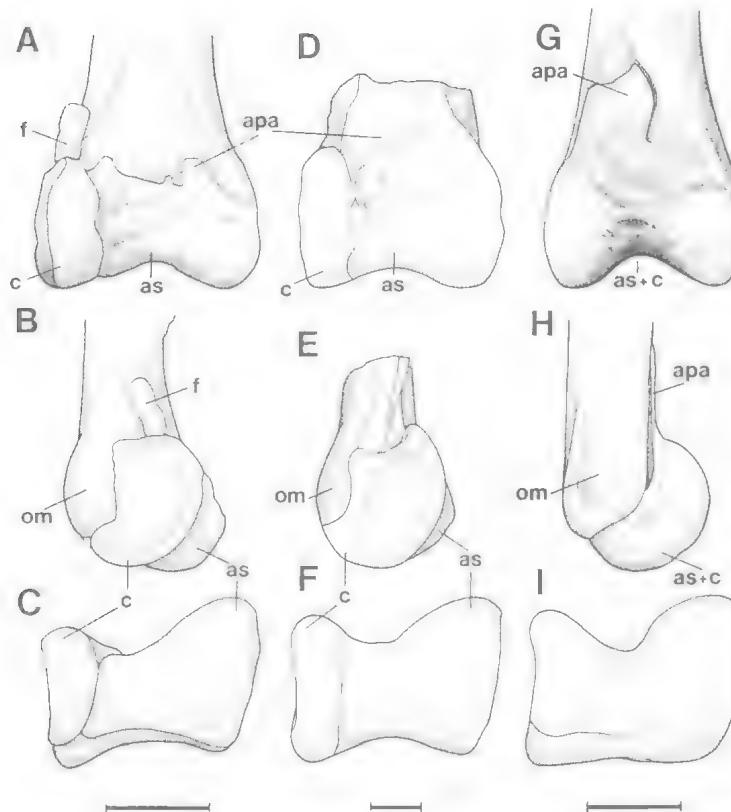
FIG. 11. Right distal tibia and astragalocalcaneum of Alvarezsauridae. A, B, C, *Alvarezsaurus calvoi* (MUCPV 54). D, E, F, *Patagonykus puertai* (PVPH 37). G, H, I, *Mononykus olecranus* (GI N107/6). (A, D, G, cranial view; B, E, H, lateral; C, F, I, distal; reconstruction indicated by dashed lines). as=astragalus, apa=ascending process of astragalus, c=calcaneum, f=fibula, om=out tibial malleolus; scale = 10mm.

Archaeopteryx, both anterior and greater femoral trochanters are separated by a cleft. In contrast *Mononykus* exhibits a femoral trochanteric crest (e.g., anterior trochanter undivided from the greater trochanter), a derived condition that is shared with more derived birds.

M23) Fibula does not articulate with the tarsus (Fig. 11). This feature was originally considered by Perle et al. (1993) as synapomorphic of Metornithes, because it is shared by *Mononykus* and the Ornithothoraces. However, other alvarezsaurids exhibit the plesiomorphic condition: in *Patagonykus* the fibula is incomplete, but the presence of a deep socket on the proximal calcaneal surface suggests that in this taxon the fibula articulated with the tarsus, a condition that also found in *Alvarezsaurus* (Bonaparte, 1991).

INGROUP RELATIONSHIPS. *Patagonykus* and *Mononykus* share seventeen characters which are absent or unknown in *Alvarezsaurus*. The monophyly of Alvarezsauridae is supported here by eleven derived characters.

Patagonykus + *Mononykus* clade. Several features support the conclusion that *Patagonykus* and *Mononykus* are more closely related than either is to *Alvarezsaurus*. Some of these features are absent in *Alvarezsaurus* and are readily interpreted as synapomorphic of the *Patagonykus* + *Mononykus* clade (characters 1 & 2), others are contingent upon the results of the cladistic analysis (characters 3 & 4). However, the condition of most of the apomorphies uniting *Patagonykus* and *Mononykus* is unknown for *Alvarezsaurus*, because of the fragmentary nature of the available material. Consequently, a large set of characters (5 through 17) used to unite *Patagonykus* + *Mononykus* may become synapomorphic of a more inclusive group (e.g., Alvarezsauridae), pending additional information on *Alvarezsaurus*:

1) Caudal articular surface of the centra of the last sacral and proximal caudal vertebrae strongly spherical. *Mononykus, Patagonykus* and *Alvarezsaurus* clearly differ from other theropods since they share last sacral and most of the caudal vertebrae with a ball-shaped caudal surface (character 19). However, *Alvarezsaurus* seems to be less derived than other alvarezsaurids because the caudal surfaces of the last sacral vertebra and caudal vertebrae are not as spherical as in *Patagonykus* and *Mononykus*. Moreover, the procoelous condition in *Alvarezsaurus* appears to be confined to the last sacral and to the caudal vertebrae, since the cranial articular surface of the presumed sacral 2 of *Alvarezsaurus* is almost planar.

2) Sacral vertebrae ventrally keeled (Fig. 7). In *Allosaurus* (Gilmore, 1920), *Gallimimus*

(Osmólska et al., 1972) and *Archaeornithomimus* (AMNH 6567) the ventral surface of sacral centra is smooth and convex in cross-section. This condition also applies to *Ornithomimus* (USNM 2164; see Gilmore, 1920), although in this taxon the sacral centra are ventrally grooved. The sacral centra of *Deinonychus* (MCZ 4371), *Ornitholestes* (AMNH 619) and *Archaeopteryx* (Wellnhofer, 1974, 1993) are not keeled ventrally. Sacral vertebrae are not keeled in *Iberomesornis* and *Sinornis* (Sanz et al., 1988; Chiappe, pers. comm.) and the same is true for more derived birds (e.g., *Ichthyornis, Hesperornis*; Marsh, 1880): other avialans, instead, bear a ventral groove (e.g., *Baptornis, Patagopteryx*; Martin & Tate, 1976; Chiappe, 1992; Perle et al., 1994). Alvarezsaurids differ from the remaining Coelurosauria in the presence of a ventral keel in the caudal sacral vertebrae. However, the degree of transverse compression of this keel varies among alvarezsaurids: in *Alvarezsaurus* (MUCPV 54) the presumed sacral 1 is transversely wide and ventrally convex in cross-section, while the sacrals 2-3 are ventrally grooved, resembling the condition present in *Ornithomimus* (Gilmore, 1920). The penultimate sacral vertebra of *Alvarezsaurus* (presumably sacral 4) is more compressed transversely than more cranial sacrals; this vertebra is slightly keeled, but a rudimentary ventral canal is still present. The last sacral (presumably sacral 5) of *Alvarezsaurus* bears a ventral keel, but it is not so prominent and transversely compressed as in *Patagonykus* and *Mononykus*. In *Patagonykus* (PVPH 37) the transverse compression of the ventral keel increases caudally, show-
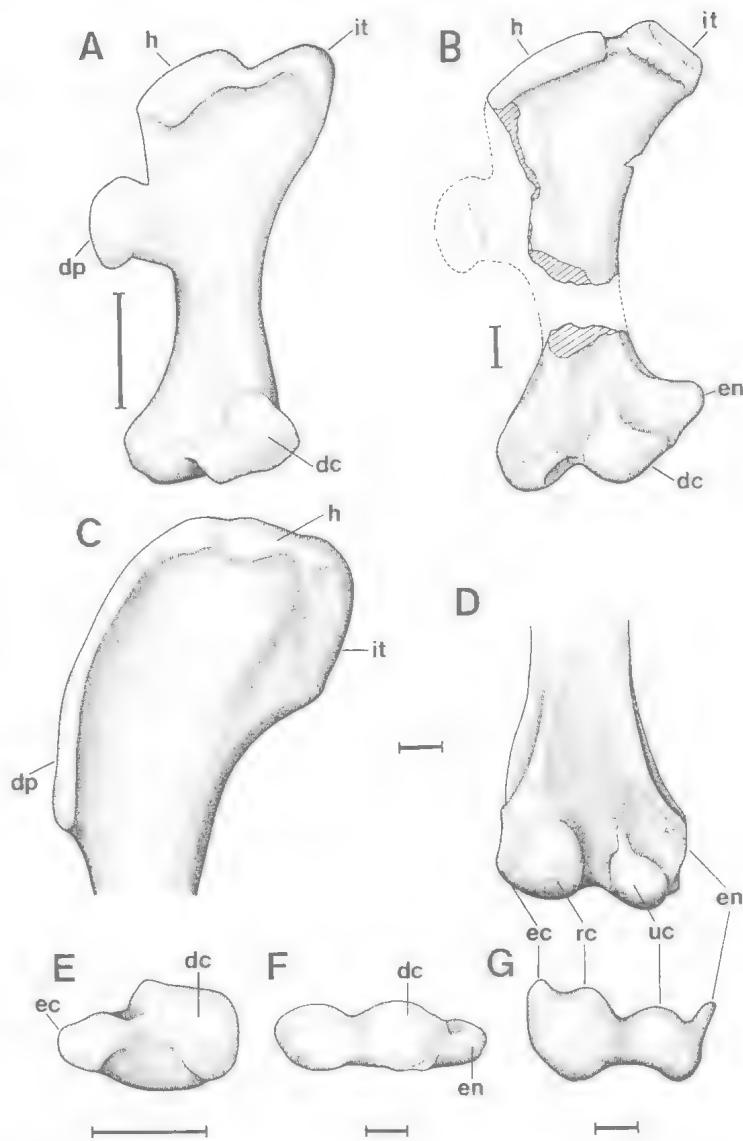

FIG. 12. Humeri of theropod taxa. A, E, *Mononykus olecranus* (modified from Perle et al., 1994). B, F, *Patagonykus puertai* (composite reconstruction based on left and right humerus of PVPH 37). C, D, G, *Deinonychus antirrhopus*; C, proximal end (from Ostrom, 1969), D, G, distal end of humerus (reconstruction based on AMNH 3015 and MCZ 4371). (A, B, C, D, cranial view; E, F, G, distal). dc=distal condyle, dp=deltopectoral crest, h=humeral head, ec=ectepicondyle, en=entepicondyle, it=internal tuberosity, rc=radial condyle, uc=ulnar condyle; scale = 10mm.

ing the maximum compression in the last sacral (presumably sacral 5). In *Mononykus* the first sacral is transversely more compressed than the dorsal vertebrae (Perle et al., 1994) and exhibits a slight longitudinal ridge along its ventral surface. I interpret *Mononykus* as more derived than
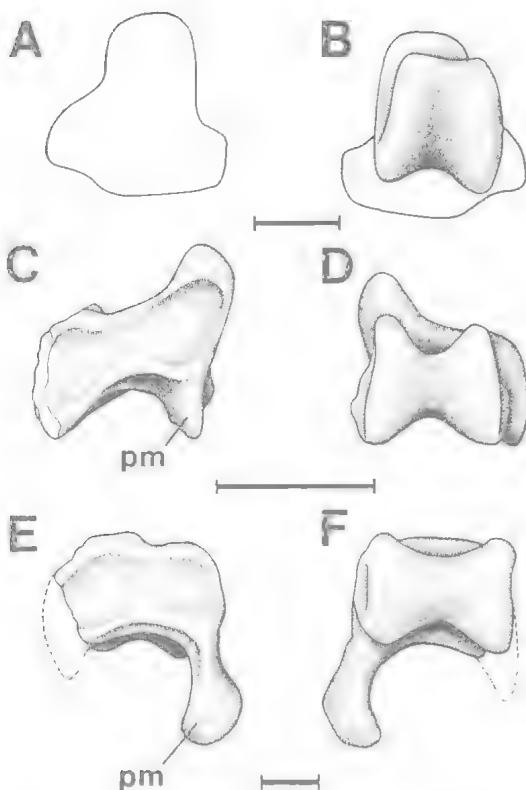
FIG. 13. First phalanx of digit I of maniraptoran theropods. A, B, *Deinonychus antirrhopus* phalanx of the left manus (A, taken from Ostrom, 1969; B, from YPM 5206). C, D, *Mononykus olecranus* phalanx of the right manus (C, from Perle et al., 1994; D, from GI N107/6). E, F, *Patagonykus puertai* phalanx of the right manus (PVPH 37). (A, C, E, proximal view; B, D, F, distal). pm=proximomedial ridge; scale = 10mm.

other alvarezsaurids in this respect, since the sacrals are extremely compressed laterally (Perle et al., 1994; see character M7).

3) Femoral fourth trochanter present. A femoral fourth trochanter is present in basal coelurosaurs (e.g., Ornithomimidae, Tyrannosauridae). This structure has been retained, albeit reduced, in dromaeosaurids as it is seen in *Deinonychus* (MCZ 4371; contra Ostrom, 1976b). *Archaeopteryx, Alvarezsaurus,* and Ornithothoraces lack the fourth trochanter, a condition interpreted as synapomorphic of Avialae. In the context of the evidence, the shared presence of a fourth trochanter in *Mononykus* and *Patagonykus* is considered as an apomorphic reversal.

4) Supracetabular crest present. The absence of a supracetabular crest is hypothesised as

synapomorphic of Maniraptora, because such a crest is lacking in *Deinonychus, Archaeopteryx, Alvarezsaurus* and the Ornithothoraces. Following that, the presence of such a crest in the ilium of *Patagonykus* and *Mononykus* is interpreted as a secondary reversal.

5) Posterior dorsal vertebrae procoelous (Fig. 6). *Patagonykus* and *Mononykus* share procoelous caudal dorsal vertebrae. However, in the first taxon the convexity of the caudal articular surface is considerably less marked than in *Mononykus*, in which this surface is ball-shaped. Interestingly, the development of a ball-shaped, caudal articular surface in sacral vertebrae is almost the same in *Patagonykus* and *Mononykus* (Fig. 7) suggesting that the procoelous condition evolved from caudal to dorsal vertebrae. Mid and caudal dorsal vertebrae are unknown in *Alvarezsaurus* (Bonaparte, 1991), but it is possible that they may have been amphiplatyan or amphicoelous, since the disarticulated second sacral vertebra of the holotype (MUCPV 54) has a flat caudal surface. *Alvarezsaurus*, however, is coded as a question mark for this character.

6) Bicipital tubercle of coracoid absent (Fig. 3). A bicipital tubercle is absent in the coracoids of *Mononykus, Patagonykus* and presumably also in *Alvarezsaurus* (unfortunately, most of the caudal and distal portions of the coracoid are missing in the holotype). This condition sharply contrasts with that present in Theropoda ancestrally. For example, in *Allosaurus* the bicipital tubercle is slightly marked, but it forms a distinct prominence on the lateral surface of the coracoid, as is seen in caudal view (Madsen, 1976). In ornithomimids (e.g., *Ornithomimus* AMNH 5355; *Archaeornithomimus* AMNH 6567, 6566) the biceps tubercle is also prominent, but it is even more developed in maniraptorans. Such is the case for *Deinonychus* (YPM 5236), which exhibits a biceps tubercle more developed than in most theropods (Ostrom, 1974) and *Archaeopteryx* in which the tubercle is proportionally larger than that of *Deinonychus* (Ostrom, 1974; Wellnhofer, 1988, 1993). In avialians more derived than *Archaeopteryx* (e.g., Enantiornithes; Walker, 1981) the acrocoracoid (hypothesised as the homologue of the bicipital tubercle; Ostrom, 1976a), consists of a robust structure, that in the Ornithothoraces is proximally placed with respect to the glenoid facet (Chiappe, 1992).

7) Forelimbs less than 20% of hindlimb length. In Theropoda ancestrally the forelimbs represent 40-53% of hindlimb length, as it occurs in

Herrerasaurus, Coelophysis, Syntarsus, Dilophosaurus, Piatnitzkysaurus and *Compsognathus* (Raath, 1969, Colbert, 1989; Ostrom, 1978; Welles, 1984; Novas, 1994; Sereno, 1994). Possession of extremely short forelimbs (with respect to hindlimb length) seems to have evolved more than once in theropod evolution (Novas, 1992; Perle et al., 1994). Examples of such shortening are seen in the neoceratosaurian theropods (e.g., *Ceratosaurus, Carnotaurus*; Bonaparte et al., 1990; Novas, 1992), the basal tetanurine *Torvosaurus* (Galton & Jensen, 1979; Holtz, 1994) and the coelurosaurian Tyrannosauridae (Novas, 1991, 1992; Holtz, 1994). In the latter taxon the forelimbs represent 22-26% of the hindlimb length (Lambe, 1917), but in *Mononykus* the forelimbs are even shorter than in tyrannosaurids, since they represent nearly 18% of the length of the hindlimbs (Perle et al., 1993, Fig. 2). In *Patagonykus* (PVPH 37) the forelimbs are known from portions of humerii, ulnae and the almost complete left manus (carpometacarpus plus digit I). Although it is not possible to obtain a ratio of forelimb versus hindlimb length for *Patagonykus*, the proportions of the currently available bones of this taxon suggest that the forelimbs also were very short. Bonaparte (1991) arrived at the conclusion that *Alvarezsaurus* possibly had reduced forelimbs on the basis of the proportionally reduced scapular girdle of this theropod. This suspicion is supported by the stout aspect and large size of the ungual phalanx of digit I (Fig. 4). The morphology of this ungual allows the prediction that the proximal elements of the forelimb of *Alvarezsaurus* were morphologically similar to those of *Mononykus* and *Patagonykus* (Perle et al., 1993, 1994).

8) Humeral head with major transverse axis ventrolaterally inclined with respect to the longitudinal axis of the humerus, and internal tuberosity proximally projected (Fig. 12). In *Mononykus* the humeral head is lateroventrally inclined with respect to the longitudinal axis of the humerus. Additionally, the internal tuberosity is proximally projected, reaching nearly the same level as the humeral head. By contrast, in other theropods (e.g., *Deinonychus*; Ostrom, 1969) the major transverse axis of the humeral head is horizontally held with respect to the longitudinal axis of the humerus, or it is inclined ventromedially (e.g., *Ichthyornis*; Marsh, 1880) with respect to the longitudinal axis. Also, in most theropods the internal tuberosity is a cone-shaped structure (e.g., Ceratosauria, Tyrannosauridae, *Ornitholestes* AMNH 619; Rowe & Gauthier,
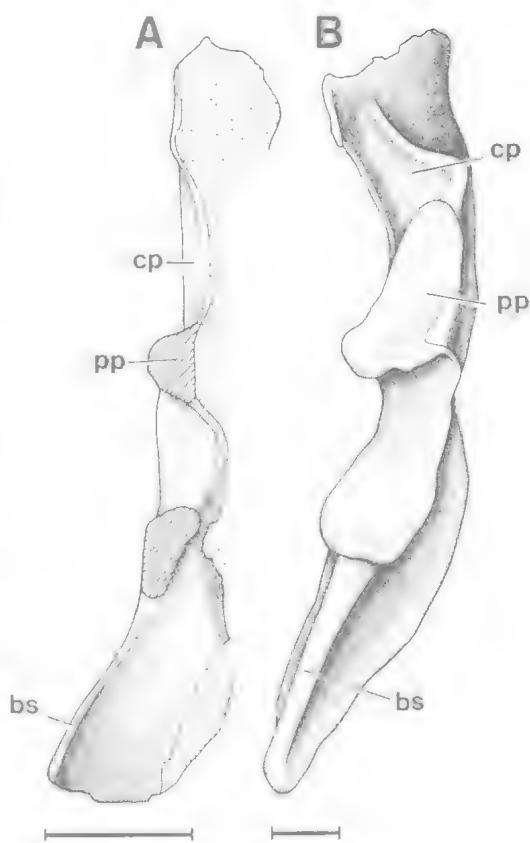

FIG. 14. Ilium of maniraptoran theropods in ventral aspect. A, right ilium of *Alvarezsaurus calvoi* (MUCPV 54). B, left ilium (reversed) of *Deinonychus antirrhopus* (AMNH 3015). Sandstone matrix indicated by stippling. bs=brevis shelf, cp=fossa for origin of M. cuppedicus, pp=pubic peduncle; scale = 20mm.

1990; Osborn, 1917), or it forms a longitudinally expanded prominence that is medially and slightly caudally projected, and distally placed with respect to the humeral head (e.g., *Deinonychus, Ichthyornis*; Marsh, 1880; Ostrom, 1969). The known humerus of *Patagonykus* has unconnected proximal and distal portions, such that determination of the orientation of the humeral head and internal tuberosity with respect to the humeral shaft is difficult to assert. However, the proximal end of the humerus of *Patagonykus* closely resembles that of *Mononykus*, and the features described above for the later taxon seem to apply also to the Patagonian species. Since the humerus is unknown in *Alvarezsaurus* (Bonaparte, 1991) the peculiar morphology of the proximal end of the humerus shared by *Patagonykus* and

Mononykus is considered as an ambiguous synapomorphy of the Alvarezsauridae.

9) Humerus with a single distal condyle; ulna and radius tightly appressed proximally, forming a cup-like articular surface for the humerus (Fig. 12). In Theropoda, ancestrally (for example, *Piatnitzkysaurus* MACN-CH 895; *Deinonychus* AMNH 3015, MCZ 4371; *Ornitholestes* AMNH 619; Ornithomimidae; Barsbold & Osmólska, 1990), the distal end of the humerus exhibits two distal condyles, the radial one being larger than the ulnar condyle. Both ulnar and radial condyles are separated by an intercondylar groove, a condition that is retained in recent birds (Baumel & Witmer, 1993). Also, the humeral cotylus of the ulna is subtriangular in proximal view, with an acute cranial projection and a craniolateral concavity for the reception of the radius. In Theropoda, ancestrally, the radius and ulna lack proximal articular facets between them. Also, the ulna and radius bear independent proximal articular surfaces for the ulnar and radial condyles of the humerus, respectively. Alvarezsaurids, instead, are unique among archosaurs in the peculiar propodial-epipodial articulation, consisting in the presence of a single, and well developed, condyle in the distal humerus which articulates with a continuous, cup-like articular surface formed by both radius and ulna. In *Patagonykus* and *Mononykus* the humeral cotylus of the ulna is subelliptically shaped and lacks the lateral concavity to accommodate the radius. The latter bone has moved entirely over the cranial aspect of the ulna and both bones are tightly articulated proximally.

Some minor differences exist in the propodial-epipodial articulation of alvarezsaurids (Fig. 12): while in *Patagonykus* the humeral distal condyle is ball-shaped and elliptical in contour, in *Mononykus* it is trochlear and trapezoidal in distal aspect. The complex morphology of the distal humeral condyle of *Mononykus* is due to the strong craniocaudal expansion of its medial side, equalling its transverse axis (Fig. 12A, E). Furthermore, the proximal articulation between the radius and ulna is extremely extended in *Mononykus* (Perle et al., 1994) and is readily interpreted as autapomorphic for the Mongolian taxon (see character M11).

10) Olecranal process of ulna strongly developed (Fig. 8). The development of the olecranal process is variable within Dinosauria, although it is feebly developed in most theropods (e.g., *Syntarsus, Piatnitzkysaurus, Allosaurus,* Ornithomimidae, *Deinonychus, Archaeopteryx,*

Ornithothoraces; Ostrom, 1969, 1976a; Raath, 1969; Madsen, 1976; Bonaparte, 1986a; Baumel & Witmer, 1993; Barsbold & Osmólska, 1990). *Patagonykus* and *Mononykus* differ from the remaining dinosaurs because they share a strongly developed ulnar olecranon process: that in *Mononykus* represents 40% of the whole length of the bone (Perle et al., 1994). The relative size and the stout morphology of the ungual phalanx of manual digit I of *Alvarezsaurus* (see characters 7 & A5) suggests that the presence of a well developed olecranal process probably had a distribution wider than thought.

11) Ulnar caudal margin straight (Fig. 8). Gauthier (1986) considered *'ulna bowed posteriorly'* as a diagnostic character of Maniraptora. Avialae and *Deinonychus*, and apparently also in *Troodon* and *Sinornithoides* (Russell, 1969; Russell & Dong, 1993b) the caudal border of the ulna is uniformly convex, excepting the distal extremity that, as in other tetanurines, is posteriorly projected (the ulna is slightly bowed in the Ornithomimidae, although it is not convex caudally but cranially — that is towards the radius; Nicholls & Russell, 1985; Barbold & Osmólska, 1990; Osmólska et al., 1972). In *Mononykus* (Perle et al., 1994) the ulna is straight in lateral and cranial aspects. Preserved portions of the ulna of *Patagonykus* show that the caudal margin is straight. The straight shaft of the ulna in alvarezsaurids is interpreted as an evolutionary reversal that might be related to the strong reduction of the forelimbs.

12) Carpometacarpus massive, short and quadrangular (Fig. 8). *Patagonykus* and *Mononykus* share a carpometacarpus (= semilunate carpal + first metacarpal) that is dorsoventrally compressed and quadrangular in dorsal view, a condition quite unusual for a theropod (Perle et al. 1994; Novas, in press a). In *Patagonykus* and *Mononykus* the distal condyle of metacarpal I is transversely wide and dorsoventrally compressed, with a shallow dorsoventral groove. In contrast to other theropods such as *Herrerasaurus* (PVSJ 373; Sereno, 1994), *Coelophysis* (Raath, 1969), *Torvosaurus* (Galton & Jensen, 1979), *Allosaurus* (Madsen, 1976) and *Deinonychus* (Ostrom, 1969), metacarpal I is proximodistally long and transversely narrow and the distal end forms a ginglymoid articulation. *Mononykus*, and presumably also *Patagonykus*, differ from other coelurosaurs (e.g., *Oviraptor, Deinonychus, Velociraptor, Archaeopteryx*; Ostrom, 1976a; Barsbold et al., 1990) in that the semilunate carpal articulates

distally only with metacarpal I, instead of with both metacarpal I and II as in Maniraptora ancestrally (Gauthier, 1986). Size disparity between metacarpal I and the semilunate carpal is readily apparent in alvarezsaurids: the transverse width of metacarpal I nearly matches that of the semilunate carpal. This disparity is probably due to hypertrophy of the metacarpal I.

The main difference between *Mononykus* and *Patagonykus* is that in the first taxon the semilunate articulation of the carpometacarpus is considerably more extended cranially and distally than in *Patagonykus*, resulting in a very close approximation between the semilunate articulation and the distal condyle of the metacarpal I. In *Deinonychus* and *Archaeopteryx* (Ostrom, 1969, 1976a) the medial (cranial, if rotated) margin of the metacarpal I forms a narrow ridge, resembling the condition described for *Mononykus* (Perle et al., 1994).

13) Digit I larger than the remaining digits of the hands (Fig. 8). The hand of most coelurosaurs is characterised by being gracile and elongate, with the first digit smaller than the second digit, both in length and in transverse diameter (Ostrom, 1969; Gauthier, 1986; Barsbold et al., 1990). In *Mononykus*, instead, digit I is much larger (in both transverse width and proximodistal length) than digits II and III. As noted by Perle et al. (1994), metacarpals II and III are not only strongly reduced, but they are fused to each other and with metacarpal I, without the delimitation of any intermetacarpal space. Interestingly, the oviraptorosaur *Ingenia* (Barsbold et al., 1990) constitutes the only known non-alvarezsaurid theropod in which digit I is proportionally larger than the outer digits, although the degree of the reduction of the external digits is not so marked as in *Mononykus*. Close resemblances of the available manual bones of *Patagonykus* and *Alvarezsaurus* suggest that the South American taxa also shared the condition described above for *Mononykus*.

14) Phalanx I of manual digit I showing B-shaped proximal articular surface, hook-like proximomedial processes, symmetrical distal ginglymus and deep extensor ligamentary pit (Fig. 13). *Patagonykus* and *Mononykus* are unique among Archosauria in the morphology of the first phalanx of digit I. This phalanx is craniocaudally wide and lateromedially compressed, resulting in a curious proximal articulation, which describes a horizontal 'B' in proximal aspect. This morphology sharply contrasts with that seen in other theropods, in which the

proximal contour of the first phalanx of digit I is triangular (e.g., *Deinonychus*; Ostrom, 1969), or describes a vertical rectangle (as in *Allosaurus*; Madsen, 1976). Another peculiarity is the presence of a pair of strongly developed proximomedial ridges bearing muscle scars. Distally, the ginglymus of the first phalanx forms a craniocaudally wide, symmetrical pulley, proximally preceded by a deep extensor ligamentary pit (Figs 8 & 13). By contrast, in other dinosaurs (e.g., *Mussaurus* MLP 68-II-27-1; *Deinonychus* YPM 5206; *Allosaurus*; Madsen, 1976), the ginglymus is transversely more compressed and the extensor pit is absent. Further, the flexor ligamentary pit is more marked in *Mononykus* and *Patagonykus* than in other theropods.

15) Medial condyle of femur transversely wide and distally flat (Fig. 10). The medial condyle of the distal femur is transversely narrow and distally convex in non-avialian theropods (e.g., *Allosaurus* CM 21726; *Tyrannosaurus* CM 9380; *Deinonychus* MCZ 4371), *Archaeopteryx* (Eichstatt specimen, cast) and early Ornithothoraces (e.g., Enantiornithes, MACN unnumbered cast). In *Patagonykus* and *Mononykus*, instead, the medial condyle of the distal femur is rectangular and distally flat. In the Patagonian taxon the transverse axis of this condyle represents nearly 66% of its craniocaudal extension, while in *Mononykus* it is 75%. The transverse extension of the medial condyle of the distal femur resembles that present in recent birds, such as *Rhea* (pers. collection).

16) Ectocondylar tuber caudally projected, well behind the medial distal condyle (Fig. 10). In *Allosaurus* (Gilmore, 1920), *Ornitholestes* (AMNH 619), *Gallimimus* (Osmólska et al., 1972), *Tyrannosaurus* (USNM 10.754) and *Deinonychus* (MCZ 4371), the ectocondylar crest of the femur does not caudally surpass the level of the medial femoral condyle. In *Patagonykus* and *Mononykus*, instead, the ectocondylar crest strongly projects caudally, surpassing the medial femoral condyle. This condition resembles that present in modern birds (e.g., *Rhea*) in which the crista tibiofibularis (the caudal portion of which is considered to be homologous with the ectocondylar tuber; Chiappe, 1996) is more caudally projected than the medial condyle of the femur.

17) Fibular condyle of femur conical and projected distally (Fig. 10). In *Mononykus* and *Patagonykus* the fibular condyle of the femur constitutes a well defined, cone-shaped structure, which is strongly projected distally. This condi-

tion contrasts with that seen in other theropods (e.g., *Allosaurus*; *Archaeornithomimus*, AMNH 6570; *Deinonychus*) in which the lateral condyle of distal femur is only slightly more projected distally with respect to the medial condyle. The lateral condyle of the femur is conical in some ornithomimids (e.g., *Gallimimus*, Osmólska et al., 1972, pl. 46), as well as in the tyrannosaurid *Alectrosaurus* (AMNH 6554), but in neither case is it so prominent as in alvarezsaurids. The condition of this femoral condyle in *Archaeopteryx, Iberomesornis* and the enantiornithine *Sinornis* is unknown (Ostrom, 1976a; Wellnhofer, 1974; Sanz et al., 1988; Sereno & Rao, 1991, Chiappe, 1995c), but in more derived avialians (e.g., *Hesperornis, Ichthyornis, Patagopteryx*, Enantiornithes; Marsh, 1880; Walker, 1981; Alvarenga & Bonaparte, 1992) the fibular condyle of femur is not conical but smoothly convex craniocaudally and transversely.

Alvarezsauridae Bonaparte, 1991. Alvarezsauridae is here defined to encompass *Patagonykus puertai, Alvarezsaurus calvoi, Mononykus olecranus* and all the descendants of their most recent common ancestor. Alvarezsauridae is diagnosed on the basis of nine unambiguous synapomorphies, plus other two ambiguous traits, which are listed and analyzed below:

18) Cervical vertebrae with craniocaudally short and dorsoventrally low neural spines (Fig. 2). *Alvarezsaurus* and *Mononykus* exhibit strongly reduced neural spines on the cervical vertebrae (Bonaparte, 1991; Perle et al., 1994). This condition strongly differs from those in other coelurosaurs. As an example, in *Ornitholestes* (AMNH 619) the neural spine of cervical ?4 is dorsoventrally deep and craniocaudally short, similar to *Deinonychus* (Ostrom, 1969). The neural spine of a mid-caudal cervical of *Ornitholestes*, instead, is dorsoventrally low but axially long. In *Archaeopteryx*, cervicals 4 and 5 (Wellnhofer, 1974) exhibit neural spines proportionally taller than *Mononykus* (Perle et al., 1994) and *Alvarezsaurus* (Bonaparte, 1991). Unfortunately, the neck vertebrae of basal avialians is almost unknown (e.g., *Iberomesornis, Sinornis*; Sereno & Rao, 1992) and the condition is unknown in *Patagonykus*. As originally noted by Bonaparte (1991), gracile cervical vertebrae with reduced neural spines are present in ornithomimids, a condition that is here interpreted as independently evolved.

19) Sacral and caudal vertebrae procoelous (Fig. 7). In Theropoda ancestrally the sacral and caudal vertebrae are amphiplatyan or slightly amphicoelous (e.g., *Piatnitzkysaurus* MACN-CH 895; *Archaeornithomimus* AMNH 6567; *Albertosaurus* AMNH 5458; *Deinonychus* MCZ 4371). In the recently described seventh specimen of *Archaeopteryx* (Wellnhofer, 1993), the disarticulated and well preserved proximal caudals appear to be amphiplatyan, as suggested by the straight cranial and caudal margins of the caudal centra, parallel to each other in lateral view. The condition is unknown in basal Ornithothoraces (e.g., *Iberomesornis*; Sanz et al.,1988) due to the firm articulation among caudal segments forming a pygostile. A procoelous condition of caudal dorsals, sacrals and caudals has been documented only in *Patagopteryx* among ornithothoracines (Chiappe, 1992, 1995a), a condition that was previously interpreted as convergently acquired with Alvarezsauridae (Perle et al., 1993, 1994). In Hesperornithiformes, ancestrally (e.g., *Baptornis*; Martin & Tate, 1976), the caudal centra are amphicoelous or amphiplatyan. In *Ichthyornis* (Marsh, 1880) the cranial surface of the first sacral centrum and the caudal surface of the last sacral vertebra are concave and the caudal vertebrae are amphicoelous.

Mononykus, Patagonykus and *Alvarezsaurus* exhibit the last sacral and most of the caudal vertebrae with a ball-shaped caudal surface. As commented above (character 1) some variation exists in the convexity of the caudal surface within Alvarezsauridae.

The resemblances between the proximal caudals of *Patagonykus* and eusuchian crocodiles (e.g., *Caiman*; pers. collection) are noteworthy, mainly because they share ball-shaped caudal articular surfaces, robust, craniocaudally short neural spines, transversely thin ligamentary scars at the base of the neural spines, and the base of the neural spines with a deep excavation between pre- and postzygapophyses. It is not possible to assert whether these osteological resemblances between *Patagonykus* and extant crocodiles correspond with similarities in distribution and development of the epaxial musculature, but the existence of a strong procoelous condition suggests a high degree of movement all along the tail, in contrast with most tetanurine theropods, including birds (Gauthier, 1986).

20) Caudal sacral centra transversely compressed. As noted above (character 2) the sacral vertebrae of alvarezsaurids are transversely compressed, in contrast with other theropods in which the sacrum does not exhibit such a condition.

21) Haemal arches of proximal caudals dorsoventrally elongate. This feature was interpreted by Martin & Rinaldi (1994) in support of non-avialian affinities of *Mononykus*. However, in the context of all the evidence, the presence of elongate haemal arches in *Mononykus* and *Alvarezsaurus* is interpreted here as an apomophic reversal, and consequently as diagnostic of the Alvarezsauridae.

22) Ungual phalanx of manual digit 1 stout and robust (Figs 4 & 8). Perle et al. (1993, 1994) have noted that the ungual phalanx of digit I of *Mononykus* is robust and less arched than in other theropods (e.g., *Deinonychus, Archaeopteryx*) and with the proximoventral area forming a flat surface lacking a flexor tubercle. These authors have indicated also, that the ungual of the first digit represents 226% of the proximodistal length of the carpometacarpus (Perle et al., 1994). As commented above, the manual ungual of *Alvarezsaurus* is remarkably similar to that of *Mononykus*, in being quadrangular in proximal aspect, with the proximoventral surface flat and the flexor tubercle absent. This manual ungual, outstandingly larger than any ungual of the foot, exhibits deep proximal concavities for articulation with the first phalanx of digit I. These concavities are separated by a prominent ridge. The ungual phalanx of digit I of *Alvarezsaurus* lacks the foramina that pierce the proximoventral surface of that of *Mononykus* (Perle et al., 1994).

23) Pubic pedicle of ilium slender (Fig. 9). Like other dinosaurs the pubic pedicle of the ilium of *Patagonykus* and *Mononykus* is subtriangular in cross-section and lateromedially compressed. However, in alvarezsaurids the pubic pedicle is elongate and craniocaudally narrow, in contrast with other tetanurines (e.g., *Allosaurus*, Ornithomimidae, *Ornitholestes, Deinonychus, Archaeopteryx*, Enantiornithes; Madsen, 1976; Osborn, 1917; Ostrom, 1969, 1976b; Walker, 1981; Barsbold & Osmólska, 1990) in which the pubic peduncle of the ilium is craniocaudally thick.

24) Pubic peduncle cranioventrally projected. In Theropoda, ancestrally (e.g., *Compsognathus, Allosaurus, Ornitholestes*, Tyrannosauridae, Ornithomimidae, *Ingenia, Chirostenotes*), the pubic pedicle is anteroventrally oriented. This condition is also seen in *Oviraptor* (AMNH 6517). In *Deinonychus* and *Archaeopteryx* the pedicle clearly surpasses ventrally the level of the ischiac pedicle. Also, the cranial margin of the pubic pedicle is straight and slopes caudoventrally. The caudal margin of the pedicle is more curved caudoventrally increasing the participa-

tion of the ilium in the acetabular surface. In *Deinonychus* (Ostrom, 1969; 1976b) and *Archaeopteryx* (Martin, 1983) the pubic pedicle inclines caudoventrally 115-130° with respect to the longitudinal axis of the iliac blade (where the dorsal margin is assumed horizontal). In Enantiornithes (Martin, 1983) the angle is 140° approximately. In contrast, in *Gallimimus* (Osmólska et al., 1972, pl. 50) and *Ornitholestes* (AMNH 619) the pubic pedicle inclines 50-60° with respect to the longitudinal axis of the blade and in *Tyrannosaurus* (Osborn, 1917) the angle is nearly 70°. *Alvarezsaurus* (Bonaparte, 1991), *Mononykus* (Perle et al., 1993) and *Patagonykus* retained the ancestral condition, with the pubic pedicle cranioventrally oriented. The angulation is not possible to calculate in *Patagonykus*.

The ilio-pubic articulation is too highly modified in *Hesperornis* to discern the inclination of the pubic peduncle. Unfortunately, most of the ilium is lost in *Iberomesornis* (Sanz et al., 1988). In *Apatornis*, and presumably also in *Ichthyornis* (Marsh, 1880), the cranial margin of the pubic pedicle slopes caudoventrally. In *Patagopteryx* neither specimen preserves the pubic peduncle complete, but judging from the available material (Chiappe, 1992) the pubic peduncle seems to be vertical, but not caudoventrally oriented. Caudoventral orientation of the pubic peduncle is also seen in neornithine birds (e.g., *Apteryx*).

25) Fossa for M. cuppedicus absent (Fig. 14). A strongly developed fossa for the femoral protractor M. cuppedicus (Rowe, 1986) is present in the cranioventral corner of the ilium of *Albertosaurus* (AMNH 5458), *Ornithomimus* (USNM 2164), *Deinonychus* (AMNH 3015, MCZ 4371), *Archaeopteryx* (HMN MB 1880/81) and Enantiornithes (Walker, 1981). On the contrary, the lateral surface of the preacetabular blade of the ilium of *Alvarezsaurus* (Bonaparte, 1991), *Patagonykus* (PVPH 37) and *Mononykus* (Perle et al., 1994) is strongly convex dorsoventrally, lacking a fossa for the M. cuppedicus on the ventral margin of the iliac blade. The absence of a fossa for the M. cuppedicus has been interpreted as synapomorphic of the avialian clade formed by *Patagopteryx* and the Ornithurae (Chiappe, 1996) and more recently (Chiappe et al., this volume) as an ambiguous synapomorphy of Metornithes. This uncertainty rises from the unknown condition in *Iberomesornis* (Sanz et al., 1988) and the presence of such an iliac fossa in enanthiornithine birds (Walker, 1981). I prefer to interpret the presence of an iliac fossa as primitive for Ornithothoraces (see character matrix in the

Appendix). Consequently, the lack of an iliac fossa for the M. cuppedicus is interpreted, with reservations, as an apomorphic character convergently acquired by alvarezsaurids and the clade formed by *Patagopteryx* plus Ornithurae.

26) Supraacetabular crest ending cranially above the pubic pedicle. In *Patagonykus* (PVPH 37) and *Mononykus* (GI N107/6) the supraacetabular crest is almost restricted to the dorsal portion of the acetabular aperture, ending abruptly above the pubic pedicle. A similar condition is present in *Alvarezsaurus* (MUCPV 54) in which the feebly developed supraacetabular crest does not extend over the pubic pedicle of the ilium. This condition contrasts with that present in other theropods (e.g., *Piatnitzkysaurus* MACN-CH 895; *Allosaurus*, AMNH 813; *Archaeornithomimus* AMNH 6576; *Ornithomimus* AMNH 5421; *Albertosaurus* AMNH 5458, 5664; *Ornitholestes* AMNH 619; *Deinonychus* MCZ 4371, AMNH 3015; *Archaeopteryx* HMN MB 1880/81) in which the supraacetabular crest (even in the reminiscent condition present in derived theropods) extends cranially in continuity with the lateral border of the pubic pedicle.

27) Postacetabular blade of ilium with brevis shelf caudolaterally oriented and medial flange ventrally curved (Fig. 9). In *Alvarezsaurus* and *Mononykus* the brevis fossa is present (e.g., a caudoventral basin bounded by a well developed brevis shelf and the medial flange of the ilium; Novas, in press b). The fragmentary nature of the ilium of *Patagonykus* prevents knowledge of this character. The loss of a discrete brevis shelf and fossa apparently constitutes a synapomorphy of the Maniraptora, and its re-acquisition is considered an apomorphic reversal diagnostic of Alvarezsauridae. Interestingly, the ornithothoracine *Patagopteryx* also exhibits a brevis shelf and fossa and, along with alvarezsaurids, constitutes one of the few avialians in which this feature is present (Chiappe, 1996).

28) 'Posterior' trochanter on proximal femur absent. This feature was originally described by Ostrom (1976a, b) for *Deinonychus* and *Archaeopteryx*. After that, the presence of such a prominence was recognised also in Enantiornithes (Chiappe & Calvo, 1994; Chiappe, 1996) and *Sinornithoides* (Russell & Dong, 1993b). The absence of a 'posterior' trochanter in the femur of *Patagonykus, Mononykus* and *Alvarezsaurus* is interpreted as an apomorphic reversal.

DISCUSSION

Alvarezsaurids have been recorded at present in Late Cretaceous formations in Patagonia and Mongolia. The recorded taxa are: *Patagonykus puertai* from the Río Neuquén Formation (Turonian; Cruz et al., 1989), *Alvarezsaurus calvoi* from the overlying Río Colorado Formation (Coniacian-Santonian; Bonaparte, 1991; Cruz et al., 1989; Chiappe & Calvo, 1994) and *Mononykus olecranus* documented in the Nemegt Formation (Maastrichtian; Perle et al., 1993, 1994). Chiappe et al. (this volume) have identified bones of species related to *Mononykus* in palaeontological collections previously made by Mongolian and American palaeontologists from the Chinese Iren Dabasu Formation, and the Mongolian Tugrugeen Shireh, Bayn Dzak, Ukhaa Tolgod and Barun Goyot (Khermeen Tsav) formations, thought to be Campanian in age (Jerzykiewicz & Russell, 1991; Currie & Eberth, 1993). More recently Holtz (1995: 511) considered '*Ornithomimus*' *minutus* (Laramie Formation, Late Maastrichtian; Marsh, 1892; Weishampel, 1990) as a possible member of the '*Mononykus* lineage'. However the description given by Marsh (1892) is insufficient to support such an assignment, since the features described for the metatarsals of '*O*'. *minutus* are not unique to *Mononykus*, but are also shared by other theropods with the arctometatarsalian condition, as for example Troodontidae, Ornithomimidae, *Avimimus*, Tyrannosauridae (Holtz, 1994). In sum, although presence of alvarezsaurids may be expected in other continents (e.g., North America), reliable records are only known from South America and Asia.

On the basis of the analysis presented above, the common alvarezsaurid ancestor evolved eleven evolutionary novelties (e.g., sacral vertebrae procoelous; caudal sacral centra transversely compressed and sharply keeled ventrally; ungual phalanx of manual digit I stout and robust; pubic pedicle of ilium slender; fossa for M. cuppedicus absent; supraacetabular crest ending cranially above the pubic pedicle; haemal arches dorsoventrally elongate; brevis fossa present; 'posterior' trochanter on femur absent; etc.). However, this list of diagnostic traits for the Alvarezsauridae may be larger with the inclusion of several characters, the condition of which is unknown for *Alvarezsaurus*. For example, the stout morphology of the first digit ungual of the manus of *Alvarezsaurus* (see characters A5 & 22) suggests that the first manual digit of this taxon was

powerfully constructed and on the basis of this evidence it is also expected that *Alvarezsaurus* possessed extremely short forelimbs plus all the synapomorphic traits described for *Mononykus* and *Patagonykus* (characters 7-14).

The Patagonian alvarezsaurids *Patagonykus* and *Alvarezsaurus* are more primitive than those from Asia, in accordance with their greater age. However, despite their close geographic and stratigraphic provenance, *Patagonykus* and *Alvarezsaurus* do not exhibit derived characters in common suggesting closer affinities within Alvarezsauridae. On the contrary, there are four features that *Patagonykus* shares with *Mononykus*, exclusive of *Alvarezsaurus*: caudal articular surface of the centra of the last sacral and first caudal vertebrae strongly spherical, sacral vertebrae ventrally keeled, supraacetabular crest present and femoral fourth trochanter present. These features suggest that *Patagonykus* and *Mononykus* are descendants from a common ancestor not shared with *Alvarezsaurus* (Fig. 1).

Discovery of alvarezsaurids less derived than *Mononykus* suggests that the surprisingly modern avialian features present in the later taxon are the result of convergent evolution. Such derived avialian (e.g., ornithothoracine) characters of *Mononykus* are: lack of hyposphene-hypantrum articulation, pubis caudoventrally directed, femoral popliteal fossa distally closed, accessory cnemial crest, fibula not contacting tarsus and astragalar ascending process transversely narrow and laterally displaced. *Mononykus* makes a good case for evolutionary convergence, showing that at least some derived features were acquired more than once in the early evolution of birds. In a more general context, the arctometatarsalian condition of the metatarsals (Holtz, 1994) was acquired at least twice in theropod evolution: once in the Arctometatarsalia clade of theropods (Holtz, 1994) and independently in the derived alvarezsaurid *Mononykus*.

A phylogenetic diagram (Fig. 15) depicting the phylogenetic relationships of the alvarezsaurids, complemented with biochronological information of terminal taxa (e.g., *Patagonykus, Alvarezsaurus* and *Mononykus*) and immediate outgroups (e.g., Ornithothoraces), suggests that the origin and diversification of the Alvarezsauridae occurred before the Turonian, probably during Valanginian times (131-138my; Haq & Van Eysinga, 1994). This suspicion about the time of origin of the Alvarezsauridae is in agreement with the currently known biochronology of the Ornithothoraces, the oldest representative of
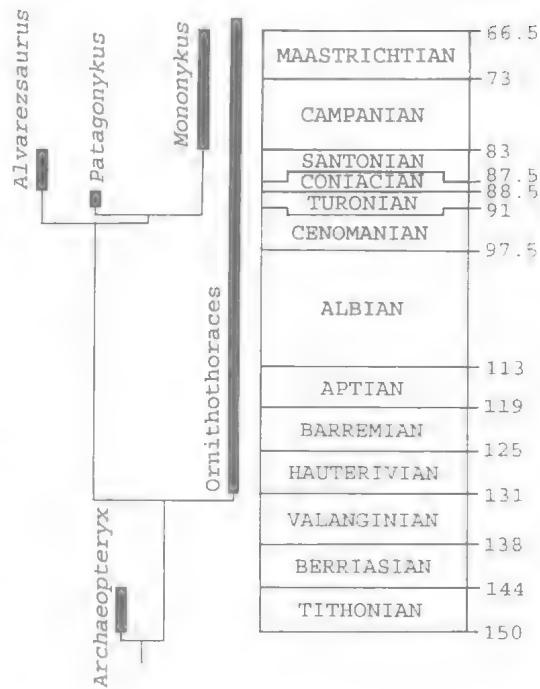

FIG. 15. Phylogenetic diagram depicting phylogenetic relationships of the Alvarezsauridae, complemented with biochronological information.

which (*Sinornis santensis*; Sereno & Rao, 1992) is known from Valanginian rocks. This information indicates that the Alvarezsauridae has a long evolutionary history, the recorded portion of which approximately spans 24.5my; i.e., from Turonian (91my) to Maastrichtian times (66.5my; Haq & Van Eysinga, 1994).

Presence of alvarezsaurids in the Late Cretaceous rocks in Mongolia and Patagonia is puzzling, mainly because alvarezsaurids are one of only two taxa (the other is the Titanosauridae, represented in Mongolia by *Opisthocoelicaudia skarzynskii*; Giménez, 1993; Salgado & Coria, 1993) which are shared by the sharply different Late Cretaceous faunas of South America and Asia (e.g., Bonaparte,1986b; Bonaparte & Kielan-Jawarowska, 1987; Russell, 1993). There are numerous examples of Cretaceous Gondwanan terrestrial vertebrates which appear to lack close phylogenetic affinities with those from Laurasia. Bonaparte (1986b) and Bonaparte & Kielan-Jawarowska (1987) pointed out the remarkable differences in faunal composition among Laurasian and Gondwanan continents, considering such dissimilarities as a direct consequence of the physical separation of both super-

continental landmasses, which lasted almost the entire Cretaceous period, a time span of 70 to 80my. Russell (1993) has also agreed that several dinosaur taxa evolved separately in Gondwanaland, although he considered that the grouping of terrestrial vertebrates into 'Laurasian' and 'Gondwanan' assemblages was established by Aptian-Albian times.

The shared presence of alvarezsaurids in South America and Asia admits two possible alternatives. One explanation considers alvarezsaurid species from South America and Asia as vicariant taxa descended from an ancestral species widely distributed over northern and southern landmasses; this wide distribution would have occurred before major barriers to overland dispersal among Laurasia and Gondwana were emplaced during Aptian to Cenomanian times (Lillegraven et al., 1979). Following this interpretation, the origin of the Alvarezsauridae must be traced back to Valanginian times, during which Gondwanan and Laurasian continents occupied closer positions than in later times (Scotese et al., 1992). The alternative explanation considers *Alvarezsaurus* and *Patagonykus* as endemic taxa from Gondwana (e.g., South America; Novas & Coria, 1990a; Bonaparte, 1991), which evolved in isolation during Cenomanian to Santonian times; in this context, alvarezsaurids may be interpreted as later emigrants to Asia (via North America?) when continental connections occurred during the Campanian (Bonaparte, 1986b). This later hypothesis agrees with the available fossil record of alvarezsaurids (Fig. 15) and also with palaeogeographic reconstructions (e.g., Lillegraven et al., 1979; Scotese et al., 1992) and palaeobiogeographic interpretations of the evolution of the vertebrate faunas of Gondwana as a whole (e.g., Bonaparte, 1986b; Bonaparte & Kielan-Jawarowska, 1987).

Current geographic documentation of the Alvarezsauridae in South America and Asia suggests that this clade successfully occupied a wide range of environmental conditions. For example, the Neuquén Group, which includes among others the Río Neuquén and Río Colorado Formations, constitutes a succession of sandstones and mudstones deposited under fluvial and lacustrine conditions (Digregorio & Uliana, 1980; Legarreta & Gulisano, 1989). The fauna recorded at the Portezuelo Member of Río Neuquén Formation is made up of gastropods (Cazau & Uliana, 1973), fishes, amphibians, turtles, crocodiles, small ornithischians, small to large theropods and large sauropods (Novas & Coria, 1990b). That of the Río Colorado Forma-

tion is a very rich fauna, including the following taxa (Bonaparte, 1991; Alvarenga & Bonaparte, 1992; Chiappe & Calvo, 1994): notosuchid and sebecosuchid crocodiles, dinilysid booids, sauropods, basal ornithothoracine birds (e.g., *Patagopteryx*, *Neuquenornis*) and ceratosaurian theropods (*Velocisaurus*). In the other extreme of sedimentological conditions in which alvarezsaurids were recorded, are the Asiatic Djadokhta (Tugrugeen Shireh) and Barun Goyot (Khermeen Tsav) Formations, deposited under subaerial conditions of sand dunes, small lakes and streams, in hot and semi-arid climate in areas lacking a permanent fluvial system (Gradzinsky et al., 1977; Osmólska, 1980). It seems to be clear that alvarezsaurids inhabited a wide range of palaeoenvironments (from desertic environments, as those indicated by the sedimentology of the Djadokhta Formation, to more humid conditions as suggested by the fluvial deposits of the Nemegt, Río Neuquén and Río Colorado Formations).

As currently known, Alvarezsauridae includes small forms the size of a turkey (nearly 1m long) such as *Alvarezsaurus* and *Mononykus*, and larger animals, up to 2m, such as *Patagonykus*. They seem to have had a role of predators of small animals, presumably insects (Perle et al., 1994), a suspicion based on the small size of the head and tooth reduction. However, other food items can not be dismissed. Chiappe (1995b) has recently speculated that alvarezsaurids may have used the hand claws to strip bark or perhaps stems from low-growing vegetation. In fact, alvarezsaurids repeat the case of almost uncertain feeding habits as with the ornithomimosaurians, for which carnivorous, herbivorous, or omnivorous habits were variously proposed (e.g., Sanz & Perez-Moreno, 1995). The unusual morphology of the forelimbs is not readily interpreted in reference to behavior and does not help in the elucidation of feeding habits. As commented by Perle et al. (1993, 1994) the sternum and forelimbs of *Mononykus* resemble those of moles mainly due to the presence of a keeled sternum, humerus short and expanded, ulna with elongate olecranon process and stout, slightly curved unguals. These resemblances have been interpreted by Ostrom (1994) as indicative of fossorial habits for *Mononykus*. However, Chiappe (1995b) has dissmissed this interpretation. *Mononykus* differs from a mole because in the latter the manus is proportionally large, not only because the number of digits is unreduced, but each digit is robust and a lunate sesamoid is added on the medial side of the manus, enlarging its palmar surface. Also, the

body proportions of *Mononykus* sharply contrast with that of digging mammals (e.g., moles and edentates; Hildebrand, 1975), in which the body is compact and the neck, forelimbs and hindlimbs are shortened.

ACKNOWLEDGMENTS

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APPENDIX

TERMINAL TAXA. Character list and taxon-character-state matrix.

The coding of 34 characters used to diagnose three of the six maniraptoran terminal taxa are given below. Some features (e.g., characters M8, M22, M23) have been incorporated in the list below, but have emerged as autapomorphies of some terminal taxa after a cladistic numerical analysis of ingroup relationships was carried out. Data from Bonaparte (1991), Perle et al. (1994), Chiappe et al. (this volume) and Novas (in press a). Scoring: 0, primitive; 1, derived; ?, missing or uncertain.

Patagonykus puertai

P1. Dorsal vertebral postzygapophyses. *0.* with lateral margin describing a continuous convex curve in ventral aspect. *1.* ventrally sinuous, with a tongue-shaped lateral projection.

P2. Base of the neural arch in postcervical vertebrae. *0.* caudally smooth and flat. *1.* with a bulge on both sides of the neural canal.

P3. Humeral articular facet of coracoid. *0.* transversely wide, being nearly as wide transversely as it is anteroposteriorly. *1.* transversely narrow, being as wide transversely as the surface for the articulation for the scapula.

P4. Internal tuberosity of humerus. *0.* conical, craniocaudally flattened, or pyramid-shaped. *1.* sub-cylindrical, wider at its extremity rather than in its base.

P5. Humeral entepicondyle. *0.* longitudinal prominence on the anteromedial margin of distal humerus, and it is almost anteriorly projected. *1.* conical-shaped and strongly projected medially.

P6. First phalanx of manual digit I. *0.* ventral surface bounded at both sides by slightly marked ridges on its proximal portion. *1.* with proximomedial hook-like processes.

P7. Ectocondylar tuber of femur. *0.* robust and elliptical-shaped in distal aspect. *1.* transversely compressed, rectangular in distal view.

Alvarezsaurus calvoi

A1. Cervical centra. *0.* amphiplatyan or opisthocoelous. *1.* amphicoelous.

A2. Cervical postzygapophyses. *0.* rectangular in dorsal view, not constricted at their bases, and with convex dorsal surface. *1.* paddle-shaped in dorsal view, dorsoventrally flattened, and with a pair of strong craniocaudal ridges.

A3. Length of distal caudals with respect to proximal caudals. *0.* less than 175%. *1.* more than 200%.

A4. Scapular blade. *0.* craniocaudally wide and distally expanded. *1.* slender and reduced.

A5. Ungual phalanx of digit I. *0.* with ventral surface transversely rounded or flattened. *1.* ventrally keeled.

Mononykus olecranus

M1. Pleurocoels in cervical vertebrae. *0.* present. *1.* absent.

M2. Sulcus caroticus in cervical vertebrae. *0.* absent. *1.* present.

M3. Relative position of parapophyses in presacral vertebrae. *0.* below the level of the diapophyses. *1.* occupying the same level as the diapophyses.

M4. Hyposphene-hypantrum in dorsal vertebrae. *0.* present. *1.* absent.

M5. Centra of cranial dorsal vertebrae. *0.* transversally rounded. *1.* strongly compressed transversally, forming a pronounced ventral keel.

M6. Centra of caudal dorsal vertebrae. *0.* slightly concave or convex. *1.* strongly procoelous, with caudal articular surface hemispherical.

M7. Last sacral centrum. *0.* elliptical or transversely compressed in cross-section. *1.* extremely compressed transversally, forming a pronounced ventral 'keel'.

M8. Coracoidal shaft. *0.* dorsoventral depth not exceeding its anteroposterior width. *1.* expanded ventrally, subrectangular in profile, dorsoventral depth more than 130% of anteroposterior width.

M9. Coracoidal shaft. *0.* with distal half strongly inflected medially. *1.* transversely flat and craniocaudally concave.

M10. Sternal carina. *0.* slender. *1.* thick.

M11. Ulnar articular surface of the radius. *0.* small and restricted to the proximal portion of the radius. *1.* extensive.

M12. Carpal articular facet of radius. *0.* restricted to the distal portion of the bone. *1.* hypertrophied, extended proximally over the caudal and cranial surfaces of the radius.

M13. Proximocaudal process on the first phalanx of digit I. *0.* absent. *1.* very prominent.

M14. Pubic shaft orientation. *0.* almost perpendicular to the iliac surface of pubis. *1.* caudoventrally oriented, describing an angle of 70° with the iliac surface of pubis.

M15. Pubic foot. *0.* present. *1.* absent.

M16. Ischiac articular surfaces for ilium and pubis. *0.* well developed. *1.* extremely reduced.

M17. Femoral distal condyles. *0.* separated below popliteal fossa. *1.* transversely expanded, nearly confluent below popliteal fossa.

M18. Accesory (medial) cnemial crest on tibia. *0.* absent. *1.* present.

M19. Outer malleolus of distal tibia. *0.* craniocaudally narrow in respect to the calcaneum. *1.* craniocaudally thick.

M20. Astragalocalcaneal intercondylar groove. *0*. shallow. *1*. deep.

M21. Astragalar ascending process. *0*. transversally wide and not displaced laterally, without overlap onto the lateral margin of distal tibia. *1*. transversally narrow and laterally displaced, with overlap onto the lateral margin of distal tibia.

M22. Femoral trochanteric crest. *0*. anterior trochanter separated from greater trochanter by a cleft. *1*. undivided.

M23. Fibula. *0*. articulates with the tarsus. *1*. does not articulates with the tarsus.

INGROUP CLADES. Character list and taxon-character-state matrix.

The coding and distribution are shown below for 74 characters in six coelurosaur taxa and in two proximate outgroups. All characters are binary. Characters gathered from Gauthier (1986), Russell & Dong (1993a,b), Chiappe (1995, 1996), Chiappe et al. (this volume) and Novas (in prep.).

1. Caudal articular surface of the centra of the last sacral and first caudal vertebrae. *0*. slightly convex. *1*. strongly spherical.

2. Sacral vertebral centra. *0*. transversely rounded or craniocaudally grooved. *1*. strongly keeled ventrally.

3. Femoral fourth trochanter. *0*. present. *1*. absent.

4. Supracetabular crest. *0*. present. *1*. absent.

5. Caudal dorsal vertebrae. *0*. amphiplatyan or amphicoelous. *1*. procoelous.

6. Bicipital tubercle of coracoid. *0*. present. *1*. absent.

7. Forelimbs to hindlimb length. *0*. 40-53%. *1*. less than 26%.

8. Proximal humerus. *0*. major transverse axis of humeral head horizontally oriented with respect to longitudinal axis of the humerus, and internal tuberosity distally placed with respect to humeral head. *1*. major transverse axis of humeral head ventrolaterally inclined with respect to longitudinal axis of the humerus, and internal tuberosity proximally projected.

9. Radial and ulnar condyles of distal humerus. *0*. Separated by an intercondylar groove, and radius and ulna loosely articulated proximally, retaining independent articular surfaces for both radial and ulnar condyles of humerus, respectively. *1*. a single condyle on distal humerus for articulation with radius and ulna, which are tightly appressed proximally, and provided with a cup-shaped proximal articular surface.

10. Olecranal process of ulna. *0*. feebly developed. *1*. strongly developed.

11. Ulnar posterior margin. *0*. sigmoid. *1*. uniformly convex.

12. Carpometacarpus. *0* slender, elongate, with intermetacarpal space. *1*. massive, short, quadrangular with no intermetacarpal space.

13. Digit I proportions. *0*. transverse dimension subequal to digit II, and longitudinally shorter than digit II. *1*. digit I larger than the remaining digits of the hands.

14. Phalanx 1 of manual digit I. *0*. with triangular-shaped proximal articular surface, proximoventral sur-

face almost flat, distal gynglymus transversely compressed, and the extensor pit absent. *1*. with B-shaped proximal articular surface, hook-like proximomedial processes, symmetrical distal ginglymus, and deep extensor ligamentary pit.

15. Medial condyle of femur. *0*. transversely narrow and distally convex. *1*. transversely wide and distally flat.

16. Ectocondylar tuber of distal femur caudally projected, well behind the medial distal condyle. *0*. absent. *1*. present.

17. Fibular condyle of femur. *0*. convex or forming a depressed low cone, and slightly surpassing distally the medial condyle. *1*. sharply conical and distally projected respect to the medial condyle.

18. Cervical vertebrae neural spines. *0*. dorsoventrally deep and craniocaudally short. *1*. craniocaudally short and dorsoventrally low.

19. Sacral and caudal vertebrae. *0*. amphiplatyan or amphicoelous. *1*. procoelous.

20. Last sacral centra. *0*. ventrally convex in cross-section, sometimes bearing a longitudinal groove. *1*. transversely compressed and keeled ventrally.

21. Haemal arches of proximal caudals. *0*. dorsoventrally elongate. *1*. dorsoventrally depressed.

22. Ungual phalanx of manual digit I. *0*. dorsoventrally deep, with proximal articular surface elliptical shaped. *1*. stout and robust, dorsoventrally depressed, with proximal articular surface quadrangular.

23. Pubic pedicle of ilium. *0*. craniocaudally wide. *1*. craniocaudally narrow.

24. Pubic pedicle of ilium. *0*. cranioventrally projected. *1*. caudoventraly projected.

25. Fossa for M. cuppedicus on ilium. *0*. transversely wide, with sharp bounding margins. *1*. absent.

26. Supraacetabular crest. *0*. extended cranially in continuity with the lateral border of the pubic pedicle. *1*. ending cranially above the pubic pedicle.

27. Postacetabular blade. *0*. brevis shelf caudolaterally oriented, and medial flange ventrally curved (viz., brevis fossa present). *1*. postacetabular blade vertical, and medial flange strongly reduced, perpendicular to iliac blade (viz., brevis fossa absent).

28. Posterior trochanter on proximal femur. *0*. absent. *1*. present.

29. Vertebral foramen. *0*. small. *1*. wide.

30. Number of caudals. *0*. 35 or more. *1*. less than 25.

31. Neural spines of caudal vertebrae. *0*. present on caudals 1-23. *1*. confined to caudals 1-12.

32. Transverse processes in caudal vertebrae. *0*. reduction begins in caudal 25-16. *1*. in caudal 12 at least.

33. Haemal arches. *0*. become longer than deep behind caudal 17. *1*. behind caudal 10.

34. Mid-caudals prezygapophyses. *0*. elongate. *1*. short.

35. Length of distal caudals. *0*. as long as the proximal caudals. *1*. distal caudals more than 130% of the length of proximals.

36. Ossified sternal carina. *0*. absent. *1*. present.

37(=M8). Coracoidal shaft. *0*. dorsoventral depth not exceeding its anteroposterior width. *1*. expanded

ventrally, subrectangular in profile, dorsoventral depth more than 130% of anteroposterior width.

38. Coracoidal shaft with respect to the proximal articular surface for the scapula. *0*. shaft transversely flattened or slightly medially inflected in posterior view. *1*. strongly inflected posteromedially.

39. Dorsal fossa on caudal process of coracoid. *0*. present. *1*. absent.

40. Bicipital tubercle of coracoid. *0*. slightly marked or absent. *1*. strongly developed.

41. Forelimbs. *0*. no more than 53% of hindlimb length. *1*. exceeding 75% of hindlimb length.

42. Forelimbs. *0*. not exceeding 75% of hindlimb length. *1*. 86% or more of hindlimb length.

43. Shape of the internal tuberosity (= bicipital tubercle) of humerus. *0*. conical. *1*. craniocaudally compressed and longitudinally elongated.

44. Radius/humerus length ratio. *0*. no more than 0.71. *1*. 0.76 or more.

45. Carpometacarpus. *0*. carpals and metacarpals unfused. *1*. carpometacarpus present.

46. Distal carpal. *0*. proximodistally flattened. *1*. semilunate.

47. Digit I proportions. *0*. digit I ends at level of mid-length of phalanx 2, digit II. *1*. digit I ends at level of mid-length of phalanx 1, digit II.

48. Posterodorsal margin of ilium. *0*. straight. *1*. curves ventrally in lateral view.

49. Posterior end of ilium. *0*. dorsoventrally deep, squared or rounded. *1*. dorsoventrally low and sharply pointed.

50. Antitrochanter on ilium. *0*. slightly marked. *1*. prominent.

51. Pubic apron. *0*. transversely wide and proximodistally long. *1*. strongly reduced transversely and restricted to the distal 1/3 of the pubic length.

52. Pubis. *0*. cranioventrally oriented. *1*. caudoventrally oriented respect to the pubic pedicle of ilium.

53. Pubic apices. *0*. in contact. *1*. not in contact.

54. Obturator process on ischium. *0*. present. *1*. absent (the cranioventral margin of ischium is almost straight).

55. Ischial to pubic length. *0*. elongate ischium, slightly shorter than pubis or femur. *1*. nearly half of pubis or femoral length.

56. Medial condyle of femur. *0*. dorsoventrally deep. *1*. dorsoventrally depressed.

57(=M22). Femoral trochanteric crest. *0*. anterior trochanter separated from greater trochanter by a cleft. *1*. undivided.

58. Adductor fossa and associated craniodistal crista of distal femur. *0*. present, prominent. *1*. reduced or absent.

59. Tibia-femur proportions. *0*. tibia no more than 15% longer than the femur. *1*. tibia 25% longer than the femur.

60(=M23). Fibula. *0*. articulates with the tarsus. *1*. does not articulate with the tarsus.

61. Articulations of quadrate and squamosal. *0*. quadrate articulates only with squamosal, the latter contacting both the quadratojugal and the postorbital. *1*.

quadrate articulates with both prootic and squamosal, and the latter contacting neither the quadratojugal nor the postorbital.

62. Serration of teeth. *0*. present. *1*. absent.

63. Teeth crown-root constriction. *0*. absent. *1*. present.

64. Ulnar distal condyle. *0*. transversely compressed and craniocaudally extended approximately in the same plane as humero-ulnar flexion-extension. *1*. subtriangular in distal view, with a dorsomedial condyle, and twisted more than 54° with respect to proximal end.

65. Calcaneum. *0*. posteroventral projection present. *1*. strongly reduced.

66. Pubic distal foot. *0*. cranial projection present. *1*. absent.

67. Prominent ventral processes of cervico-dorsal vertebrae. *0*. absent. *1*. present.

68. Large, rectangular ossified sternum. *0*. absent. *1*. present.

69. Terminal processes of ischia. *0*. in contact. *1*. not in contact.

70. Fibular tubercle for M. iliofibularis. *0*. craniolaterally projected. *1*. laterally, caudolaterally, or caudally directed.

71. Proximal and distal humeral ends. *0*. twisted. *1*. expanded in nearly the same plane.

72. Pelvic elements. *0*. unfused. *1*. fused or partially fused.

73. Proximal end of fibula. *0*. excavated by a medial fossa. *1*. nearly flat.

74(=M4). Hyposphene-hypantrum in dorsal vertebrae. *0*. present. *1*. absent.

TAXON CHARACTER STATES.

Ornithomimidae
00000 00000 00000 00100 00000 00000 00000 00000
00000 00000 00000 00000 00000 00000 0000

Tyrannosauridae
00000 00000 00000 00000 00000 00000 00000 000?0
00000 00000 00000 00000 00000 00000 0000

Deinonychus
00010 00000 10000 00000 10010 01100 11101 01000
10110 10100 01001 10100 00001 00000 0000

Archaeopteryx
00110 000?0 10000 0?000 10010 011?1 11111 01111
11110 11110 01001 ?0110 01101 100?? 00??

Ornithothoraces
00110 00000 10000 00?00 10010 01111 11111 11111
11111 11111 11110 01111 1111? 11111 1111

Mononykus
11001 11111 01111 11111 01101 10011 11110 10010
00001 10101 11110 11111 11110 11111 1111

Patagonykus
11001 11111 01111 11?11 ?1101 1?01? ???10 ??010
?00?1 1???1 110?? 101?0 ???10 0???? ?010

Alvarezsaurus
0011? ????? ????? ??111 011?1 100?? 10111 ??0??
????? ??10? ????? ?0??0 ???0 ????? ????

EARLIEST EVIDENCE OF DINOSAURS FROM CENTRAL GONDWANA

M.A. RAATH

Rocks of the Elliot Formation and its regional equivalents in southern Africa, which straddle the Triassic-Jurassic boundary, have traditionally been regarded as the earliest dinosaur-bearing sediments in this region. The identification of tridactyl *Grallator*-like tracks at a site in the Eastern Cape Province, South Africa, and the discovery of an isolated fragment of a prosauropod femur in the central Zambezi Valley of Zimbabwe, both in rocks assigned to equivalents of the underlying Molteno Formation on stratigraphic and palaeobotanical grounds, indicate the presence of an earlier dinosaurian fauna. These traces constitute the earliest known evidence of dinosaurs in this region of Central Gondwana. □ *Triassic, dinosaur tracks, rhynchosaur, prosauropod, South Africa, Zimbabwe, Molteno.*

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Two fossil discoveries during the last decade in two far-flung localities in southern Africa — Maclear in the north-eastern Eastern Cape Province of South Africa, and the Cabora Bassa Basin of the Central Zambezi Valley of Zimbabwe (Fig. 1) — have yielded evidence of a dinosaur fauna predating that of the Elliot Formation of the Stormberg Group in South Africa (Raath, Kitching, Shone & Rossouw, 1990; Raath, Oesterlen & Kitching, 1992).

The Elliot Formation and its regional equivalents have generally been regarded as the earliest dinosaur-bearing formations in this part of Africa. According to Olsen & Galton (1984) the Elliot spans the Triassic-Jurassic boundary (Carnian to Sinemurian). On the basis of its fossil content in South Africa, Kitching & Raath (1984) recognised two distinct biozones in the Elliot Formation: a lower *Euskelosaurus* Range Zone characterised by the presence of the relatively large prosauropod dinosaur *Euskelosaurus*, accompanied by capitosaurid amphibians, unidentified rauisuchid thecodontians and rare cynodont therapsids. This zone is followed by the *Massospondylus* Range Zone, characterised by the abundance of the smaller prosauropod dinosaur *Massospondylus* and a diverse fauna which includes amphibia, a chelonian, crocodilians, dinosaurs other than prosauropods, therapsids and even rare primitive mammals (Kitching & Raath, 1984).

The discoveries which are the subject of this contribution have only recently come to the attention of scientists, although one of them has been known to the local populace for a long time. From the early years of this century, trout anglers fishing along the Pot River in the vicinity of the town of Maclear (Fig. 1) in the Eastern Cape Province of South Africa have known of the presence of unusual markings in the rocks lining the river's banks, which have long been known locally as 'petrified spoor' (animal tracks). Although these tracks have featured in local newspapers from time to time, they escaped the notice of geologists and palaeontologists. As far as I can determine, ours was the first detailed investigation of the site (Raath et al., 1990). It confirmed that the marks included vertebrate tracks and that animals of probably more than one kind were involved, at least one of them a dinosaur. It was further concluded that the rocks in which the tracks are preserved belong to the Molteno Formation (Raath et al., 1990), which underlies the Elliot Formation.

Until now, no unequivocal evidence of tetrapod vertebrates has been found in Molteno rocks — other than reports by P. Ellenberger of vertebrate tracks of many kinds in Lesotho in beds which he assigned to the Molteno, including tracks of a variety of dinosaurs (see synthesis in Ellenberger, 1970). Persistent doubts about the reliability of these stratigraphic assignments has meant that this work has been largely overlooked. The only unquestionable animal fossils previously recovered from the Molteno have been some palaeoniscid fish (*Semionotus* sp.) and a variety of invertebrates, mainly insects. Anderson & Anderson (1984: 40) state in their summary of Molteno fossils: '*Tetrapods — Bone is not preserved in the Molteno Formation*'.

The early Mesozoic deposits of Zimbabwe are palaeontologically very similar to their South

African counterparts. In that country, the main dinosaur-bearing unit, the Forest Sandstone Formation, contains a typical but rather depauperate 'terminal Karoo fauna' which is dominated by prosauropod and small theropod dinosaurs, like the South African middle and upper Elliot Formation fauna. However, the Zimbabwean fauna lacks many of the other elements represented in South Africa, particularly the ornithischian dinosaurs, advanced therapsids and early mammals.

As in South Africa, the Zimbabwean beds which underlie the traditional dinosaur-bearing beds have until now also been considered barren of tetrapods (see e.g., Bond, 1973). The

FIG. 1. Reconstruction of Gondwana prior to separation, showing approximate positions of the two localities referred to in the text (modified from Colbert, 1975: fig. 5).

fossils usually associated with these beds in Zimbabwe include silicified logs (cf. *Dadoxylon* spp), particularly from the Pebbly Arkose Formation and plant leaf impressions (mainly the pteridosperm genus *Dicroidium*) and rare invertebrates (freshwater bivalve molluscs) (see summary in Bond, 1973). On the basis of the dominance of the characteristic Triassic fossil plant genus *Dicroidium*, Bond (1973) concluded that these beds in Zimbabwe (including the Pebbly Arkose, the Ripple Marked Flags and the Fine Red Marly Sandstone) were equivalents of the Molteno Formation of the Karoo Supergroup in South Africa (late Triassic: Carnian, Anderson & Anderson, 1984). Some lungfish remains were recovered from beds of this age in Lake Kariba in 1973, and until the recent tetrapod discoveries in the Central Zambezi Valley (Raath, Oesterlen & Kitching, 1992), they were the only vertebrate remains known from these strata in Zimbabwe.

SUMMARY OF THE TWO OCCURRENCES

MACLEAR DINOSAUR TRACKS, SOUTH AFRICA. The most prominent trace in the tracksite at Maclear, Eastern Cape Province, South Africa, is a straight groove ploughed into the mud (Fig. 2a), with other less obvious similar traces nearby. Raath et al. (1990) tentatively interpreted

these grooves as the tail drags of quadrupedal dinosaurs, but no clear unequivocal footprints can be associated with them, so this suggestion is doubtful at best. It has been suggested that a more likely interpretation is that they are drag marks from an object floating in the river, although the remarkably detailed preservation of the rolled edges of the groove indicate very low velocity of the current responsible.

On the other hand, the majority of the tracks are clear and well preserved, consisting of plentiful tridactyl footprints of a small bipedal dinosaur (Fig. 2b, c). Similar tracks are well known from a number of other places in southern Africa, especially in Lesotho (Ellenberger, 1970; Olsen & Galton, 1984) and from one locality in Zimbabwe (Raath, 1972). Since publication of the report by Raath et al. (1990), several more reports of similar well-preserved tridactyl dinosaur footprints have been received from the farming districts south and west of Maclear.

Raath et al. (1990) concluded that the tridactyl tracks are assignable either to the ichnogenus *Grallator* (see Olsen & Galton, 1984: fig. 3H) or *Atreipus* (Olsen & Baird, 1986: figs 6.3, 6.4). But *Atreipus* is defined as '*habitually quadrupedal ichnites*' (Olsen & Baird, 1986: 62), and since no manus impressions are associated with any of the tridactyl pes impressions at Maclear, it appears that this ichnogenus can be eliminated. Accord-
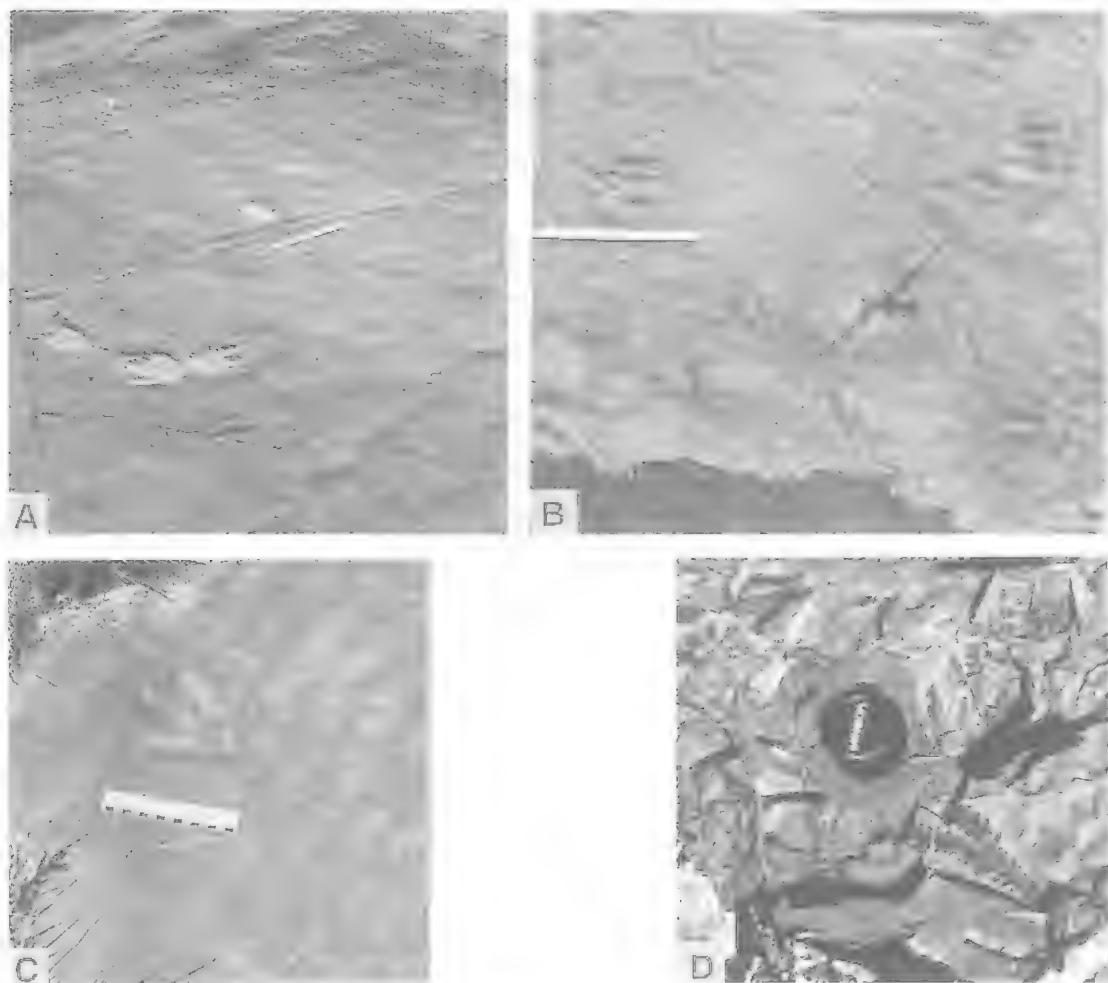
FIG. 2. Maclear dinosaur tracksite. A, the straight ploughed trace — possibly a tail-drag. B, tridactyl prints arranged in several trackways (note the infilled desiccation cracks on the surface). C, single isolated tridactyl print, *Grallator* sp., from a ripple-marked surface. D, frond impression of the pteridosperm genus *Dicroidium* from near the tracksite.

ing to Olsen & Galton (1984: 97), *Grallator*-like tracks were '*almost certainly made by small theropod dinosaurs*', which therefore indicates the presence of small theropods at Maclear when these sediments were laid down.

RHYNCHOSAURS AND DINOSAUR, ZIM-BABWE. The rhynchosaur fossils from the Dande Communal Lands in Zimbabwe consist mainly of scattered, isolated, often fragmentary bones and teeth, including the unmistakable tooth-studded maxillary dental plates of these highly specialised herbivorous archosauro-morphs (Fig. 3a). They evidently belong to a

single rhynchosaur taxon, showing a consider-able range in size.

Rhynchosaur taxa are well-known to be useful for dating the beds from which they come (Chat-terjee, 1980; Benton, 1983) and the state of the diagnostic dental and other cranial characters in the Zimbabwean rhynchosaurs identifies them as *Hyperodapedon*, of the family Rhynchosauridae, sub-family Hyperodapedontinae (Raath et al., 1992). This has significance for dating the strata from which they come.

The single fragmentary non-rhynchosaur bone found with rhynchosaur material at one of the Dande sites bears the characteristic crest-like fourth trochanter of a prosauropod dinosaur

femur (Fig. 3b, c). The fragment is broken off just below the trochanter and most of the head is missing, but enough remains to be reasonably confident of its identification as a prosauropod. Although it is small compared to most of the known southern African prosauropods, such as *Euskelosaurus* and *Massospondylus*, the specimen is taken to be from an adult based on the degree of ossification of scars of minor surface features like the vascular groove running along the anterior surface to the nutritive foramen opposite the fourth trochanter (Fig. 3c).

If this identification is correct, it demonstrates the presence of prosauropod dinosaurs when the Dande beds were laid down.

GEOLOGY AND AGE OF THE TWO OCCURRENCES

MACLEAR TRACKSITE. The Maclear tracks are preserved in a medium-to-finegrained cross-bedded silty sandstone belonging to the Stormberg Group, from somewhere near its base. The Stormberg succession consists of the thick, coarse fluvial sandstones and finer shales of the Molteno Formation at its base, overlain by the brick-red mudrocks and sandstones of the Elliot Formation, which in turn are overlain by the pale, finer-grained, mainly aeolian sandstones of the Clarens Formation. The thick Drakensberg lavas cap the sequence (Fig. 4). This entire sequence is well exposed in the Barkly Pass — a road pass through the Drakensberg mountains just 50km west of the Maclear tracksite. Visser (1984) notes that in this area, the Molteno Formation makes up the valley floor at the base of the Drakensberg mountains. The mountains themselves are made up of Elliot Formation mudrocks at the base, with the pale sandstones of the Clarens Formation above, and capping the sequence on the mountain peaks are the Drakensberg lavas. Visser (cited in Raath et al., 1990) locates the Molteno-Elliot contact '*right at the foot of the (Barkly) pass in the Tsomo River and this position agrees with the boundary defined by (A.L.) du Toit on his map (?1910) of the area.*'.

The Pot River has cut its deep valley through the flat plains at the foot of the mountains — i.e., through Molteno deposits. The beds through which it has cut might be described as 'uppermost Molteno', and one coarse sandstone ledge from this unit overlooks the fossil tracksite about 100m below. This sandstone is lithologically reminiscent of the Indwe Sandstone Member, a persistent and highly characteristic marker horizon in the

FIG. 3. Zimbabwean rhynchosaur locality. A, snout of a juvenile rhynchosaur, *Hyperodapedon*, in palatal view, showing the characteristic maxillary toothplates. B, fragmentary prosauropod left femur in lateral view; note crest-like fourth trochanter (arrowed). C, anterior surface of the femur in (B) showing the vascular groove (arrowed) leading to the nutritive foramen. Scales = 1cm.

Molteno Formation, all of which suggests that the fossil tracks are in Molteno beds, substantially below the contact with the Elliot Formation.

Moreover, within a kilometre of the tracksite, and on a stratigraphic level either the same as or

slightly above it, a finegrained shale outcrop contains abundant plant fossils dominated by the characteristic Molteno pteridosperm genus, *Dicroidium* (Fig. 2d).

No bones of dinosaurs are known from Molteno beds in South Africa, but they are certainly known from the higher levels of the Stormberg Group and its equivalents in many southern African localities (see Raath, 1980; Cooper, 1981; Kitching & Raath, 1984 and references therein); in fact, there are several good bone-producing sites in the Barkly Pass, within 50km of the Maclear tracksite.

GROUP	FORMATION	DIVISION	BIOZONE
STORMBERG GROUP	Drakensberg Formation		[Lavas]
	Clarens Formation	Upper	
		Middle	
		Lower	*Massospondylus* Range-zone
	Elliot Formation	Upper	
		Middle	
		Lower	*Euskelosaurus* Range-zone
	Molteno Formation	Upper	New "pre-Elliot" dinosaur fauna
BEAUFORT GROUP			

FIG. 4. Summary of Stormberg stratigraphy in South Africa.

The apparently consistent stratigraphic distribution of dinosaurs in the Stormberg led Kitching & Raath (1984) to propose the two biozones mentioned earlier — the *Euskelosaurus* Range Zone in the lower parts of the Elliot Formation, and the *Massospondylus* Range Zone in the middle and upper parts, extending into the base of the overlying Clarens Formation.

A complicating factor in the Maclear case is that the only dinosaurs so far known from the *Euskelosaurus* Range Zone are prosauropods — no theropods have been discovered to date. However, at least one theropod taxon, *Syntarsus*, is relatively common in the overlying *Massospondylus* Range Zone (Raath, 1980; Kitching & Raath, 1984). Tracks attributed to *Syntarsus* are known from Zimbabwe in beds which correlate with the upper Elliot Formation (Raath, 1972). In terms of general morphology, the Zimbabwe ?*Syntarsus* tracks are similar to the Maclear tridactyl prints, but *Syntarsus* is too small to have made the Maclear tracks. The identity of the track-maker therefore remains unresolved.

The conclusion that these tracks are in Molteno sediments also demands a reassessment of the validity of Ellenberger's (1970) stratigraphic assignments.

ZIMBABWEAN RHYNCHOSAUR AND DINOSAUR SITE. The rhynchosaur specimens and the prosauropod from Zimbabwe were discovered during mapping by P.M. Oesterlen of the Zimbabwean Geological Survey, in the Dande Communal Lands in the Lower Zambezi Valley during the late 1980s (Raath et al., 1992). The rocks exposed here range in age from late Palaeozoic to early Mesozoic (Broderick, 1984; 1989; Oesterlen, 1989) and the rhynchosaur material came from beds which Oesterlen mapped as Pebbly Arkose Formation (Fig. 5). This formation is of late Triassic age and is considered an equivalent of the South African Molteno Formation (Bond, 1973).

Chatterjee (1969; 1980) and Benton (1983) point out that rhynchosaurs fall into three family or subfamily groups whose stratigraphic distribution neatly coincides with the division of the Triassic into early, middle and late divisions. The subfamily Hyperodapedontinae is characteristic of, and apparently confined to, the late Triassic. Benton (1983) includes in this subfamily the East African form '*Supradapedon*', which comes from the late Triassic beds of Tunduru, Tanzania, and is very similar to the Zimbabwean form. On these grounds, the Zimbabwean rhynchosaurs are assigned to the late Triassic, and, by association, so is the dinosaur found with them.

A late Triassic (Molteno-equivalent) age for the Zimbabwean occurrences is further supported by the fact that, as in the South African case, the typical late Triassic plant genus *Dicroidium* is found in the vicinity of the Dande rhynchosaur localities, although so far not in direct stratigraphic association with the vertebrates.

It is therefore concluded that on stratigraphic and palaeontological grounds, the Maclear (South Africa) and Dande (Zimbabwe) sites show

Era	Period	Group	Formations in the Cabora Bassa Basin, Zimbabwe	South African Equivalents
Mesozoic	Cretaceous		--	[Post-Karoo]
	Jurassic		Dande Sandstone	
		Upper Karoo	Forest Sandstone	
	Triassic		**Pebbly Arkose** (from which the rhynchosaurs and the dinosaur bone come)	Stormberg Group
			Angwa Sandstone	

FIG. 5. Stratigraphy of Stormberg equivalents in Zimbabwe (adapted from Raath, Oesterlen & Kitching, 1992).

the presence of dinosaurs during Molteno times (?lower Carnian, Anderson & Anderson, 1984: 40) and, subject to a reassessment of Ellenberger's (1970) stratigraphic assignments, these are therefore the earliest indications of dinosaurs in this part of Central Gondwana.

ACKNOWLEDGEMENTS

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SIGNIFICANCE OF POLAR DINOSAURS IN GONDWANA

THOMAS H. RICH

Polar dinosaurs have been found at four localities in the southern hemisphere and eight in the northern. Three groups of dinosaurs, neoceratopsians, ornithomimosaurs and oviraptorosaurs, previously known only from the Late Cretaceous of the northern hemisphere were present in the Early Cretaceous polar dinosaur fauna of southeastern Australia. Labyrinthodont amphibians were also represent, but do not occur in the same deposits as crocodilians. Enlarged optic lobes of the hypsilophodontid *Leaellynasaura*, suggesting enhanced ability to see under low light conditions, is the only adaptation to a polar environment yet recognised in a dinosaur. Polar dinosaurian taxa are not unique at the familial level, but belong to more widespread families. Polar dinosaurs probably lived under cold climates quite unlike those tolerated by modern reptiles. □ *Early Cretaceous, southeastern Australia, dinosaurs, labyrinthodonts, palaeoclimate.*

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Only one area within the palaeo-Antarctic Circle has produced dinosaurs — southeastern Australia (Aptian-Albian, early Cretaceous). Four more are known to have been close to the palaeo-Antarctic Circle — southeastern Queensland, Australia (early or middle Jurassic), Beardmore Glacier, Antarctica (early Jurassic), James Ross and Vega Islands, Antarctica (Campanian and Maastrichtian, late Cretaceous) and North Island, New Zealand (probably Maastrichtian, late Cretaceous). In the Northern Hemisphere, eight areas (late Jurassic? to late Cretaceous) are known to have produced dinosaurs within the palaeo-Arctic Circle (Fig. 1). Most of the polar dinosaur material from both hemispheres was acquired during the past twenty years and much of it remains to be described (Table 1).

Polar Gondwana may have served as both a refuge and birthplace for some dinosaur groups.

From the early or middle Jurassic of southeastern Queensland has come a partial skeleton of one of the earliest sauropods, *Rhoetosaurus brownii* Longman, 1927.

A single astragalus suggests that the well-known form *Allosaurus* may have persisted into the Aptian of southeastern Australia after having become extinct elsewhere at the end of the Jurassic.

On the basis of one or a few bones, the presence of three groups previously known in the late Cretaceous of the Northern Hemisphere has been suggested in the early Cretaceous of southeastern Australia. An ulna from the Aptian there bears an uncanny resemblance to that of the Maastrichtian protoceratopsian *Leptoceratops gracilis* from Alberta, Canada. This suggests that Polar Gondwana may have been the place of origin for the neoceratopsians, for they are known nowhere else prior to the Late Cretaceous.

Ornithomimosaurs are represented in the Albian of southeastern Australia by femora distinct enough to base a new genus and species, *Timimus hermani* Rich & Vickers-Rich, 1994. As yet undescribed ornithosaur vertebrae are known from both the same Albian site that produced femora from southeastern Australia as well as Aptian sites a few hundred kilometres to the east. This material suggests a presence for this group on the Gondwana continents prior to when ornithomimosaurs are best known in the northern hemisphere, the late Cretaceous. However, the recent publication of *Shuvosaurus inexpectatus* Chatterjee, 1993 from the late Triassic of Texas, implies that ornithomimosaurs have had a much longer history in the northern hemisphere than previously suspected. The late Jurassic *Elaphrosaurus bambergi* from Tendaguru, Tanzania, formerly regarded as an ornithomimosaur, has recently been allocated to the abelisaurs (Holtz, 1994).

Oviraptorosaurs, previously represented exclusively in the late Cretaceous of the northern hemisphere, appear to have been present in the Albian of southeastern Australia based on a partial surangular and a vertebra (Currie, Vickers-Rich & Rich, 1996).

Associated with these dinosaurs is the most unexpected and best documented temporal range extension of a major tetrapod group. Two decades ago, labyrinthodont amphibians were thought to have become extinct at the end of the Triassic.
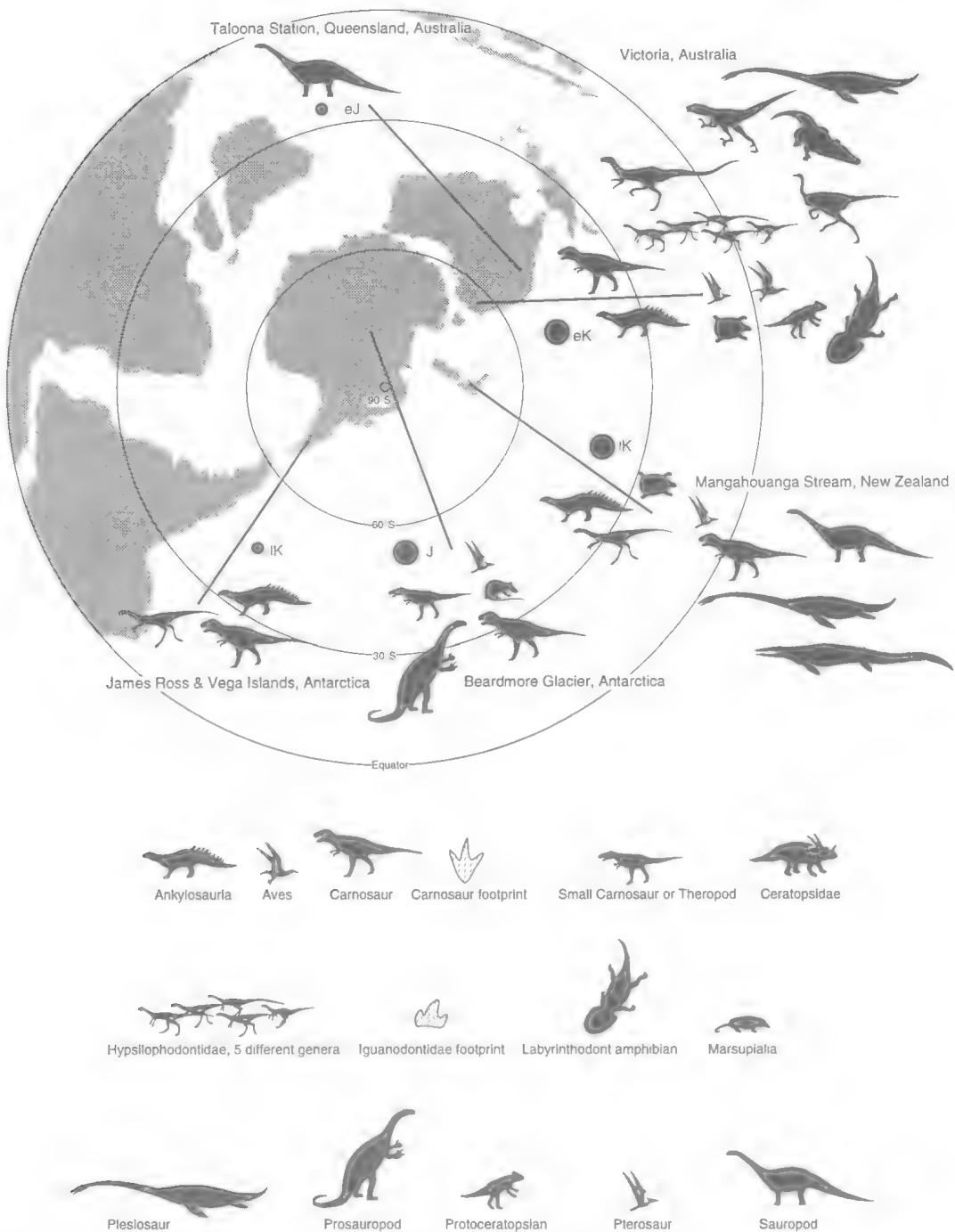
FIG. 1. Distribution of polar dinosaurs, Southern Hemisphere (this page) and Northern Hemisphere (facing page). Dinosaur sites in polar latitudes are not common, most having been discovered in the last 20 years. None are fully studied. The higher diversity in southeastern Australia is probably due to greater collecting effort and easier accessibility. When some of the other sites are more fully studied, they may provide similar diversity. Base map from Smith, Hurley & Briden (1981).

Spitzbergen
eK

Sangarskaya Svita, Siberia
lJ - eK

Kakanaut, Siberia

lK

Colville River, Alaska

Black Lake, Alaska
lJ

lK

Talkeetna Mountains,
Alaska

Bylot Island,
Canada

lK

Northwest Territories,
Canada

lK

Yukon Territory, Canada

Equator

90 N
60 N
30 N

Crocodilia   Dromaeosauridae   Hadrosauridae   Hypsilophontidae

Mosasaur   Multituberculata   Ornithomimosauridae   Oviraptosauridae   Placentalia

Stegosauridae   Tritylodontid   Troodontidae   Turtle

Geological Age of Site or Sites

J - Jurrassic, 145 - 208 million years
eJ - Early Jurassic, 178 - 208 million years
lJ - Late Jurassic, 145 - 157 million years
eK - Early Cretaceous, 97 - 145 million years
lK - Late Cretaceous, 65 - 97 million years

Quantity of Fossil Material

Greater than 1,000 bones

100 - 1,000 bones

Less than 100 bones

FIG. 1 (*cont.*).

Subsequent to that, they have been described from the early Jurassic of Australia (Warren & Hutchinson, 1983), middle Jurassic of China (Dong, 1985) and late Jurassic of Mongolia (Shishkin, 1991). Nearly complete lower jaws with teeth, pectoral girdle elements, and ver-

tebrae form the basis for recognition of their presence in the Aptian of southeastern Australia (Warren, Kool, Cleeland, Rich & Rich, 1991; Warren, Rich & Vickers-Rich, in press).

Crocodilian-like in their overall morphology, the latest survivors of this once dominant group of amphibians may have found a final refuge in Aptian polar southeastern Australia because of a greater tolerance of cold, as is true of modern frogs and salamanders, than the crocodilians which appeared there subsequently in the Albian when conditions became warmer. There is no trace of an Albian labyrinthodont in the southeastern Australian deposits where crocodilians are represented by a few dermal scutes.

Among polar dinosaurs from either hemisphere, only one feature of one individual has yet been interpreted as an adaptation to life in a high latitude environment. This may reflect more the fact that very little is known about these animals and less published, than that they rarely displayed marked differences between themselves and their lower latitude contemporaries. The feature in question is the enlarged optic lobes of the brain that occurred on the holotype of the hypsilophodontid *Leaellynasaura amicagraphica* Rich & Rich, 1989 from the Aptian of southeastern Australia. Hypertrophy of this structure formed the basis for the suggestion that this animal had enhanced ability to see under the low light conditions that would have prevailed during the prolonged periods of continuous darkness each Winter.

Hypsilophodontid dinosaurs are generally a rare element in most dinosaur assemblages. Even where specimens are relatively common, as on the Isle of Wight, their taxonomic diversity is not great. Southeastern Australia is a marked exception to that generalisation. At least six species in five or six genera occur there; just over half the total dinosaurs recognised to date. Currie (pers. comm.) has suggested that hypsilophodontids may have been primarily an upland group at lower latitudes, hence their general rarity there, and are better represented in southeastern Australia because of its cooler conditions.

In this regard it may be noteworthy that the dinosaur known from the late Cretaceous of Vega Island is a hypsilophodontid or dryosaurid (Milner & Hooker, 1992) and that of the four found at Mangahouanga Stream, New Zealand, one is a probable dryosaurid, a family closely related to hypsilophodontids (Wiffen & Molnar, 1989). This explanation for the apparent preponderance of these groups at high latitude may well be true.

However, in the much more fossiliferous Liscomb Bonebed locality on the Colville River, Alaska, hypsilophodontids are all but unknown despite the extensive sieving programme carried out there (Clemens & Nelms, 1993; pers. obs.). The age of the site is Maastrichtian and by that time there may not have been the variety of hypsilophodontids there was earlier in the Cretaceous. But that does not explain why the one known to occur there is not more abundant.

Today, there are no avian or terrestrial mammalian families restricted to the polar regions. As far as the available record has been analysed, the same can be said of the polar dinosaurs as previously independently noted by Molnar & Wiffen (1994). Although new genera and species have been recognised among them, they all belong to families also known at lower latitudes.

However, given the fragmentary nature of much of the evidence for the existance of various groups, this could be an artefact. If one had a single tooth of a litoptern and that group was otherwise unknown, depending on the species, the most parsimonious familial identification might be Equidae. In that case one would be parsimonious but one would be wrong. The recent identification of protoceratopsians in the Aptian of Australia (Rich & Vickers-Rich, 1994) could be a parallel case. On the basis of a single bone, rather than propose an entirely new group of vertebrates which would share an uncanny resemblance in the form of the ulna to protoceratopsians but would in some other way be distinct from them, the specimen was allocated to this known taxon which extended its record not only to another continent but also backwards in time by at least 15 million years. At our present state of knowledge that is an identification which is quite plausible but could well eventually prove to be fundamentally in error.

The Gondwanan polar dinosaur localities that form groups of the same age are quite meagre in their total faunal lists, making comparisons quite preliminary. It is fortuituous, however, that in the broadest terms, they share a common facies. Both early Jurassic sites are flood plain deposits and the three late Cretaceous ones, nearshore marine. It may be of some note that the New Zealand late Cretaceous locality shares ankylosaurs and dryosaurids/hypsilophodontids with the two sites in the Antarctic Peninsula, the only two dinosaurs known to occur in the latter region.

There is no evidence such as tillites to suggest that continental ice sheets existed during the Mesozoic at high latitudes (Frakes, Francis &

TABLE 1. Gondwana Polar Dinosaur Localities.

1, Mt Kirkpatrick, Beardmore Glacier area, Transantarctic Mountains, Antarctica, 165°E, 84°S
Rock unit. Falla Formation (fluviatile)
Age. Jurassic on stage-of-evolution of dinosaurs
Palaeolatitude. 61°S (Smith, Hurley & Briden 1981)
Palaeoenvironment. Foreland basin flood plain
Recent Reference. Hammer & Hickerson (1994)
Fauna. *Cryolophosaurus ellioti*, plesiomorphic allosaurid (Hammer, pers. comm. to Molnar 1995); Small theropod; Prosauropod; Tritylodontid; Pterosaur

2, Australia, Southeastern Queensland, Taloona Station near Roma, 149°03±3'E, 26°05±3'S.
Rock unit. Walloon Coal Measures (Injune Creek Group)
Age. Early Jurass ic [?Bajocian]
Palaeolatitude. 65°S (Douglas & Williams 1982), 56°S (Smith, Hurley & Briden 1981)
Palaeoenvironment. Intracratonic flood plain
Reference. Longman (1927)
Fauna. Sauropoda: *Rhoetosaurus brownei*

3, Victoria, Australia, numerous sites centred on 38°45'S, 143°30'E. (Otway Group) and 38°40'S, 145°40'E (Strzelecki Group)
Rock units. Strzelecki and Otway Groups (fluviatile)
Age. Strzelecki Group Aptian except Koonwarra locality which is Albian; Otway Group Albian
Palaeolatitude. Strzelecki Group, 77.8°S; Otway Group, 66.8°S. Minimum estimates because of thermal overprinting between 75 & 100my BP (Whitelaw 1993).
Palaeoenvironment. Rift valley flood plain
Recent Reference. Rich & Vickers-Rich (1994)
Fauna. Hypsilophodontidae: *Fulgurotherium australe, Leaellynasaura amicagraphica, Atlascopcosaurus loadsi*, Victorian hypsilophodontid Type 1, Victorian hypsilophodontid Type 2, Victorian hypsilophodontid Type 3
  Ornithomimidae: *Timimus hermani*
  Ankylosauria, cf. *Minmi*
  Protoceratopsidae: Aff. *Leptoceratops*
  Oviraptorosaur?
  Carnosauria: *Allosaurus* sp.
  Testudines: *Chelycarapookus arcuatus* (testudines)
  Testudines: Cryptodira

Plesiosaur
Pterosaur
Aves
Labyrinthodont: New genus and species (Warren et al., in press)
Ceratodontidae: *Ceratodus avus, Ceratodus nargun*, Ceratodus sp., *Coccolepis woodwardi, Wadeicthys oxyops, Koonwarria manifrons, Leptolepis koonwarri*

4, Antarctica, Antarctic Peninsula, James Ross Island, 57.9°W, 63.9°S
Rock unit. *Santa Marta Formation (Marambio Group)*
Age. Campanian
Palaeolatitude. 65°S (Scotese et al. 1988)
Palaeoenvironment. Nearshore marine
Recent Reference. Gasparini, Pereda-S. & Molnar (1996, this volume)
Fauna. Nodosauridae

5, Antarctica, Antarctic Peninsula, James Ross Island, 57.9°W, 63.9°S
Rock unit. Hidden Lake Formation
Age. Coni acian-Santonian
Palaeolatitude. 65°S (Scotese et al. 1988)
Palaeoenvironment. Nearshore marine
Recent Reference. Molnar, Angriman & Gasparini (1996, this volume)
Fauna. Theropod

6, Antarctica, Antarctic Peninsula, Vega Island, 57.5°W, 63.7°S
Rock unit. Cape Lamb Member of the Lopez de Bertodano Formation
Age. Late Campanian - early Maastrichtian
Palaeolatitude. 65°S (Scotese et al. 1988)
Palaeoenvironment. Near shore marine
Recent Reference. Milner & Hooker (1992).
Fauna. Hypsilophodontidae

7, New Zealand, North Island, Mangahouanga Stream, 176°45'E, 39°S
Rock unit. Maungataniwha Sandstone
Age. Late Cretaceous, Campanian - Maastrichtian
Palaeolatitude. 55°S (Scotese et al. 1988)
Palaeoenvironment . Nearshore marine
Recent Reference. Molnar & Wiffen (1994)
Fauna. Dryosauridae, Theropod, Ankylosauria, Sauropoda, Testudines, Plesiosauroidea, Mosasauridae, Pterosauria

Syktus, 1992). However, it has been inferred on the basis of the occurrence of dropstones as large as 3m across in finegrained marine sediments deposited during the late Jurassic and early Cretaceous that winter seasonal ice did form at high palaeolatitudes in both hemispheres (Frakes, Francis & Syktus, 1992).

In southeastern Australia, studies assessing the mean annual palaeotemperature have been carried out on the sediments producing the dinosaurs. Palaeobotanical evidence based on leaf margin and stomatal structure together with the overall composition of the flora have been taken to suggest a mean annual temperature of +10°C (Parrish et al., 1991) while an oxygen isotope estimate is -6°C (Gregory et al. 1989), the difference between Chicago and Point Barrow, Alaska, today. While the biological implications of these two estimates are quite different, they are concordant in that the palaeoclimate was far from tropical.

No matter what the palaeotemperature was, polar dinosaurs would had to have adapted to prolonged periods of annual darkness each Winter. There have been suggestions that in the geological past the earth's rotational axis might have been significantly closer to being oriented perpendicular to the plane of the ecliptic (e.g., Douglas & Williams, 1982). If this had occurred, the length of continuous darkness each Winter at high latitudes would have been reduced. However, the criticism of Laplace (1829) against the earth's obliquity having shifted more than a few degrees from its present orientation as it does over a period of about 41,000 years (one of the components of the Milankovitch cycle), has never been refuted.

Of all the polar dinosaur sites, that on the Colville River, Alaska (Fig. 1), has the greatest potential to yield a detailed picture about these animals. For more than 200km on the left bank of that river are beautifully exposed outcrops that range in age from Albian to Maastrichtian. Fossil bones have been found at many places along that river. By contrast, the potential of sites which are shown as having less than 100 bones is much more problematical.

The work on the polar dinosaurs of Gondwana is just beginning. Just how distinctive they were from their lower latitude contemporaries is all but unknown. The Falla Formation of Antarctica seems the most promising area at the moment in terms of future potential. Southeastern Australian outcrops are limited to just 4 square kilometres which have been thoroughly prospected. In another four years, the major sites there may be worked out. Outcrops of the Wallon Coal Measures are rare in southeastern Queensland. In the Mangahouanga Stream locality of New Zealand the fossil vertebrates are recovered from loose boulders in the stream itself and dinosaur remains are quite rare. The Ross Island occurrences, like the New Zealand ones, are marine but unlike there, partial skeletons rather than isolated bones have been found. Although Ross Island is unlikely to produce major concentrations of dinosaur remains, with persistent prospecting over the large available area, it may be expected to continue to contribute significantly to our knowledge of Gondwana polar dinosaurs. Clearly, to find significantly more information about Gondwana polar dinosaurs outside the area of the Falla Formation, new areas need to be investigated such as the Cretaceous coalfields of New Zealand (Rich, 1975).

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EARLY CRETACEOUS POLAR TETRAPODS FROM THE GREAT SOUTHERN RIFT VALLEY, SOUHTEASTERN AUSTRALIA

PATRICIA VICKERS-RICH

Early Cretaceous deposits from southeastern Australia record a cold, extensively forested environment. Tetrapod fossils in channel fills, gravity flows, lag and point bar deposits in the Aptian Wonthaggi and Albian Middle Eumeralla formations. The fossils occur mainly in horizontally-stratified, clast-supported conglomerates and massive, matrix-supported conglomerates. Leaf mats indicate that several species of deciduous plants shed their leaves together, presumably in winter. Taphonomy of the lake beds at Koonwarra indicate seasonal freezing. A variety of dinosaurs — including hypsilophodonts, ankylosaurs, neoceratopsians, allosaurs, dromaeosaurs, oviraptorosaurs and ornithomimosaurs — were present as well as pterosaurs, plesiosaurs, temnospondyls and crocodilians. The latter two groups did not occur together and the temnospondyls lived under either cooler or higher-energy conditions than the crocodilians. □ *Cretaceous, Australia, dinosaur, environment of deposition, palaeoclimate, temnospondyl.*

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Breakup of Gondwana began in the Late Triassic. Australia and Antarctica were the last two continents of the supercontinent to separate, commencing in the Late Jurassic. During the Early Cretaceous, between 125 and 105 million years ago, what is now the southern coast of Victoria, Australia, was part of a rift valley formed between the two continents during the initial phase of that separation. As separation continued and sped up, the floor of the rift valley sank. As a consequence of that event, volcanoes that probably lay near the Lord Howe Rise, poured quantities of ash (estimated at 50,000 cubic kilometres) into the rift valley where it was then reworked by the rivers and streams, the precursors to the green sandstones and mudstones that now form prominent cliffs for about 200km of the Victorian coastline (Fig. 1).

Since that rift valley was formed, Australia has drifted far to the north, while Antarctica remained close to its Early Cretaceous position straddling the South Pole. In the Early Cretaceous southeastern Australia lay well within the Antarctic Circle. The dinosaurs, other fauna and plants that lived in this region thus contended with prolonged periods of continuous darkness each year, just as musk ox and reindeer do today. However, the geochemical and botanical climatic indicators suggest that the environment in the Early Cretaceous of Victoria was not frigid as are similar latitudes today, and extensive forests clothed many parts of the rift valley and its flanks at times.

ENVIRONMENTAL SETTING OF THE TETRAPOD FAUNA

A small, but growing, collection of fossil tetrapods are known from several locales in southeastern Australia (Currie, Vickers-Rich & Rich, 1996; Gross, Rich & Vickers-Rich, 1993; Molnar, Flannery & Rich, 1981; 1985; Rich & Rich, 1989; Rich & Vickers-Rich, 1994; Rich et al., 1988; 1992; Vickers-Rich & Rich, 1993; Warren et al., 1991). These fossils have been collected from three geologic units: 1, the younger Middle Eumeralla Formation of Early Albian age in the Otway Group; 2, the older undifferentiated Wonthaggi Formation of Aptian age in the Strzelecki Group; and 3, the Aptian San Remo Member near the base of the Wonthaggi Formation.

Fossils are concentrated in a few facies within these units: i.e., 1, mainly those preserved as a consequence of rapid deposition in a new channel cut as a consequence of a single major flood; 2, as gravity flows of sediment, either mud or rock debris; and to a lesser extent, 3, lag and point bar deposits within major river systems (A. Constantine, pers. comm.).

The bones are most commonly preserved in horizontally stratified, clast-supported conglomerates and massive, matrix-supported conglomerates. A 'clast-supported conglomerate'

refers to one in which the individual pebbles or boulders contact one another, whereas a 'matrix-supported conglomerate' is one in which the quantity of finegrained rock between the pebbles or boulders is so great that they do not contact one another. If the matrix could be removed from a clast-supported conglomerate, the volume occupied by the conglomerate would not decrease, whereas in the case of a matrix-supported conglomerate, it would.

The horizontally stratified, clast-supported conglomerates are typically of the order of 5-20cm thick and are characterised by pebble to cobble-sized clasts formed of clay and mudstone. Such deposits are stratified and contain little carbonaceous material. This type of bone-bearing conglomerate typically occurs at the base of channel complexes where significant erosion into underlying floodplain claystones and mudstones is evident. Such deposits are interpreted as having formed by streams or rivers breaking their banks during major floods, with the resultant flood waters flowing out over the surrounding floodplain, picking up bones and plant debris and concentrating them in erosion scours.

The massive, matrix-supported conglomerates, on the other hand, differ in that the pebble to boulder-sized clasts are not touching each other. Instead, they appear to be suspended in a finer-grained matrix composed of fine to medium-grained sandstone. Mudstone is again the dominant clast type, and plant remains are not as common. Conglomerates of this type are interpreted as debris flows, which form as the result of bank collapses within the confines of channels.

The regional setting for the two geological units that have produced significant fossil collections shows distinct change through time, from a predominantly 'meandering' to a 'braided' system upsequence. The older Wonthaggi Formation is characterised by thick floodplain deposits and channels with moderate to high sinuosity. There are thick accumulations of horizontally stratified to low angle crossbedded sediments, which indicate rapid aggradation under transitional to high flow regimes — suggestive of occasional flash flooding. The formation consists of about 60% sandstone and 40% mudstone and reflects varying flow regimes, perhaps due to discharge levels controlled by snow melt. Vertebrate fossils have been recovered from a variety of lithofacies within the formation, but mainly from horizontally stratified, clast-supported conglomerates and massive, matrix-supported conglomerates.

The younger Middle Eumeralla Formation consists primarily of sandstone (more than 70%) and is characterised by a classic braided river lithofacies and architecture. Sinuosity of channel deposits is low, and the channels were wide and shallow. There are thick sequences of both floodplain and lacustrine sediments with lenses of sand-sized particles representing individual channels stacked one on top of another. Vertebrates occur in only a few environmental settings, somewhat in contrast to the situation in the Wonthaggi Formation — in the Middle Eumeralla bones occur predominantly in sediments formed when a channel broke its bank and flowed out over the surrounding floodplain, or in those formed by loading and collapse of non-vegetated sand bars in the main channel during a peak flood stage that caused liquefaction of sand and then down-slope mass flow.

THE BIOTA: PALAEOFLORA AND INVERTEBRATE FAUNA AS PALAEOCLIMATIC INDICATORS

The palaeoflora of southeastern Australia during the Early Cretaceous was dominated by conifers, ferns, cycads, ginkgoes and lower-growing horsetails and bryophytes. Angiosperms were present, but only as prostrate or small herbaceous forms. The structure and diversity of this flora suggest a mean annual temperature of 8-10°C (Douglas, 1969; 1971; Drinnan & Chambers, 1986; Parrish et al., 1991). Some plants in this flora were evergreens, while others were clearly deciduous, the best evidence being fossilised leaf mats suggestive of simultaneous shedding of leaves by several species. The evergreen plants possessed leaves with thick cuticle and micro-phyllus (small) leaves. Such leaf morphology is consistent with a climate characterised by significant variation in temperature throughout the year or a fluctuating water supply — conditions that would be expected within a continental land mass distant from the ocean. Leaf mats themselves are indicative of leaves having fallen in a short period of time — which can be brought on by pronounced seasonal changes in light, temperature or water availability or a combination of these factors. Pronounced seasonal contrasts are expected of such inland environments at such latitudes as was the case in southern Victoria in the Early Cretaceous (Parrish et al., 1991).

One unusual locality to have produced fossil plants, invertebrates, fishes and birds, is Koonwarra. Koonwarra is an inland site in the Won-
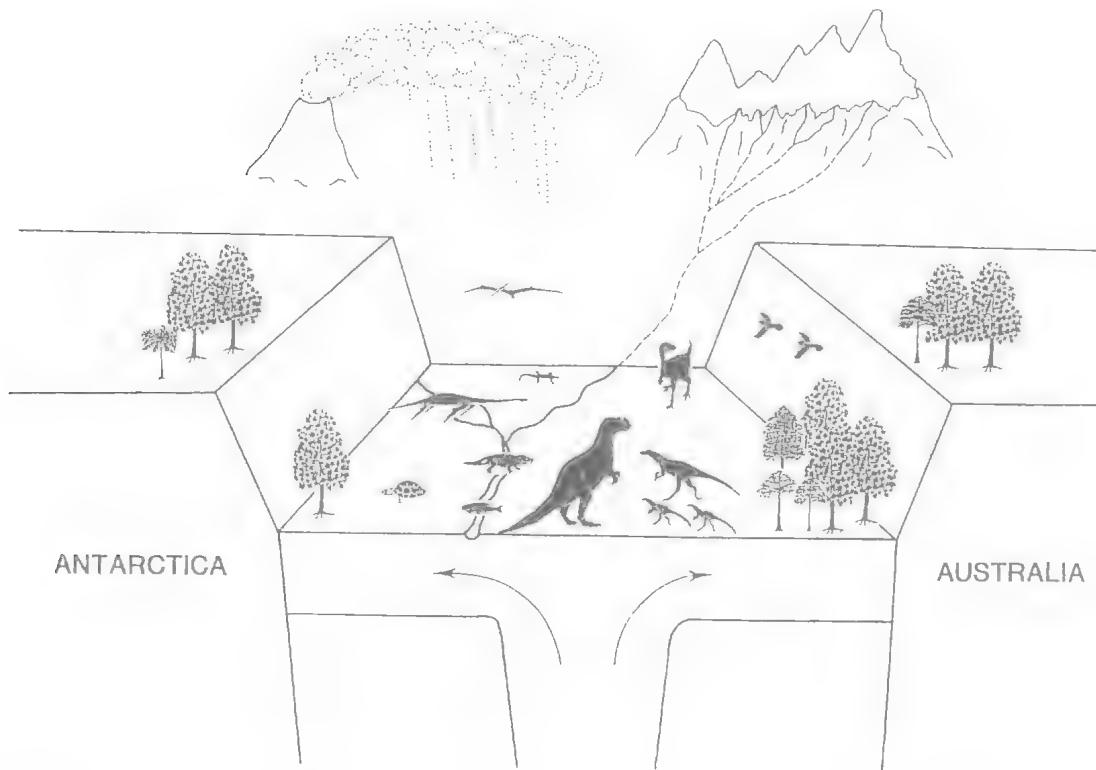
FIG. 1. Sketch of junction between SE Australia and E Antarctica in the Early Cretaceous. Separation began in the Late Jurassic and resulted in a rift valley being formed on the interplate boundary. Into this rift valley poured a vast quantity of volanogenic sediments derived from volcanoes perhaps laying to the east in the vicinity of the Lord Howe Rise. Large rivers flowed across the floor of this rift valley, fed perhaps in part by meltwater of snow presumably located at high altitude on mountains on the margins of the rift valley or the volcanoes which produced the volcanogenic sediments. The Early Cretaceous tetrapod and plant fossils occur for the most part in sediments that were laid down in small streams feeding into the larger rivers on the floor of the rift valley. Subsequent to the Early Cretaceous, the sediments deposited on the floor of the rift valley were first lithified as they were buried under additional sediment. Then late in the Cainozoic, these sediments were uplifted to form the Strzlecki and Otway Ranges.

thaggi Formation of the Strzelecki Group and represents the remains of an ancient lake. Most other vertebrate sites in southeastern Victoria are coastal exposures, and fossils were deposited not in the quiet waters of large lakes, but in the more energetic riverine and floodplain environments. Insects and other invertebrates, primarily larval forms, recovered from the Koonwarra locality are most closely related to forms typical of cool Tasmanian mountain lakes today (Jell & Duncan, 1986), relationships that are indicative of temperatures similar to those reflected by the palaeoflora. Waldman (1971), who studied the Koonwarra fish concentration, suggested that the entire fossil accumulation may have been due to winterkill — when the lake froze over and oxygen supply was greatly reduced.

Further evidence that temperatures were cool and that ice may have formed at times during the year occurs in contemporaneous sequences in central Australia. Boulders up to 3m in diameter have been found in otherwise finegrained marine sediments of the Bulldog Shale near Andamooka, South Australia (Frakes & Francis, 1988). Frakes & Francis have suggested that these boulders dropped to the bottom of the shallow sea as icebergs in which they floated, melted away. Although there is no preserved evidence — such as tillites — for glacial activity in Australia at this time, unlike for the earlier Permian time, Frakes has suggested that montane glaciation could have been active and, in places, these glaciers might have reached the sea at the base of drainage systems.

In summary, the suite of animals, plants and sedimentological data suggest that the climate of southeastern Australia during the late Early Cretaceous when dinosaurs are known to have lived there, was somewhat cooler than at present, but temperatures were by no means frigid as similar high polar latitudes are today. O^{18}/O^{16} evidence, however, suggests that mean annual temperatures approached 0°C at times during deposition of the dinosaur-bearing sediments.

VERTEBRATE ASSEMBLAGES OF THE EARLY CRETACEOUS OF POLAR AUSTRALIA

The Early Cretaceous terrestrial vertebrate assemblages of southeastern Australia are dominated by dinosaurs, in particular hypsilophodontids. There are at least five genera and six species of this family known from Victoria, half as yet unnamed. The diversity of hypsilophodontids in these south polar latitudes is unmatched anywhere else in the world, including localites with hundreds of thousands of bones and high diversity in the total dinosaur assemblage. Currie (pers. comm.) has suggested that at lower palaeolatitudes, hypsilophodontids may have been upland forms and thus not frequently represented at the lower elevations where most dinosaur fossils accumulated. Hypsilophodontids, then, may well have been preadapted for the conditions of southeastern Australia and consequently thrived there. Hyspilophodonts are known from both the Otway and Strzelecki Groups and thus have an age range in these sequences from Aptian to Albian, with some sites perhaps being as old as Valanginian in the Strzelecki Group.

On the basis of femoral morphology, five genra of hypsilophodontids have been recognised. To date, formal scientific names have been assigned to only three of these: *Fulgurotherium*, *Leaellynasaura* and *Atlascopcosaurus*. Prominent optic lobes preserved on an endocast of *Leaellynasaura* suggest that this dinosaur had unusually enhanced ability to process visual signals. In a polar setting, the most plausible explanation for this acuity would be that it improved visual ability under the low light conditions, which would have prevailed during the months of continuous darkness of the polar Winter. Since both palaeobotanical and geochemical studies suggest that Winter temperatures would have probably dipped below freezing, and since this is a prohibitive temperature for activity of modern reptiles, it is tantalis-

ing to think that *Leaellynasaura* may have been homeothermic — thus allowing the increased visual acuity to have an adaptive advantage.

Other ornithischians in the fauna include an ankylosaur (based on the cross-sectional outline of a rib, a scute and a few teeth) and an Aptian neoceratopsian (based on an ulna with a remarkable resemblance to that of *Leptoceratops gracilis* from the latest Cretaceous of Alberta).

Allosaurids, oviraptorosaurs and ornithomimid theropods are known. An astragalus resembling that of *Allosaurus* has been recognised in the Aptian Wonthaggi Formation of the Strzelecki Group (Molnar, Flannery & Rich, 1981; 1985). Oviraptorosaurs (Currie, Vickers-Rich & Rich, 1996) and ornithomimids (Rich & Vickers-Rich, 1993) are both known from the Middle Eumeralla Formation in the Otway Group, and ornithomimids have also been recovered from the older Strzelecki Group (Wonthaggi Formation). Footprints of small theropods have been recorded in the Otway Group.

The neoceratopsian, dromaeosaur and oviraptorosaur fossils from Australia are among the oldest records of these groups anywhere in the world. Other components of the fauna include the young temnospondyl amphibians, which are represented by more than twenty bones, including a pair of mandibles with the teeth in situ. Two bones of pterosaurs and half a dozen plesiosaur teeth have also been recovered. Evidently the plesiosaurs were freshwater animals, as all sedimentological and palaeontological data point to a fluviatile source for the containing sediments.

A few remains of crocodiles have been recovered in the Middle Eumeralla Formation in the Otway Group, but never have they been found together with temnospondyl remains, restricted as they are to the older Strzelecki Group. A warming trend up section in the Aptian-Albian sequence may explain this apparent faunal change — the replacement of temnospondyls by crocodiles.

The Victorian Aptian record of temnospondyls is the most recent for the group anywhere in the world. These amphibians were very crocodile-like functionally — in body form and in tooth morphology. Temnospondyls occur in the older Aptian sediments where temperatures were lower than in the younger Albian sediments that bear a few dermal scutes of crocodiles. Perhaps the rising temperatures allowed the invasion of crocodilians into an area from which they had been excluded by the cold waters, thus bringing them into direct competition with the temnospon-

dyls, followed by extinction of the latter. Today amphibians, such as frogs and the Giant Japanese Salamanders are able to cope with temperatures well below those tolerated by living reptiles.

The evidence is suggestive, but not definitive, however, for there is one other possible explanation that cannot be ruled out. Temnospondyl fossils are known from the Strzelecki Group only in the high energy sediments that represent fanglomerates pouring off the margins of the rift valley. This coarse facies occurs widely in the western exposures of the Aptian Strzelecki Group, but is less common in the younger Aptian Otway Group. Perhaps temnospondyls were facies controlled, and thus their absence is owing to sparsity of the coarse fanglomerate facies in the younger sediments of the Otway Group, rather than their extinction by the Albian owing to temperature increase or some other factor.

CONCLUSION

Although genera endemic to southeastern Australia occur in these Early Cretaceous assemblages, there is nothing yet recognised as unique as the modern day koala or kangaroo. All of the tetrapods found to date can be readily accommodated in families known from other continents. But what is clear is that in the Early Cretaceous, southern Australia served as a refuge allowing some groups to live well beyond their time elsewhere in the world (e.g., *Allosaurus,* temnospondyls and some fish and plant groups). This area also nurtured novelty — it may have been the cradle for such groups as the neoceratopsians, dromaeosaurs and oviraptorosaurs — a cradle from which they dispersed later, northwards, to meet with great success in North America and Asia.

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DINOSAURIAN PALAEOBIOLOGY: A NEW ZEALAND PERSPECTIVE

J. WIFFEN

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The first known dinosaur bone from New Zealand was identified from the Late Cretaceous marine sandstones at the Mangahouanga Stream site in 1980 (Molnar, 1981). Since then isolated bones indicate that a variety of herbivores and carnivores were present after the separation from Gondwana 80-85 million years ago until their extinction. Though geographically polar in origin, survival for a long period on an island landmass suggests a temperate climate prevailed as New Zealand drifted north. □ *New Zealand, Cretaceous, dinosaur, palaeoclimate, palaeobotany, taphonomy.*

J. Wiffen, 138 Beach Road, Haumoana, Hawke's Bay, New Zealand, 5 July 1996.

The only dinosaur fossils so far found in New Zealand come from the Late Cretaceous Maastrichtian-Campanian marine sediments in the Mangahouanga Stream fossil site, North Island, New Zealand. These bones represent a diverse dinosaur fauna and the only record of terrestrial life from Mesozoic New Zealand. They include vertebrae and phalanges from 2-3 species of theropod, vertebrae (Fig. 1A) and a rib from an ankylosaur, an ilium (Fig. 1B) from an ornithopod and a rib fragment (Fig. 1C) from a sauropod (Molnar, 1981; Wiffen & Molnar, 1989; Molnar & Wiffen, 1994).

The bones are found in hard calcareous concretions, locally derived from the upper layers of the Maungataniwha Sandstone. This was laid down on the eastern coastline of ancient New Zealand in Campanian-Maastrichtian (Haumurian-Piripauan) times and is now exposed at the Mangahouanga Stream (Fig. 2). Isolated bones were carried from the adjacent landmass by rivers probably in seasonal floods — the larger bones dropped as the flow slowed through lagoonal or estuarine areas — prior to burial in riverborne debris in nearshore wave base deposits (Crampton & Moore, 1990; Moore & Joass, 1991; Wilson & Moore, 1988). They occur along with fossils of marine origin.

The described terrestrial bones are easily recognised (Fig. 3) and well preserved, with diagnostic features. So it seems likely that the bones weren't transported far from land to the site. When extracted from the rock, there is little apparent abrasive damage on the bone surface that occurred prior to burial. Most of the damage seen is recent, from exposure after the concretions have eroded out of the enclosing rock and split due to temperature extremes (i.e., winter frosts and hot dry summers), with resulting surfaces worn by running water.

SIGNIFICANCE

By and large the record of terrestrial life from ancient New Zealand isn't as good as those from elsewhere. Acid conditions produced by the high rainfall and extensive forest cover are thought to account for the generally poor fossil record (Fleming, 1962).

Consequently although the number of dinosaur bones identified to date is small, they are significant for several reasons:

1) They show that dinosaurs inhabited this part of Gondwana prior to its separation from the Marie Byrd Land area of western Antarctica (Stevens, 1985).

2) They are the first evidence that terrestrial vertebrates survived in New Zealand after its separation from Gondwana, as opposed to having arrived there by dispersal.

3) This is the only known Southern Hemisphere region where dinosaurs lived on a small island, for up to 15-20 million years, until their extinction.

What evolutionary changes, if any, occurred in these forms in the presumably static island environment, in the absence of migrations to New Zealand and with (presumably) decreased competition, are not known. To date no unique features have been seen to suggest morphological changes or geographic or climatic adaptations: however, considerably more complete fossil material is required to determine this.

Although similar taxa have been found from this period in Antarctica (Hooker et al., 1991; Hammer & Hickerson, 1994) no closely-related forms have been detected, in spite of the variety of taxa — ornithopod, sauropod and ankylosaur,
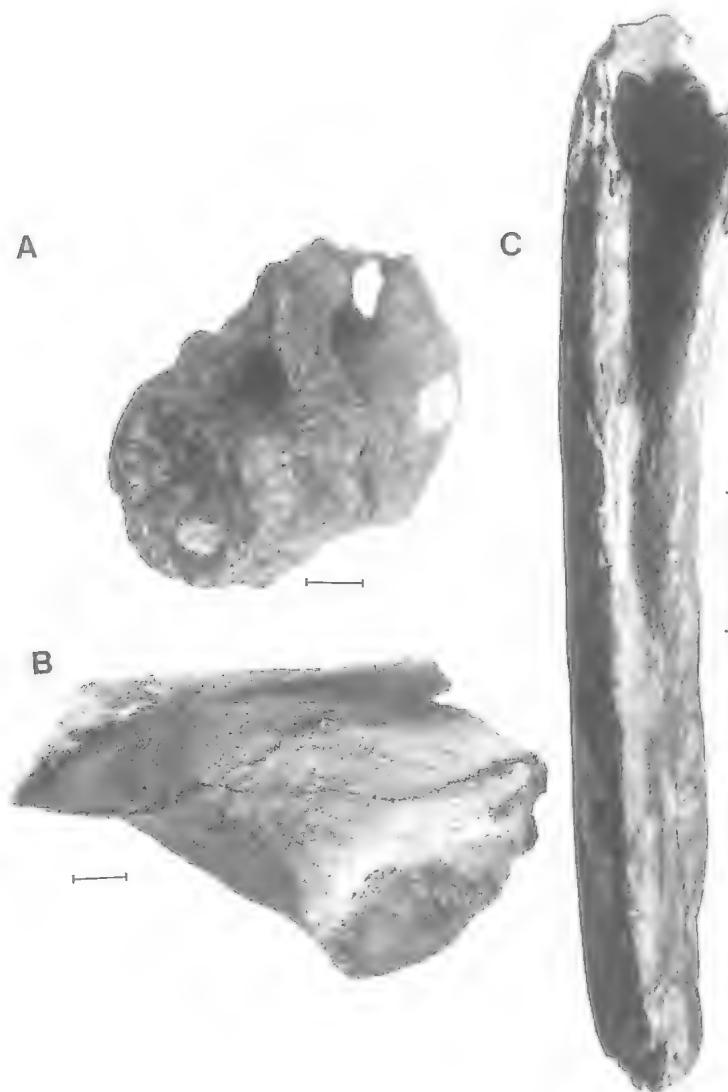
FIG. 1. A, Articulated nodosaurian caudal vertebrae (CD 546) from the Maungataniwha Sandstone, Mangahouanga Stream, in posterolateral oblique view. The specimen unfortunately exceeded the depth of focus of the camera. CD, New Zealand Geological Survey Collection, Lower Hutt. Scale = 1cm. B, Posterior part of the right ilium (CD 529) of a dryosaur-like ornithopod from the Maungataniwha Sandstone, Mangahouanga Stream. Scale = 1cm. C, Fragment of sauropod rib (CD 542) from the Maungataniwha Sandstone, Mangahouanga Stream. Scale = 5cm.

this volume) and a second skull of the large ornithopod *Muttaburrasaurus* (Molnar, this volume) from Queensland and a range of new Jurassic material from Antarctica (Hammer & Hickerson, 1994) suggest the early and widespread distribution of dinosaurs on the southern continent. So a greater understanding of the distributions of these polar dinosaurs, and their relationships to those from New Zealand, should result when more becomes known about these new discoveries.

The difficulties of close comparisons with New Zealand dinosaur bones are due to the paucity of fossil material collected and identified to date, hence the difficulty in finding homologous elements for comparison, as well as the discrepancy in geological age from most other Australasian /Antarctic sites.

FLORA AND FAUNA

The New Zealand marine fossil record is relatively good, and the Mangahouanga Stream site has contributed fossils to both marine (Crampton & Moore, 1990; Glaessner, 1980; Feldmann, 1993; Wiffen, 1981) and terrestrial records — including (possibly freshwater) turtles (Gaffney, pers. comm., 1989), flying reptiles (Fig. 4)(Wiffen & Molnar, 1988), a coleopteran (Craw & Watt, 1987) and a cockroach, which is still under study (Fig. 5).

A considerable quantity of fossil wood and plant material has been collected as well and this is currently being described by J.I. Raine. The available fossil plant material (wood, leaves, seeds and cone scales) is probably biased due to its preservation in shallow wave-base marine sediments — with only the tougher plant material surviving transportation by river to the region of deposition.

probably nodosaurian, dinosaurs — that have been identified from the Mangahouanga site (Molnar & Wiffen, 1994): the ankylosaurid bones found by the British Museum are as yet undescribed. Recent discoveries, which include a neoceratopsian, *Timimus hermani* and a possible oviraptorosaur (Rich & Rich, 1994; Currie et al., 1996) from Victoria, new ankylosaur material (Molnar,
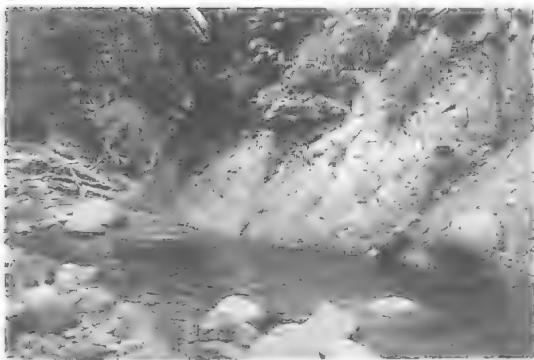
FIG. 2. The Mangahouanga Stream fossil site, showing a concretion eroding from the Maunataniwha Sandstone. Dinosaurian, and other, bones have been recovered from some of these concretions.

However eight types of angiosperm leaves and several seed capsules have been recognised and a considerable amount of podocarp-like foliage, similar to present-day material — though araucarian wood, leaves and cone scales dominate the collections (Raine, 1990; Crampton, 1990). It is hoped that ultimately the study of this material, combined with pollen and spore samples, will give a clearer indication of the botanical environment in which these dinosaurs survived.

POLAR DINOSAURS?

While it is evident that New Zealand's dinosaur population was subpolar in the geographic sense (Fig. 6) (Molnar & Wiffen 1994), it is not readily apparent that the climate and conditions in which they survived during the subsequent 15-20 million years were polar in the climatic sense. Water temperatures of 14.3°C are suggested from oxygen isotope studies by Stevens & Clayton (1971) and the marine record shows that plesiosaurs, mosasaurs and turtles were common in offshore waters in the Late Cretaceous. On land, there is evidence of continuous forest and plant growth — e.g., the Jurassic fossil forest at Curio Bay, Southland, the plant beds at Port Waikato, the lignite and plant fossils in both South and North Islands, material from Shag Point and Cretaceous material from Putarau, northwestern Nelson, Kaipara Harbour and Mangahouanga Stream (Bose, 1975; Edwards, 1926; Ettingshausen, 1891; Johnson, 1993; Kennedy, 1993; Mildenhall, 1970; Stevens, 1985) — which would have been essential to maintain a her-

bivorous dinosaur population, which in turn provided the food for the carnivorous dinosaurs.

However, palaeobotanical evidence appears to be accumulating to support the view of a cold Australasian polar climate, i.e., dominant angiosperms that were deciduous, dormant in periods of cold and darkness and dropping all their leaves over a short period to form leaf mats (Vickers-Rich & Rich, 1993; Johnson, 1993), though Pole (1993) suggests that this is still based on scant evidence. If true, presumably the deciduous plants would have, to some extent, replaced the conifers. From a practical point of view, such a deciduous vegetation would seem to have provided a meagre winter diet for the active, medium-sized dryosaur-like herbivorous dinosaur, while having the larger herbivores (sauropods) dependent on foraging for and browsing on fallen leaf mats to sustain life over prolonged periods of darkness and low temperature seems an unlikely scenario. How much nutriment could be derived from cold, semi-frozen, fallen leaves alone does not appear to have been calculated, but it was probably substantially lower than in still-attached leaves, because most nutrients are withdrawn from leaves before they are dropped. The feasibility of sauropods of even modest proportions 'grazing' on such a leaf mat is unclear, and even the question of how sauropods supported themselves in more temperate climates is unresolved (Ostrom, 1985). There is no evidence that herbivorous dinosaurs roamed New Zealand in large herds, as occurred in North America at this period, and the balance of both herbivores and carnivores would have been ultimately controlled on this island landmass by the quality, quantity, reproductive rate and availablity of the vegetation that formed the food supply. The deciduous vegetation does not appear to have been adequate to support the known dinosaurs through a cold polar winter.

Migration was not an option on this relatively small island landmass (Molnar & Wiffen, 1994). There is nothing in the dinosaur bones so far identified from the Mangahouanga Stream site to indicate dwarfism, as suggested for Victorian dinosaurs by Vickers-Rich & Rich (1993): a useful strategy if food resources or climatic conditions made hibernation necessary for survival. But hibernation for the relatively large dinosaurs (*Allosaurus*-size theropods and medium-size sauropods) found in New Zealand seems unlikely. Even remaining stationary for long periods in groups to conserve warmth would be unlikely for dinosaurs of this large size, while laying down
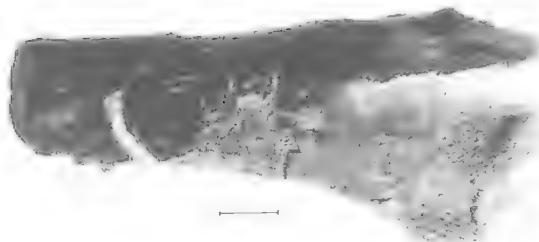
FIG. 4. Pterosaur distal ulna (CD 467) from the Maungatanwha Sandstone, Mangahouanga Stream. Scale = 1cm.

and curling up to keep the extremities warm would be improbable and finding sufficient handy caves to accommodate a number of animals of this size unbelievable. So there are no obvious behavioral strategies for the dinosaurs to have coped with a cold polar winter, either.

The difficulty of comparing the environment and dinosaurs from New Zealand and Australia arises from the difference in geological ages of these dinosaur faunas. The Australian dinosaurs range from Jurassic to Early Cretaceous, while Australia was still attached to Gondwana, whereas the only known bones from New Zealand are Late Cretaceous (Maastrichtian, 65-70 million years) when New Zealand had been adrift — and an isolated island — for approximately 15-20 million years after separation from Gondwana. It would appear that dinosaurs either adapted to whatever climatic changes they encountered over their 15-20 million years of occupation or the climate on the New Zealand landmass remained relatively stable and temperate. Doubtless even with a reasonably stable and temperate maritime climate, as probably existed, there were times when temperatures dropped or rose and conditions were unfavorable for dinosaurian life — with subsequent decreases in population size and reproduction at that time, such as occurs in the wild (and also with domesticated) animals today, but so far as is known of insufficient magnitude to wipe out any species before the end of the Cretaceous.

A living example of the resiliency that favours long-term survival is the Tuatara (*Sphenodon punctatus*): to quote Vickers-Rich & Rich (1993), '*this reptile can live in conditions down to 5°C, as long as it can sun itself*'. It must be remem-

FIG. 5. Fossil cockroach, about 43mm long, from the Maungataniwha Sandstone, Mangahouanga Stream. The head was not found, but the right antenna (a) is present.

bered that *Sphenodon punctatus* was a New Zealand resident prior to and since the separation from Gondwana and that it apparently survived everything, including the Pleistocene ice ages from around 2 million to 14,000 years ago: an example of endurance over a long period of fluctuating temperature. Admittedly, the relatively small size and lower metabolic rate of the Tuatara allowed it to hibernate using holes and tunnels made by birds, or tree roots, for shelter. On the other hand the Moas, flightless ratite birds of large proportions whose ancestors are also believed to have lived on New Zealand since it separated from Gondwana, would have had difficulty in hibernating during the Ice Age, but survived until shortly after the arrival of man — around 1,000 years ago. This in spite of their higher metabolic rates and hence increased susceptibility to low temperatures and winter food shortages.

These are just two of a number of the forms which are known to have survived, regardless of climatic changes and turbulent geological events,

FIG. 3. A, Plesiosaurian vertebrae exposed in a concretion at the Mangahouanga Stream locality. B, Pedal phalanx of a large theropod exposed in a concretion at this locality. Both specimens show the characteristic structure of fossil bone as it is seen in the field and show how the bone can be easily recognised in situ.
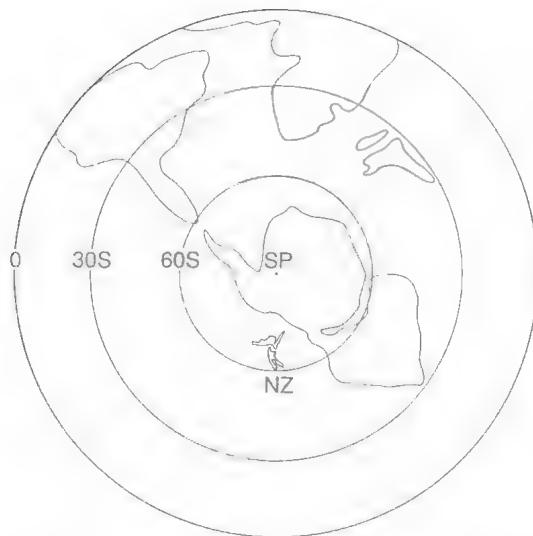
FIG. 6. Map of Late Cretaceous Southern Hemisphere in south polar projection showing the position of New Zealand (NZ). SP=South Pole.

since New Zealand's isolation 80-85 million years ago — though, as yet, there is little fossil evidence of their long period of residence. So it is not unexpected that the dinosaurs whether ectothermic or endothermic — considered by some to be the most successful forms of life on earth — were capable of surviving whatever changes occurred within their period of occupation of New Zealand. Especially as these changes seem to have been substantially less great than those undergone during the Caenozoic.

SUMMARY

Although the New Zealand contribution of dinosaur fossils is small at this stage, they do contribute to the overall knowledge of dinosaurs from the southern supercontinent, their dispersal and their survival until their worldwide extinction at the end of the Cretaceous. The fossils show that dinosaurs did inhabit New Zealand after it separated from Gondwana early in the Campanian. They are the oldest evidence for terrestrial vertebrates in New Zealand, and are the only near-polar dinosaurs from the Southern Hemisphere that lived on an island landmass.

The climate of New Zealand at that time seems to have been temperate, judging from the dinosaurian and plant fossils. Some plant material suggests that leaves were dropped during the winter forming leaf mats although conifers, not these deciduous forms, still appear to have

dominated the forests in this region. The recovered dinosaur material shows no special adaptations to cold climates. However, the survival of Tuataras and Moas through the climatic variations that occurred in New Zealand since its separation from Gondwana shows that both endothermic and ectothermic forms were capable of surviving here for long periods. There is no reason to think that dinosaurs were not able to do so, too.

It is hoped that other New Zealand sites yielding Mesozoic terrestrial fossils will be found, and that more material will add to what we already know and expand our understanding of dinosaurian life and survival here on New Zealand and our place in the evolution of Gondwanan dinosaurs.

ACKNOWLEDGEMENTS

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