Miocene geology and palaeontology of
Ad Dabtiyah, Saudi Arabia

Compiled by P. J. Whybrow

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Contents

Fig. 1 Qarn Abu Wayil. The locality where in 1933 H. St J. Philby first found Miocene fossils. Photographed in 1979 from Qatar; the Saudi Arabian–Qatar border, left to right, passes the foot of the hill.

Summary

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The importance of the eastern Saudi Arabian Miocene mammal-bearing localities lies in their intermediate palaeogeographical position between the eastern African Miocene sites and those of Turkey and Pakistan, and their proximity to the shores of the contracting Tethys epicontinental sea.

The eastern Arabian deposits consist of three units. These are, from oldest to youngest, the continental Hadrukh Formation, which unconformably overlies Eocene rocks, the marine Dam Formation and the continental Hofuf Formation. The Hadrukh can always be distinguished from the Hofuf when the intervening marine Dam is present, but where continental equivalents of the Dam occur, such as at Ad Dabtiyah, they are difficult to separate from the underlying Hadrukh.

In the Mesopotamian region of the Middle East the ancient marine connection between the Mediterranean and the Indian Ocean—the Tethys—had been lost at the time of deposition of the Dam Formation. The break in the marine sequence, indicated in part by the continental Hadrukh and its equivalent chronostratigraphic units in the region, suggests the presence of a land connection between Saudi Arabia and southwestern Asia by *at the latest* mid-Burdigalian times, at about 18 Ma (Adams, Gentry & Whybrow 1983; Whybrow 1984). Keller & Barron (1983) report worldwide low sea level between 20 and 18 Ma, while Barry, Johnson, Raza & Jacobs (1985) believe an Africa to southern Asia land connection must have existed before 18 Ma and possibly even before 20 Ma as suggested by Whybrow *et al.* (1982).

The Ad Dabtiyah fauna, described here, represents part of a fauna of cosmopolitan distribution in Africa, Europe and Asia during a time equivalent to the mid-Orleanian of Europe, 17–19 Ma. The Asian mastodon *Gomphotherium cooperi*, previously known only from the basal Miocene deposits at Dera Bugti, Pakistan, is present. Of the two rhinoceros species found, both are early and primitive members of their genera; one is not unlike the European *Dicerorhinus sansaniensis*. Even so, the poor ruminant and suid fauna, together with the mastodon and rhinoceroses, does not on balance suggest any discrete palaeobiogeographical affinities for the Ad Dabtiyah fauna. Part of its African element is a new genus of hominoid which is interpreted as the sister group of the great ape and man clade and is more closely related to the African members of that clade than to their Eurasian representatives.

The palaeoenvironment at Ad Dabtiyah appears to have been a tropical ponded area of fresh water with centropomid and cyprinid fishes. Logs, probably of palm, are found encrusted with cyanophyte algal material of fresh-water origin, and large stromatolitic bioherms occur. The ruminants and rhinoceroses suggest a woodland habitat near to the Ad Dabtiyah depositional area.

From the marine Dam Formation near its type locality at Jabal Lidam, the first cetacean fossil to be reported from Saudi Arabia is described (p. 447).

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Appendix. Table of eastern Saudi Arabian Miocene vertebrates

Hofuf Formation—vertebrate fauna from Al Jadidah

From Sen & Thomas 1979; Thomas *et al.* 1978; Thomas 1983.

Rodentia
  Sciuridae: *Atlantoxerus* sp.
  Ctenodactylidae: *Metasayimys intermedius* Sen & Thomas 1979
Carnivora
  Hyaenidae: *Percrocuta* sp.
Proboscidea
  Gomphotheriidae: *Gomphotherium angustidens*
Perissodactyla
  Rhinocerotidae: *Dicerorhinus* cf. *primaevus*
Artiodactyla
  Suidae: cf. *Lopholistriodon*
  Giraffidae: *Palaeotragus* sp.
  Bovidae:
    Pachytragus ligabuei Thomas 1983
    Caprotragoides aff. *potwaricus*
    Protragocerus sp.
    cf. *Homoiodorcas*?
Indeterminate Pisces, Chelonia and Crocodilia.

Dam Formation (continental equivalents)—vertebrate fauna from Ad Dabtiyah

Hominoidea
    Heliopithecus leakeyi Andrews & Martin 1987 (herein)
Proboscidea
  Gomphotheriidae: *Gomphotherium cooperi*
Perissodactyla
  Rhinocerotidae:
    Dicerorhinus sp. aff. *sansaniensis*
    Brachypotherium sp.
Artiodactyla
  Suidae:
    Listriodon cf. *lockharti* or *L.* cf. *akatikubas*
    ? *Kenyasus* sp.
  Tragulidae:
    Dorcatherium sp.
    Dorcatherium, larger sp.
  Giraffoidea: *Canthumeryx* sp.
  Bovidae:
    Eotragus sp.
    Bovid species 2.
    Bovid species 3.
Chelonia
Crocodilia: cf. *Crocodylus pigotti*

Osteichthyes: Cyprinidae
Acanthoptergii: ? Centropomidae

Vertebrates from the As Sarar (Al Sarrar) locality

Provisional list from Thomas *et al.* 1982.

Insectivora: Erinaceidae
? **Primates** gen. et sp. indet.
Lagomorpha: Ochotonidae
Rodentia
  Cricetidae
  Ctenodactylidae: *Metasayimys* cf. *intermedius*
  Gerbillidae
  Pedetidae:
    Megapedetes cf. *pentadactylus*
    cf. *Protalactaga*
  Thryonomyidae: *Paraphiomys* sp.
Carnivora
  Viverridae: *Viverra* sp.
  Mustelidae:
    cf. *Martes*
    Mionictis sp.
  Felidae: *Pseudaelurus turnauensis*
  Amphicyonidae: *Amphicyon* sp.
Proboscidea
  Deinotheriidae: cf. *Deinotherium*
  Gomphotheriidae: *Gomphotherium* sp.
  ? Amebelodontinae
Sirenia indet.
Hyracoidea
  Saghatheriinae: *Pachyhyrax* aff. *championi*
Perissodactyla
  Rhinocerotidae:
    Aceratherium sp.
    Dicerorhinus sp.
Artiodactyla
  Suidae:
    Listriodon sp.
    gen. et sp. indet.; giant species.
  Tragulidae: *Dorcatherium* cf. *libiensis*
  Bovidae gen. et sp. indet.
Aves
  Threskiornithidae
  Ciconiidae:
    Mycteria cinereus
    ? *Mycteria* sp.
  Scolopacidae: Charadriinae indet.
  spp. unidentified.
Crocodilia
  Crocodylidae: *Crocodylus* cf. *pigotti*

Chelonia
  Pelomedusidae:
    cf. *Schweboemys*
    aff. *Stereogenys*
  Trionychidae: aff. *Cycloderma*
  Carettochelyidae
  Testudinidae: *Geochelone* sp.
Serpentes
  Scolecophidia
  Boidea:
    Python sp.
    Eryx/Gongylophis spp.
  Colubridae
  Elapidae: *Naja/Palaeonaja* spp.
  Viperidae
Squamata
  Sauria: Lacertidae
  Amphisbaenia: Amphisbaenidae
Amphibia
  Bufonoidea
  Ranoidea
Pisces
  Mormyridae: *Hyperopisus* sp.
  Cyprinidae:
    Barbus sp.
    Labeo sp.
  Clariidae:
    Heterobranchus sp.
    Clarias sp.

  Centropomidae: *Lates* sp.
  Sphyraenidae: *Sphyraena* sp.
  Sparidae indet.
Selachii
  Hemigaleidae: *Hemipristis serra*
  Carcharhinidae:
    Carcharhinus aff. *priscus*
    Carcharhinus aff. *plumbeus*
    Galeocerdo cf. *aduncus*
    Scoliodon sp.
    Negaprion eurybathrodon
  Sphyraenidae: *Sphyraena* sp.
  Dasyatidae: *Dasyatis* sp.
  Myliobatidae:
    Myliobatis sp.
    Aetobatus arcuatus
  Rhinopteridae: *Rhinoptera*

Hadrukh Formation—vertebrates from Jabal Midra ash-Shamali

From Whybrow *et al.* 1982.

Rodentia
  Zapodidae: *Arabosminthus quadratus* Daams 1982
  Cricetidae: *Shamalina tuberculata* Daams 1982
Artiodactyla
  Bovidae: cf. *Oioceros* sp.

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Miocene stratigraphy, geology and flora (Algae) of eastern Saudi Arabia and the Ad Dabtiyah vertebrate locality

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Synopsis

Studies of the Miocene deposits in eastern Saudi Arabia are briefly reviewed. The stratigraphical succession is explained and the geological details of the vertebrate-bearing, non-marine deposits at Ad Dabtiyah presented. The stratigraphical position of the fossiliferous beds is believed to lie near the boundary of the continental sequence of the Hadrukh Formation and continental equivalents of the Dam Formation, the beds themselves locally close to, and the lateral equivalent of, the basal deposits of the Burdigalian marine carbonates of the Dam Formation. The fresh-water depositional environment at Ad Dabtiyah contains many bones of terrestrial vertebrates, found in close association with several large stromatolitic bioherms. These, and similar encrustations also of a fresh-water origin, are associated with *in situ* logs, probably of palm trees. Overall, both the stratigraphical position of the Ad Dabtiyah deposits and their contained fauna suggest an age of about 17–19 Ma; middle Orleanian (European land-mammal age equivalent); early Burdigalian (marine chronology).

Introduction

Until the 1930s, almost nothing was known of the geology of the central part of the Arabian Peninsula. Observations on its general geology had been carried out by Philby (1933) during his explorations of Saudi Arabia, and his fossil collections were presented to the British Museum (Natural History) by King Abdul Aziz ibn-Saud. Cox (1933) studied the Tertiary fossils Philby had found at a hill called Qarn Abu Wayil (Fig. 2) and identified the oyster *Ostrea latimarginata*, and natural casts of *Mytilus, Anomia, Cardium, Clementia, Anadara* and other molluscs previously known from the Lower Fars rocks of Iran. South of Qarn Abu Wayil at Jaub Anbak (Fig. 2), Philby had noted the marine beds were overlain by a considerable thickness of red sandstones which Cox suggested might also be of Miocene age, but equally might be equivalent to the Pliocene Bakhtiyari deposits of Iran (Cox, in Philby 1933: 386–387). Cox's work therefore provided the first evidence of the presence of Miocene rocks in Arabia.

Mapping and surface collecting by geologists of the Arabian American Oil Company, ARAMCO, started in the mid-1930s and revealed in detail the extent of Miocene deposits in eastern Saudi Arabia. Three formations were formally designated (Steineke *et al.* 1958), together with the lithological details at their type localities. Later, the first published evidence that vertebrate fossils occurred in the region was given by Powers *et al.* (1966: D97) who recorded 'vertebrate fragments' in their lists of the Miocene biota.

In 1974 a collection of Miocene crocodile, turtle, antelope, rhinoceros and proboscidean remains was presented to the British Museum (Natural History), representing the first known
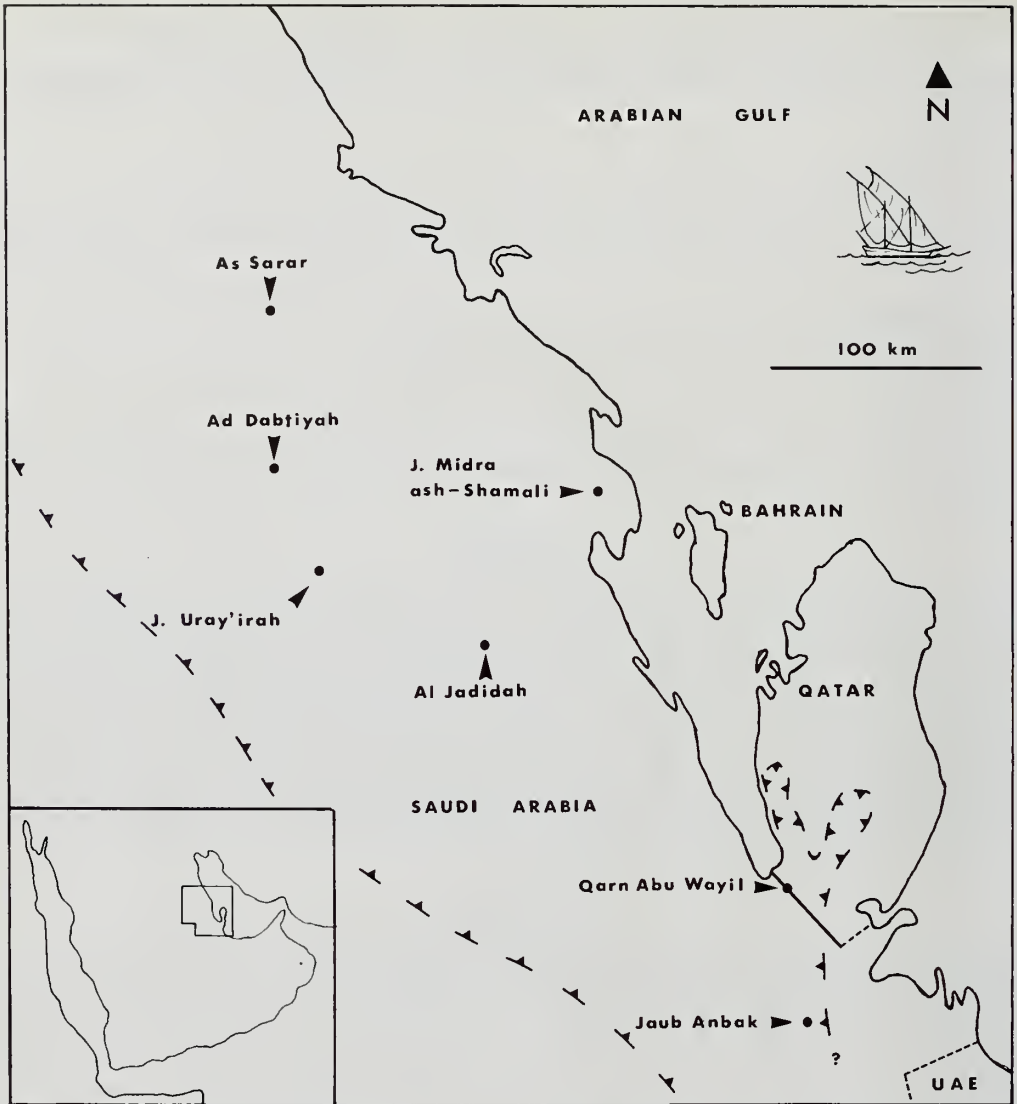
Fig. 2 Eastern Saudi Arabia, the State of Qatar and part of the United Arab Emirates showing localities referred to in the text. The most western extent of the Miocene deposits in Saudi Arabia and their location in south-western Qatar is indicated.

vertebrate palaeofauna from Arabia (BM(NH) 1975: 18). In the same year staff of the Palaeontology Department added more material by collecting from Miocene continental deposits at Ad Dabtiyah (Fig. 2). They also collected vertebrate-bearing rocks near a hill called Jabal Midra ash-Shamali, *c.* 6 km north-west of Dhahran (Fig. 2) where Tleel (1973) had discovered 'artiodactyl' remains. Chemical breakdown of these rocks yielded rodent, lagomorph and bovid teeth and preliminary reports on the faunas from both localities were published (Hamilton *et al.* 1978; Andrews *et al.* 1978). Further work on the Ash-Shamali material showed a new genus of fruits of aquatic plants, *Midravalva arabica* (Collinson 1982), to be present, together with new rodents, *Arabosminthus quadratus* and *Shamalina tuberculata* (Daams, *in* Whybrow *et al.* 1982: 111–116).

In 1978, H. Thomas of the Museum National d'Histoire Naturelle, Paris, and colleagues excavated vertebrate fossils, *Percrocuta, Gomphotherium angustidens, Dicerorhinus, Lopholistriodon, Pachytragus, Protragocerus, Caprotragoides* and a new rodent, *Metasayimys intermedius*, from red-coloured sandstones at Al Jadidah (Fig. 2); see Thomas *et al.* (1978), Sen & Thomas (1979), Thomas (1983). Later, they collected from the As Sarar region (Fig. 2) in collaboration with the Saudi Arabian Department of Antiquities. Abundant vertebrate remains were found including two gomphothere species, a deinothere, several carnivores and cricetid, ctenodactylid, dipodid, gerbellid, pedetid and phiomorph rodents (Thomas *et al.* 1982).

These discoveries of terrestrial vertebrates in eastern Arabia have now bridged the palaeo-geographical gap between the better-known Miocene faunas of Africa and those of south-western Asia. In addition, interpretations of the eastern Arabian palaeoenvironments have been made (Whybrow & McClure 1981; Thomas *et al.* 1982; Whybrow *et al.* 1982) and, because of the proximity of the fossil localities to the contracting Tethys epicontinental seaway, there have been suggestions concerning the location of a Neogene land connection between Arabia and south-western Asia (Adams *et al.* 1983; Rogl & Steininger 1983; Whybrow 1984; Thomas 1985).

The collected papers in this issue of the *Bulletin*, with the exceptions of the descriptions of a delphinoid ear bone and a gomphothere tooth from other localities, are the results of studies on the Ad Dabtiyah fauna and flora collected and donated in 1974.

Stratigraphy and the age of the deposits

Towards the end of the middle Eocene, widespread emergence of the eastern Arabian shelf coincided with continued uplift and a slight north-easterly tilting of the Arabian plate, events that began in the late Cretaceous and continue today as a consequence of the movement of the Arabian plate against the more stable south-western Asian plate. Red Sea rifting was also a contemporaneous consequence of this plate activity (Schmidt *et al.* 1983; Sellwood & Nether-wood 1984). Since that time mainly continental deposition, with the exception of a marine transgression from the Indian Ocean, has prevailed in eastern Arabia. Rocks of Oligocene age have not been recognized in the region; Miocene deposits unconformably overlie rocks of Ypresian or Lutetian age.

Where the rocks formed by the marine transgression (represented by the Dam Formation) occur, the continental Neogene has been divided into units. From the oldest, these are the Hadrukh Formation (*c.* 20–120 m thick), succeeded by the Dam Formation itself (*c.* 30–100 m thick), and the Hofuf Formation (*c.* 30–100 m thick).

Towards the western interior, where the marine marker beds of the Dam intercalate with the continental deposits, become thin and eventually disappear, the eastern divisions of Hadrukh, Dam and Hofuf no longer apply. The undifferentiated deposits are treated as a single un-named unit—Tertiary continental sandstone, marl and limestone, marked 'Tsm' in Figs 3 and 5 (Steineke *et al.* 1958). In such deposits a gomphothere $M^2 + M^3$ (M.42946) was found in the 1930s; see Gentry, p. 401 in this issue.

The age of the Hadrukh is important and is currently controversial (see Whybrow 1984) as it contains a new cricetid rodent, *Shamalina tuberculata*, whose descendant relatives appear to be present in the Miocene Lower Siwaliks of Pakistan (Daams, *in* Whybrow *et al.* 1982; E. H. Lindsay, personal communication 1985). The Hadrukh is undoubtedly coeval with the Ghar Formation of Kuwait and southern Iraq and, in the neighbouring part of Iran, 215 m (700 ft) of sandstone (subsurface section from a drill hole) is said to be the eastern wedge-end of the Ghar Formation and called the Ahwaz Sandstone (James & Wynd 1965: 2229). Adams *et al.* (1983: 278) indicated that at least part of the Ahwaz Sandstone is of Late Oligocene (Chattian) age, but Murris (1980: 614) suggested an Early Miocene, Aquitanian, age for these deposits, which he called the Ahwaz delta formed from eroded Saudi Arabian pre-Neogene rocks. Thin beds near to the top of the Hadrukh contain poorly-preserved marine molluscs and the oyster *O. latimarginata* which indicates a Burdigalian (marine chronostratigraphy) age. These beds crop out in a small area near the modern coastline; their lithology has not been described and
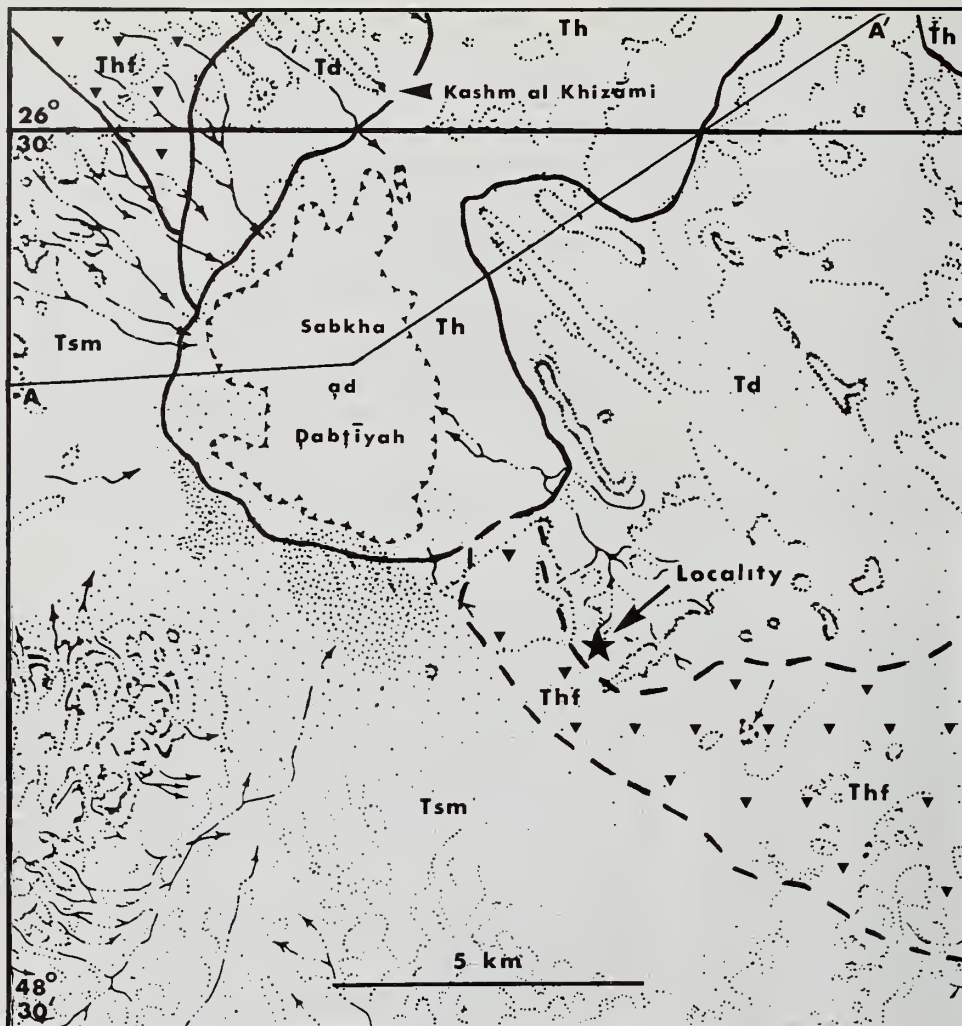
Fig. 3   Geology and topography around Sabkha Ad Dabtiyah and the position of the vertebrate-bearing locality. Tertiary units are: Th = Hadrukh Formation, Td = Dam Formation, Thf = Hofuf Formation, Tsm = undifferentiated continental equivalents of the Dam and Hofuf Formations. Broken line indicates that the contact is uncertain. A–A' refers to the schematic cross-section in Fig. 5. Adapted from Steineke et al. (1958).

they are the only evidence of marine Hadrukh in Saudi Arabia (Powers et al. 1966: D93). They may be in part coeval with the basal Miocene of Qatar; see below.

The continental Hadrukh must be older than the overlying marine carbonates of the Dam Formation, and its thickness in Kuwait of 244 m, together with regional stratigraphy, suggests that a 21–18 Ma age for its deposits in eastern Arabia is a plausible estimate.

Adams et al. (1983: 278) pointed out that there should be a distinct 'discontinuity between the Hadrukh and the overlying Dam Formation'. The top of the Hadrukh as defined by Steineke et al. (1958: 1313) is 'at the base of the Echinocyamus-bearing limestone and marl of the basal Dam'. This echinoid Echinocyamus was described by Kier (1972) as Fibularia damensis. The limestone in which it occurs is known as the 'Button bed'; it is an echinoid

coquina, which has been used as a Miocene marker horizon throughout eastern Saudi Arabia and Qatar. It also marks the change from mainly clastic continental deposition to a shallow-water marine carbonate environment. A local discontinuity has been observed in the basal Miocene sequence of Qatar. Here marine carbonates and the Button bed overlie thinly bedded ferruginous claystones showing desiccation and rainspot structures and an intraformational conglomerate in erosional contact with underlying medium-bedded sandstones (Whybrow & Bassiouni 1986).

The marine biota of the Dam Formation is of an Indo-West Pacific origin and dated as Burdigalian, about 16–19 Ma, a time when there was no marine connection the Mediterranean (Kier 1972; Adams *et al.* 1983).

Basal continental extraformational conglomerates and sandstones of the Hofuf Formation unconformably overlie the Dam Formation marine carbonates. The contact is well represented in Qatar where the Dam terminates in a regressive evaporitic phase. The vertebrate-bearing Hofuf locality of Al Jadidah lies stratigraphically about 30 m above the contact of Hofuf conglomerates with the underlying Dam Formation. Some 70 m of red-coloured sandstones overlie the vertebrate horizon (Thomas 1978; Fig. 2). From his study of the bovids found at Al Jadidah, Thomas (1983) concluded that their age is close to that of the Fort Ternan, Kenya, vertebrate locality dated at 14 Ma (Shipman *et al.* 1981).

The Ad Dabtiyah locality

Sabkha ad-Dabtiyah, a large salt flat (*sabkha*), from which the vertebrate-bearing site takes its name, is the dominant topographic feature of the area. It occupies the central part of a local drainage depression, itself probably a reflection of an underlying minor post-Miocene structure, and is surrounded by low hills and long mesa-topped escarpments of Neogene rocks. The whole region, generally bare of both vegetation and Recent sediments, is heavily dissected by small wadis (Fig. 3).

The vertebrate-bearing sediments (26° 27′ 02″ N, 48° 35′ 24″ E) were first discovered during geological mapping surveys in the late 1930s (Fig. 4). The locality is about 4 km from the

Fig. 4 Photograph of part of the Ad Dabtiyah locality taken by geologists of the Arabian American Oil Company in the early 1930s; note the Ford field vehicle. In the foreground are *in situ* 'logs' encrusted with stromatolite. View is south-west; compare drainage channel (arrow) with Fig. 6.
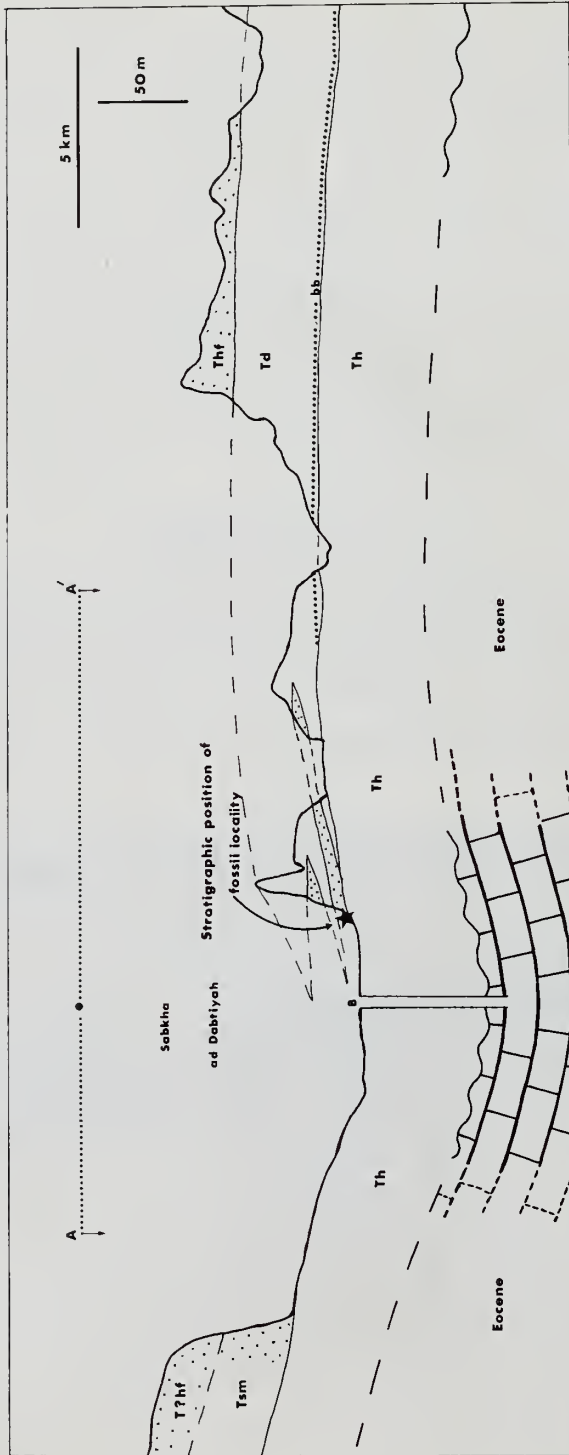
Fig. 5   Schematic cross section around the Ad Dabtiyah locality. The unconformity between Neogene and Eocene rocks is indicated; B = a bored water well that provided subsurface information, bb = 'Button bed'. See Fig. 3 for other abbreviations.

south-eastern edge of the sabkha, in hummocky terrain. The low-lying area with centripetal drainage into Sabkha ad-Dabtiyah is floored by continental sediments mapped as Hadrukh Formation. Along a north-westerly line and to the east, low hills mapped as Dam Formation flank the sabkha, while stratigraphically higher and to the north-west and south-east gravels and sandstones of the Hofuf Formation occur. To the south-west, beyond the limits of marine Dam outcrops, the Neogene formations cannot be divided, see p. 373.

Fig. 6   Similar view to Fig. 4 (photo taken 1979) showing the *in situ* 'logs'. The drainage channel, shown in Fig. 4, indicates little erosion in over 40 years. Tape = 1 metre.

Fig. 7 Large stromatolitic bioherms found to the north-east of the vertebrate locality. S measured 223 cm in width.
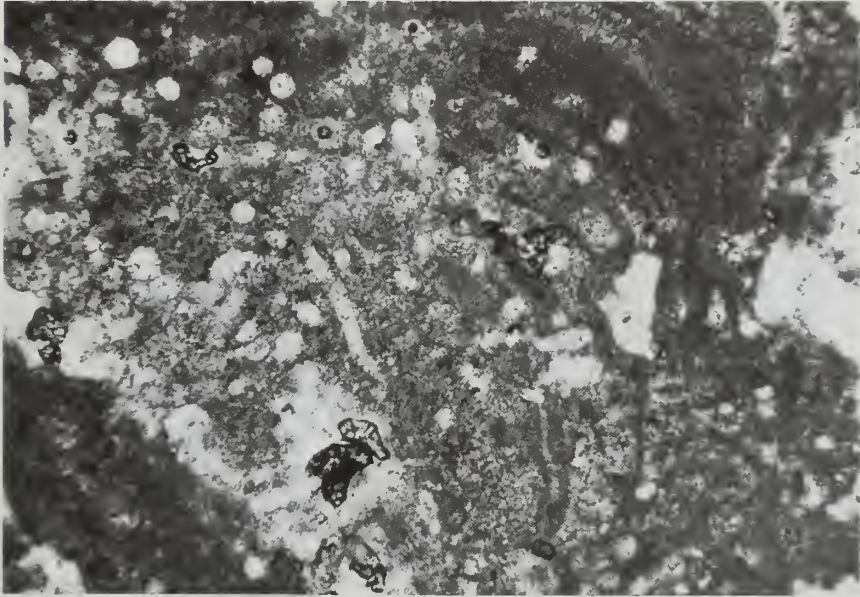
Fig. 8 Photomicrograph of a thin section of calcareous crust (V.60434c) found covering the skull of a rhinoceros. Banded algal growth of radial cyanophyte filaments are at top right. × 45.

The vertebrate site lies at or near the contact of the Hadrukh Formation with other continental sediments coeval with and laterally equivalent to the basal parts of the marine Dam sequence. The basal Dam marker horizon—the 'Button bed' with *Fibularia damensis*—is absent at the locality, but is found about 10 km to its east. The south-western limit of the Dam sea in
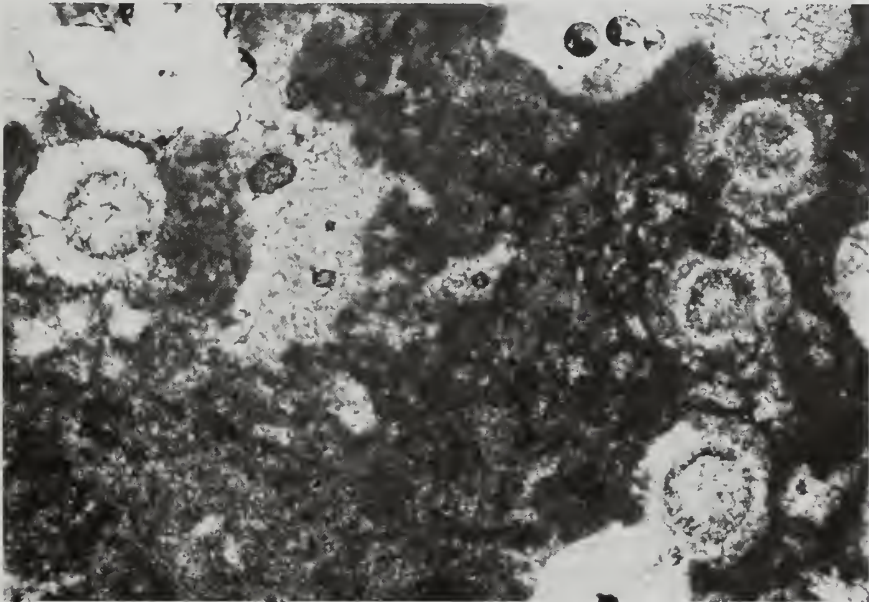
Fig. 9 Algal crust showing conspicuous charophyte oogonia, left and right. Same sample as Fig. 8.
× 45.
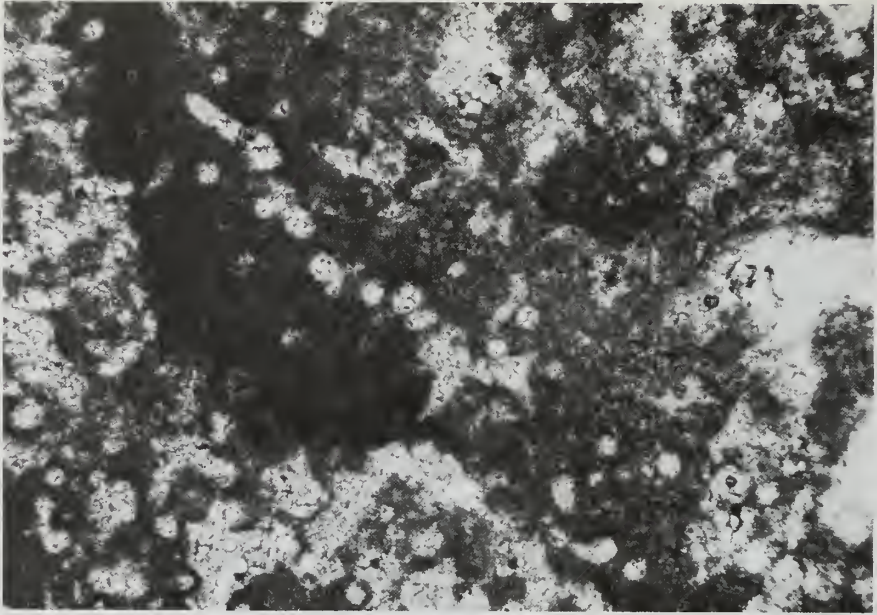
Fig. 10   Algal crust with probable traces of chironomid larval tubes, centre. Same sample as Fig. 8.
× 45.

the area appears to have been near Kashm Khizami (Fig. 3), where marine fossils are associated with beach boulder conglomerates. A schematic cross section of the area indicating the relationship of the stratigraphy to the vertebrate site is shown in Fig. 5.

The main excavation was carried out in hard, unbedded White N9 (United States Geological Survey Rock-Color Chart 1980) sandstones. These were well sorted with fine-grained (about 280 μm), angular to subrounded, micrite supported quartz clasts. Occasionally, rounded micritic pebbles were present. Voids in the sandstones were sometimes filled with sparry calcite or, rarely, a form of manganese oxide known as wad. The excavation (about 22 m × 17 m, 50–80 cm in depth) produced scores of isolated bones, mainly lower jaws, teeth, limb bones, pectoral and pelvic elements, mostly of rhinoceros. None was preferentially orientated. Vertebrae and ribs were rare and, although none of the bones showed sign of depositional transport, rhinoceros mandibles had been broken and their anterior parts were missing. Except for the dryopithecine maxilla (see Andrews & Martin, this issue, p. 383), no other cranial bones were excavated.

About 5 m stratigraphically higher than the main excavation, and 110 m to its west, the sediments exposed on a ridge trending north-east showed a change in lithology. They consisted of an unsupported conglomerate formed of pebbles and cobbles of micritic limestone. In these sediments a proboscidean scapula and incomplete but uncrushed fish skulls were found (see Greenwood, this issue, p. 451). On top of this ridge were five *in situ* fallen logs encrusted with stromatolite (Fig. 6). Three measured 3·0 m, 5·3 m and 7·2 m in length and all, including the encrustation, were about 1·5 m in diameter. At one end of each of these logs stromatolitic crusts, 2 m in diameter, suggested the position of the bole of the fallen tree. The microstructure of a large amount of silicified wood found in this area resembled palm wood. At the same level and 11 m east of the logs, a bioherm had been fractured to reveal a fragmented rhinoceros skull encrusted with a 3-cm layer of algal material. Surface collecting in the area of the conglomerate produced proboscidean, giraffoid and tragulid remains. The conglomerate facies continued to the east and on the northern flank of a parallel ridge, many large stromatolitic bioherms were present (Fig. 7).

The bioherms and the crusts are largely of cyanophyte (myxophyte) algal origin. In thin section the rock shows marked banding with differential growth, and in places a ragged radial structure survives from the original microscopic thread-algae (Fig. 8). The rock shows intrinsic evidence of freshwater origin with embedded charophyte oogonia and debris, and what are probably chironomid larval tubes. All are poorly preserved and filled with sparry calcite (Figs 9, 10).

The depositional environment

Immediately prior to or at about the time of the deposition of basal transgressive marine sediments of the Dam Formation coming from the east, the environment at Ad Dabtiyah appears to have been a fluvial regime, transporting sandy carbonate muds, with laterally discontinuous conglomerates suggestive of channel sediments. Remains of terrestrial mammals, freshwater fish, turtle and crocodile (cf. *Crocodylus pigotti*, see Buffetaut, 1984) occur in these sediments. Subsequently, clastic deposition ceased and ponded fresh water was present; this was perhaps as a lake high in dissolved carbonates and deep enough to allow continuous growth of large stromatolitic bioherms and thick stromatolite crusts on hard substrates.

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Rhinoceroses from the Miocene of Saudi Arabia

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Synopsis

Dental and postcranial remains of the rhinoceroses from the Miocene of Ad Dabtiyah, Saudi Arabia, are
compared with Oligocene and Miocene Old World representatives of *Ronzotherium*, *Diceratherium*,
Brachypotherium, *Aceratherium*, *Dicerorhinus*, *Paradiceros*, *Rhinoceros* and *Hispanotherium*. From this it is
concluded that two species are present, *Dicerorhinus* aff. *sansaniensis* and *Brachypotherium* sp. Both are
primitive, and by implication early, members of their genera. Attention is drawn to the absence of
Aceratherium and its occurrence in Africa is questioned.

The rhinoceroses suggest a woodland habitat at Ad Dabtiyah and a geological age early in the Middle
Miocene, not later than the Orleanian in European terms.

Introduction

The fossils described below were collected in 1974 from continental deposits, thought to be the
lateral equivalent of the Dam Formation, at Ad Dabtiyah, Saudi Arabia. This locality is
situated at 26° 27′ 02″ N, 48° 35′ 24″ E (Hamilton *et al.* 1978; see also Whybrow *et al.*, this issue,
p. 375).

Register numbers of individual specimens refer to the collection of the British Museum
(Natural History), London. Nomenclature for rhinoceros teeth is shown in Fig. 26, p. 410.

Systematics

Order **PERISSODACTYLA** Owen, 1848

Family **RHINOCEROTIDAE** Owen, 1845

Genus *DICERORHINUS* Gloger, 1841

Dicerorhinus sp. aff. *sansaniensis* (Lartet, 1851)
Figs. 25, 27–32, 33A, 34–37, 38A, 39A, B, 40, 42–43, 44A, B

MATERIAL. Measurements in mm.

M.36890   Anterior part of conjoined nasal bones. Fig. 25.
M.36891–2   Left M^1 and M^2, early middle wear, possibly from one individual, occlusal lengths 41·8 and
51·6. Figs 27B, C.
M.36893   Left P^4, middle wear, occlusal length 37·7. Fig. 27A.
M.36894   Right upper molar, probably M^2, early middle wear, occlusal length 49·3.
M.36895   Right M^2, middle wear, occlusal length 40·4. Figs 28B, 33A.
M.36896   Left M^2, middle wear, occlusal length 40·5.
M.36897   Right M^3, early wear, occlusal length 41·1. Fig. 28A.
M.36898   Right P^4, middle wear, occlusal length 32·4. Fig. 29B.
M.36899   Left P^3, middle wear, occlusal length 30·6. Fig. 29A.
M.36900   Left P^2, anterolabial parts missing, late middle wear.
M.36901   Right P^2, middle wear, occlusal length 27·3. Fig. 29C.
M.35012   Left deciduous P^1, late wear, occlusal length 24·1.
M.36902   Left mandible with labial side of P_1, P_2–P_4, much of M_1, much of the labial side of M_2. Early
middle wear. The front premolar is identified as P_1 and not P_2 because M_1, itself identified by being
more worn than P_4, is the fifth tooth from the front of the cheek tooth sequence. Occlusal lengths: P_1
19·4, P_2 25·4, P_3 31·7, P_4 36·8, P_1–P_4 113·4, M_1 *c*. 43·0. Fig. 30.
M.36903   Left mandible with P_3 to M_3, early middle wear. Occlusal lengths: P_3 30·3, P_4 31·2, M_1 37·2,
M_2 42·6, M_3 41·2, M_1–M_3 124·0. Fig. 31.

Fig. 25   Dorsal (above) and lateral (below) views of *Dicerorhinus* nasal, M.36890 from Ad Dabtiyah.
Anterior side to the left. × 0·5.
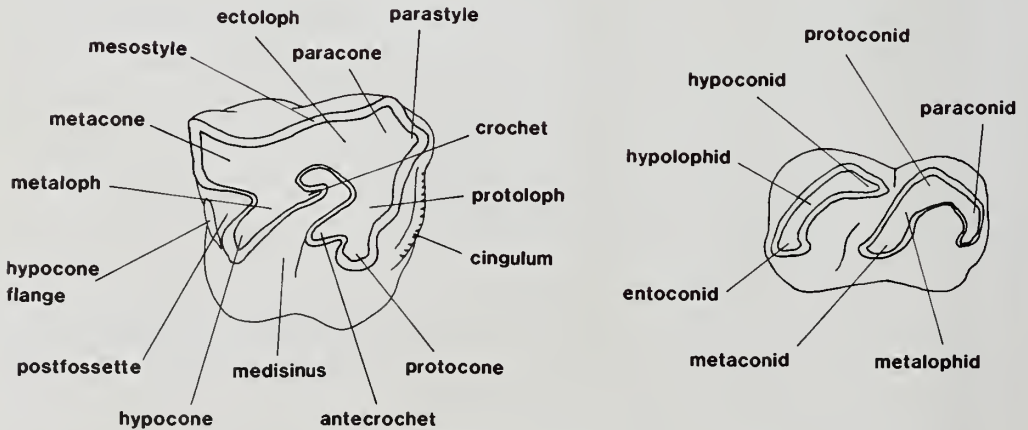
Fig. 26   Nomenclature in rhinoceros upper molar (left) and lower molar (right). Anterior side to
right and labial side to top.
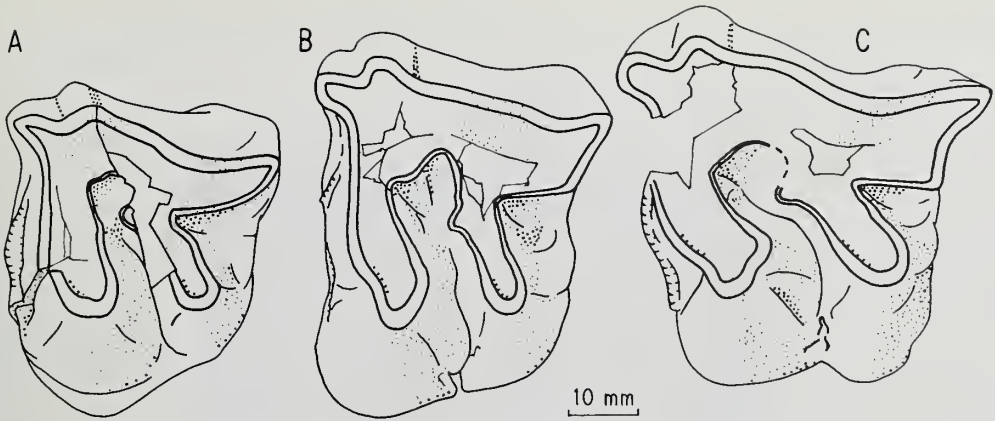
Fig. 27 Occlusal views of teeth of *Dicerorhinus* from Ad Dabtiyah. Anterior sides to left. A, left P^4, M.36893. B, left M^1, M.36891. C, left M^2, M.36892.

M.36904   Back of right mandible with M$_2$–M$_3$ and part of M$_1$, early middle wear. Occlusal lengths: M$_2$ 45·0, M$_3$ 42·7. Possibly the same individual as the last specimen.
M.36309   Right P$_4$, middle wear, occlusal length 32·8. Possibly belongs to mandible M.36904.
M.36905   Most of the crown of a right P$_3$, early middle wear, occlusal length 29·5.
M.36906   Most of the crown of a right P$_2$, middle wear, occlusal length 25·5. Fig. 32.
M.36907   Right I$_2$, little worn. Fig. 34 (top).
M.36908a, b   Paired I$_2$s, about half worn by comparison with last specimen. Fig. 34 (bottom).
M.35076   Two pieces of mandibular symphysis with alveoli for I$_1$ and I$_2$. Fig. 35.
M.35075   Ventral part of right scapula, doubtfully rhinocerotid.
M.36909   Right humerus, complete and undistorted. Length from top of lateral tuberosity to base of medial condyle 460; length from top of articular head to base of medial condyle 410; least transverse width of shaft 64. Fig. 36.
M.36910   Left humerus, less complete and crushed anteroposteriorly in proximal part.
M.36912   Right ulna, complete. Overall length 440. Fig. 37.
M.36913   Right metacarpal IV complete but partially shattered. Overall length 155; transverse width in middle of shaft 32. Fig. 39A.
M.36914   Proximal left metacarpal III.
M.36915–6   Two right scaphoids. Fig. 38A.
M.36917–8   Parts of left and right unciforms.
M.36919   Right magnum.
M.36782   Partial right magnum.

Fig. 28 Occlusal views of teeth of *Dicerorhinus* from Ad Dabtiyah. Anterior sides to right. A, right M^3, M.36897. B, right M^2, M.36895.

M.36783   Left femur, complete. Length from top of great trochanter to base of lateral trochlear ridge 520. Fig. 40.

M.36784   Left tibia, complete. Length from centre of medial facet proximally to posterior tip of medial facet distally 371; transverse width in middle of shaft 60. Fig. 42.

M.36785   Left astragalus, damaged mediodistally. Fig. 43.
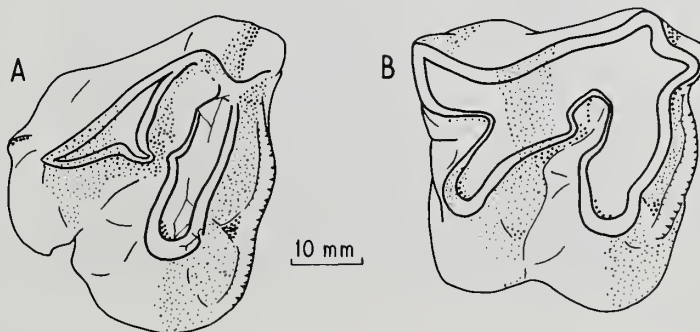
M.36786–7   Trochleae of one left and one right astragali, both slightly smaller than preceding specimen.

M.36788   Left calcaneum.

M.36789   Medial side of left cuboid.

M.36299   Left metatarsal III, proximal end damaged anteromedially. Overall length 169; transverse width in middle of shaft 41·4. Fig. 39B.

M.35077   First phalanx of median digit. Fig. 44A.

M.36911   Second phalanx of median digit. Fig. 44B.

Many other more fragmentary bones have been left unregistered.

DESCRIPTION. The nasal fragment, M.36890, has a small protuberance for a horn base, but its dorsal surface is not very rugose. The tip of the anterior end is missing but it is clear that the portion of bone in front of the horn base is neither long nor at all downturned.

The cheek teeth are brachyodont and the premolar row relatively long. The upper molars show a hypocone flange spreading up from the cingulum and meeting a corresponding but smaller flange from the ectoloph to close the postfossette, no lingual cingula, a prominent paracone rib, no mesostyle, the merest trace of constriction of the protocone and no antechrochet, a small or very small crochet on M^1 and M^2 and a moderate-sized one on the M^3, and a straight ectometaloph on M^3. However, the M^3 ectometaloph would become more curved in late wear. The upper premolars have only an occasional trace of the lingual cingulum, no fusion between hypocone and protocone, hypocone somewhat narrowly connected with more labial cusps to make a metaloph, and only a poor metacone rib on the labial wall. The lower molars have fewer distinctive characters; they show no anterolabial or posterolabial cingula, and the vertical indentation centrally on the labial wall is weak. The lower premolars show poor anterolingual cingula, a moderate depth of the ventral indentation centrally on the labial wall, an anterolabial concavity on the wall of P_2, and a large P_1 or persistent dP_1. The central vertical indentation on the labial wall of P_2 is quite narrow behind the sharp-angled protoconid, and the effect is accentuated by the labial flange developed from the protoconid. This may be an individual or a species character.

It is possible to split the adult upper teeth into two groups: M.36891–4 on the one hand and M.36895–901 on the other. The second group consists of smaller-sized teeth which are also small in comparison with the rhinocerotid mandibular and postcranial remains at Ad Dabtiyah. The premolars and molars are less wide than in M.36891–3, although M.36894 may be in an intermediate state. The upper premolars of this second group have a hypocone less completely bound in with the metaloph, and in fact in the P^3 it is altogether isolated—probably an individual variation. The metacone rib is also probably slightly larger giving a less flat or concave appearance.
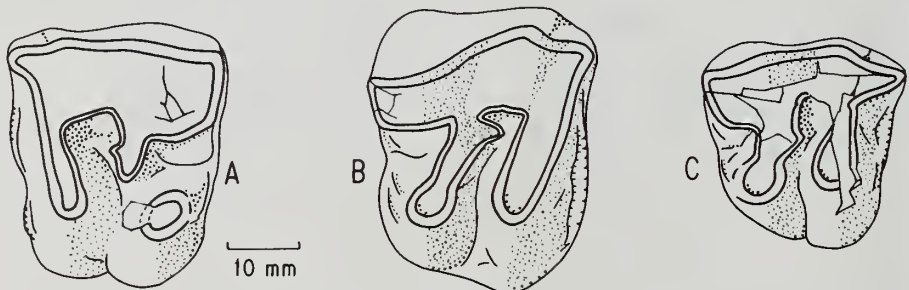

Fig. 29   Occlusal views of teeth of *Dicerorhinus* from Ad Dabtiyah. A, left P^3, M.36899, anterior side to left. B, right P^4, M.36898, anterior side to right. C, right P^2, M.36901, anterior side to right.

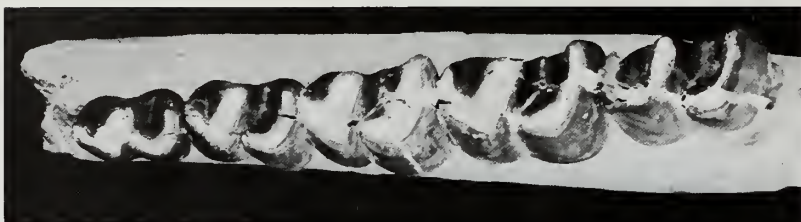**Fig. 30** Lateral view of left mandible, M.36902, of *Dicerorhinus* from Ad Dabtiyah. × 0·33.

Fig. 31 Occlusal view of P_3–M_3 in left mandible of *Dicerorhinus* M.36903. Anterior side to the left.
× 0·5.

The pair of I_2s in later wear have retained more of their roots than the unworn one and these roots are more or less straight. The unworn incisor may have a more curved course of its crown and root but this is very uncertain.

Each lower jaw has preserved nearly all of its vertical ramus. The angle of the jaws projects or bulges a little posteriorly. The lower edges of the horizontal rami are very slightly convex in outline, but only M.36902 is visible as far forwards as diastema level. The back of the symphysis in M.36902 is about level with the back of P_1.

The postcranial bones are further considered on p. 423, following the comparisons of cranial and dental remains.

GROUPS USED IN COMPARISONS. In order to identify and understand these remains, comparisons were made with fossils and illustrations of the following Eurasian and African rhinoceroses:

1. *Ronzotherium* Aymard, mainly from the illustrations of Brunet (1979), Heissig (1969) and Roman (1912). This was the earliest rhinoceros in Europe at localities like Ronzon and survived until the end of the Oligocene.

2. *Diceratherium pleuroceros* (Duvernoy), a small rhinoceros from the Upper Oligocene and basal Miocene of Europe. It has two horns side by side at the front of its nasals. Upper cheek teeth in middle wear are illustrated in Piveteau (1958: 440, fig. 77), lowers in Roman (1912: pl. 6, figs 4–6).

3. The hornless rhinoceros *Aceratherium* Kaup, mainly as illustrated in Guérin (1980), Bonis (1973) and Heissig (1969). It is first known in Europe in the middle of the Oligocene. The small Agenian 'Dicerorhinus tagicus' (Roman), possibly conspecific with *Protaceratherium minutum* (Cuvier) as used by Abel (1910: pl. 2, fig. 8), has crochets on its upper molars, at least in earlier wear, and no fifth metacarpal (Roman 1924). It could be an offshoot of Oligocene *Aceratherium*. It also occurs in the basal Miocene of Dera Bugti, Pakistan (Cooper 1934: 602) and near the Oligocene/Miocene boundary in Russia (Borissiak 1938a). Larger and smaller sized *Aceratherium* continued into the Upper Miocene (Vallesian).

4. The large, short-legged and usually hornless *Brachypotherium* is known from the Agenian onwards and replaced *Ronzotherium*. It may have originated from a form near *Diceratherium* Marsh, judged by traces of paired horns in some early examples, or one close to *Aceratherium*, judged by the difficulties with generic classification of the early species *lemanense* Pomel (Bonis 1973: 124). It is illustrated in Depéret & Douxami (1902), Hooijer (1966), Viret (1929) and Roman (1912).

5. Miocene species of the horned rhinoceros *Dicerorhinus*, as in Guérin (1980) and Hooijer (1966). [*Dicerorhinus* has been validated in preference to *Didermocerus* by the International

10 mm

Fig. 32 Occlusal view of left P_2, M.36906, of *Dicerorhinus* from Ad Dabtiyah. Anterior side to left.
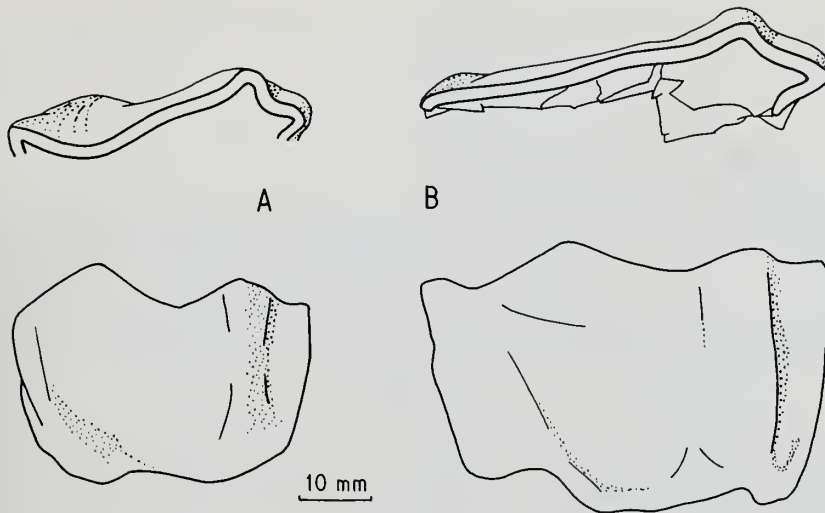
Fig. 33 Occlusal and labial views of labial sides of rhinoceros upper molars from Ad Dabtiyah. Anterior sides to right. A, *Dicerorhinus*, a right tooth, M.36895 (occlusal and reversed labial views). B, *Brachypotherium*, a left tooth, M.36300 (labial and reversed occlusal views).

Commission of Zoological Nomenclature (1977).] *Dicerorhinus sansaniensis* (Lartet) and the smaller *D. steinheimensis* Jäger are best known from the Middle Miocene of Europe, *D. leakeyi* Hooijer from the Lower Miocene of east Africa, *D. primaevus* Arambourg from the Upper Miocene of north Africa and *D. schleiermacheri* (Kaup) from the Upper Miocene (Vallesian and Turolian) of Europe. *Diceros pachygnathus* (Wagner) from the Turolian of Pikermi, Greece, lacks lower incisors but is otherwise very similar to *Dicerorhinus schleiermacheri. Dicerorhinus sansaniensis* is known back to the Orleanian or late Lower Miocene in Europe (Heizmann *et al.* 1980: 7; Guérin 1980: 201). Finally it may be mentioned that '*Aceratherium*' *abeli* Cooper (1934: 596) from Dera Bugti appears to be a *Dicerorhinus*, as already noted by Heissig (1972: 27).

6. The African horned rhinoceros *Paradiceros mukirii* Hooijer (1968) from the Middle Miocene of Fort Ternan, Kenya (Shipman *et al.* 1981), related to *Diceros.*

7. A rather incompletely known group of Miocene horned rhinoceroses held to be related to the Pliocene and Pleistocene *Elasmotherium* Fischer of Asia and centred on *Hispanotherium* Crusafont & Villalta, within which Ginsburg & Antunes (1979) would also include the Asiatic *Beliajevina* Heissig and *Caementodon* Heissig. *Hispanotherium* appeared for only a limited duration in Spain and Portugal (Antunes 1979: 20) and is known at what is probably a later horizon in Turkey (Heissig 1976). The African *Chilotheridium pattersoni* Hooijer (1971) and possibly the *Chilotherium* Ringström of the Chinese *Hipparion* faunas (Ringström 1924), as well as the much earlier *Chilotherium blanfordi* (Lydekker), the commonest true rhinoceros at Dera Bugti, could also belong here. All these rhinoceroses were hypsodont and had upper molars with constricted protocones and strong antecrochets; the (? primitive) protocone/hypocone fusion on upper premolars persisted until the start of the late Miocene. There are, however, some differences among them. In particular the Turkish *Hispanotherium* has a reduced mandibular symphysis and no enlarged lower incisors (Heissig 1976: 33, fig. 2), whereas the Bugti *Chilotherium* shares a very wide symphysis (Cooper 1915: figs 4, 5) with the *Chilotherium* of the Chinese *Hipparion* faunas. The Chinese *Chilotherium* has no horns, the state of *C. blanfordi* is unknown, *Chilotheridium* possessed a nasal horn and pneumatized frontals (Hooijer 1971: pls 2, 4) and *Beliajevina* Borissiak had what must have been a horn base towards the back of the nasals (Borissiak 1938*b*: 8). In addition to the foregoing references, see also Heissig (1972, 1974), Antunes (1972) and Antunes *et al.* (1972).

Fig. 34 Incisors of *Dicerorhinus* in medial view to show differences in root curvature. Right I_2, M.36907 (above), left I_2, M.36908b (below). × 0·5.

8. *Rhinoceros browni*, first described by Colbert (1934) under the generic name *Gaindatherium* and figured by him and by Heissig (1972). It is known from the Chinji Formation and other pre-*Hipparion* localities of the Siwaliks Group in Pakistan, where it predates other rhinoceroses like *Aceratherium* and *Brachypotherium* (Guérin *in* Pilbeam *et al.* 1979: 36; Barry *et al.* 1982: 113–4).

The taxonomy and history of Oligocene and earlier Miocene rhinoceroses is confused. Many generic names have been used besides those so far mentioned while multitudes of species-level names have been founded and used in differing combinations with the generic names.

Comparative material in the British Museum (Natural History) comprised mainly fossils and casts from the Upper Miocene of Eppelsheim, Germany and the Lower and Middle Miocene of some French localities, the Lower Miocene of Jebel Zelten, Libya, the Lower Miocene of some Kenyan localities and the basal Miocene of Dera Bugti, Pakistan.

COMPARISONS. In *Ronzotherium* upper molars it is mainly the massive lingual and posterolabial cingula, the stronger indication of a mesostyle, the posteriorly open postfossette and the curved ectometaloph of M^3 which differ from the Arabian teeth. Strong cingula also occur on *Ronzotherium* lower molars and premolars.

The upper premolars differ by having strong cingula as in the molars, a stronger metacone rib and fusion between the protocone and hypocone. Radinsky (1967: 5) and Heissig (1969: 15) agree that primitively rhinocerotid P^3s and P^4s would have had a protocone linked or almost linked by a protoloph to the ectoloph. The hypocone was definitely linked with the protocone-protoloph but only more weakly via the metaloph to the ectoloph. This is the condition found in *Ronzotherium*, whereas in other rhinoceroses the hypocone is part of a metaloph and linked only weakly or in later wear, if at all, to the protocone. They thus look much more like molars.

Fig. 35 Anterior view of mandibular symphysis of *Dicerorhinus*, M.35076. Notice alveoli for I_1s as well as I_2s. Natural size.

The change has been carried less far in *Aceratherium* in which a narrow protocone–hypocone link may be present (e.g. *A.* cf. *platyodon* Mermier, of Roman & Viret 1934: pl. 8, fig. 1). In *Hispanotherium* (Heissig 1976: pl. 1, figs 14, 15) this same link has survived undiminished from its ancestral *Ronzotherium*-like condition (or has been strengthened anew, helped perhaps by antecrochet growth from the protoloph, from an *Aceratherium*-like condition). Against this background the Arabian P^3 is interesting in that the hypocone is separated both from the

Fig. 36   Anterior view of right humerus of *Dicerorhinus*, M.36909. × 0·33.
Fig. 37   Medial view of right ulna of *Dicerorhinus*, M.36912. × 0·33.

protocone and from a metaloph growing towards it from the ectoloph. It has, however, already developed a posterolabial flange (perhaps a raising of the old posterior cingulum) which is closing off the postfossette posteriorly.

The P_1 or persistent dP_1 on M.36902 is almost as large as in a *Ronzotherium filholi* from Bournouncle I, France (Heissig 1969: fig. 15C; table 14), although in other *Ronzotherium* the P_1 may be only a single-rooted peg or altogether absent.

The upper premolars of *Diceratherium pleuroceros* do not have the primitive *Ronzotherium*-like fusion of protocone and hypocone but the teeth are otherwise little advanced. They differ from the Arabian species by being smaller, the M^3 having a curved ectometaloph (only available from the aged specimen 28845, a cast of the holotype skull), and anterolabial and antero-lingual cingula being present on the lower molars. '*Dicerorhinus*' *tagicus* has stronger cingula on the premolars and molars, stronger crochets and mesostyles, some sign of antecrochets on the upper molars and only a peg-like P_1. The only figured specimen also lacks a nasal horn.

Aceratherium differs very distinctly by its tendency to have a reduced paracone rib and by the antecrochets and constricted protocones on the upper molars, by the curved ectometaloph and localized posterolabial cingulum on M^3, and by an internal cingulum and narrow protocone–hypocone fusion on the upper premolars. The lower molars have a stronger labial indentation between the metalophid and hypolophid, and small but definite anterolabial and anterolingual cingula. P_1 is smaller.

Brachypotherium has rather primitive teeth but has nonetheless developed some special-izations of its own. The large size, wide and evenly flat or slightly concave ectoloph surface behind the rather insignificant paracone rib, persistence of internal cingula on its upper cheek teeth and of external cingula on its upper and lower molars are all different from the Arabian form. Orleanian *Brachypotherium* already had a smaller P_1 (Mayet 1908: pl. 2, fig. 2). The P^3 of '*Rhinoceros (Diceratherium) asphaltense*' Depéret & Douxami (1902: pl. 2, fig. 1), which Bonis (1973: 123), following Schlosser (1904: 443), includes in *B. lemanense*, is one of the few in which the hypocone is not linked by a metaloph to the ectoloph. Other cases are found in some *Ronzotherium* P^4s, e.g. that shown by Heissig (1969: fig. 13).

The distinctive *Hispanotherium* has hypsodont upper molars, often with abundant cement; the paracone rib is probably weaker than in the Arabian specimens, the protocone strongly constricted and an antechrochet is present. On the upper premolars the protocone and hypo-cone are fused and the metacone rib is strong. The lower molars have more of a labial
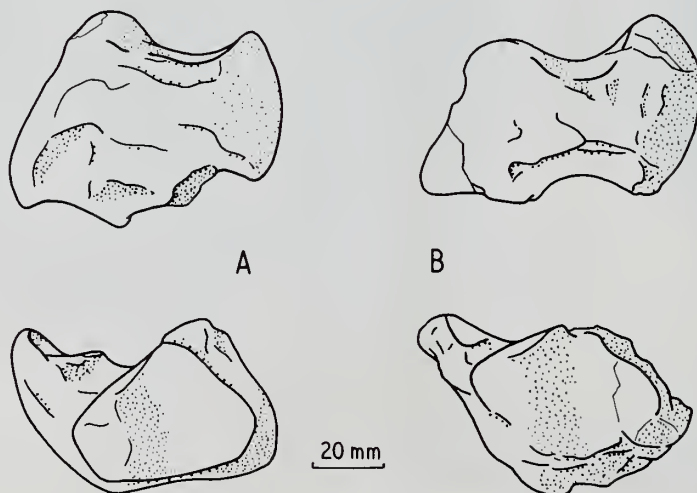

Fig. 38   Right scaphoids of rhinoceros from Ad Dabtiyah in medial view (above) and dorsal view (below). Anterior sides to left. A, *Dicerorhinus*, M.36916. B, *Brachypotherium*, M.36302.

indentation between metalophid and hypolophid. As regards reduction of the anterior premolars, even P_2 has diminished in size (Heissig 1976: 33, fig. 2).

Paradiceros mukirii was described as an early relative of the living African black rhinoceros, *Diceros bicornis*, apparently about twice as old as the well-known Turolian *Diceros pachygnathus*. *Paradiceros* differs most notably from the Arabian species by the absence of lower incisors. Other differences are its shorter premolar row without a P_1, stronger anterolingual cingula on the lower premolars, and probably the larger crochets of the upper molars.

It is not clear why *Rhinoceros browni* need be generically separated from *Dicerorhinus* as used here (cf. Groves 1983: 310). Alleged differences are that it has no sign of a horn base on the frontals, the top of the nasals are less bent downwards and the anterior border of the orbit lies above the middle of M^1. The first two characters resemble later *Rhinoceros* but could as easily fit a female *Dicerorhinus*. As to the third, the front of the orbit lies above P^4 in adult modern *R. unicornis*, above M^1, perhaps even its back half, in *D. sumatrensis*, and above the M^1/M^2 boundary in Miocene *Dicerorhinus*. Here again the state of *R. browni* could fit *Dicerorhinus* as easily as *Rhinoceros*. The union of the posttympanic and postglenoid processes beneath the external auditory meatus, mentioned by Colbert (1934), is like *Rhinoceros* and Miocene *Dicerorhinus* but unlike *D. sumatrensis*. Modern *R. unicornis* and *sondaicus* have a longer P^3 and P^2 than *D. sumatrensis* (Guérin 1980: table 5) but there is no foreshadowing of this in *R. browni*.

Rhinoceros browni differs from the Arabian species in having a smaller crochet and curved ectometaloph on M^3, a shorter premolar row, a more prominent metacone rib on the upper premolars and probably a stronger mesostyle rib on the upper molars. Crochet size on M^1 and M^2 of *R. browni* must be variable according to the illustrations of Colbert (1934: fig. 4) and Heissig (1972: pl. 1, figs 7, 8). P_1 was reckoned by Colbert (1934: 9) to be absent in *R. browni* and although Heissig (1972, pl. 2, fig. 3) figured one, it was nevertheless smaller than in the Arabian rhinoceros. The anterolabial wall of P_3 is very slightly concave in the Arabian species—more so than in many later rhinoceroses but like *R. browni* in Heissig (1972: pl. 2, fig. 3).
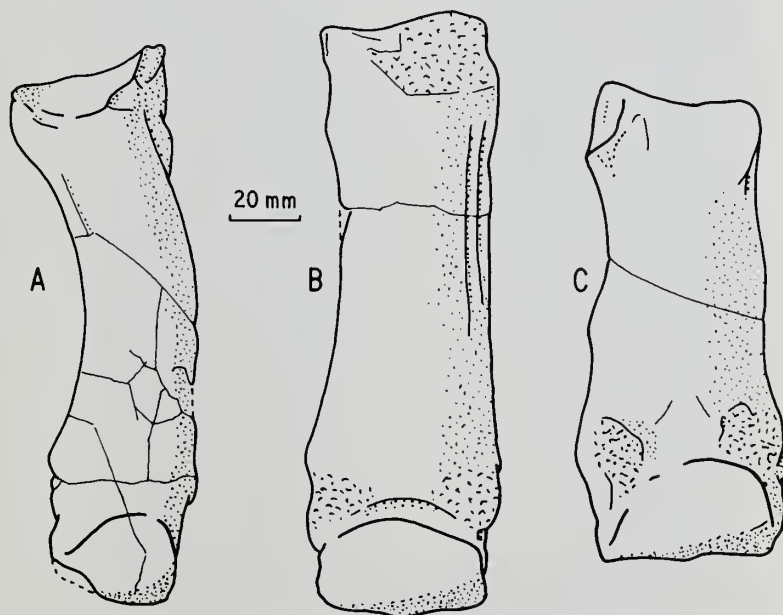

Fig. 39 Metapodials of rhinoceros from Ad Dabtiyah in anterior view. A, *Dicerorhinus*, right metacarpal IV, M.36913. B, *Dicerorhinus*, left metatarsal III, M.36299. C, *Brachypotherium*, left metatarsal III, M.36308.

Fig. 40   Anterior view of left femur of *Dicerorhinus*, M.36783. × 0·33.

Dicerorhinus shows fewer differences in its teeth from the Arabian species than genera already mentioned and some species-level comparisons are needed.

Dicerorhinus primaevus Arambourg (1959: 56) comes from the Upper Miocene of Bou Hanifia (= Oued el Hammam), Algeria. It has larger teeth than the Arabian species and larger crochets on M^1 and M^2. Unfortunately premolars are known only from the milk dentition.

Dicerorhinus abeli differs from the Arabian species by having larger crochets on its upper molars, a smaller P_1, a lingual cingulum at the medisinus entrance on the upper premolars, a stronger metacone rib on the upper premolars, antero- or posterolabial cingula on the lower molars and a shallow anterolabial concavity on the wall of P_2.

D. leakeyi appears to show fewer differences: a less straight ectometaloph in M^3 (Hooijer 1966: pl. 7, fig. 5), a more prominent metacone rib on the upper premolars, more fusion between hypocone and protocone in later wear on the upper premolars and deeper labial grooves on the lower premolars. P_1 is present in one of the two specimens but is not quite as large as in M.36902.

D. sansaniensis, known to me only from illustrations, differs by the probably stronger fusion between hypocone and protocone of the upper premolars in later wear. It also has better lingual cingula on both its upper molars and premolars and larger labial grooves on its lower molars. One mandible (Guérin 1980: pl. 9C) has a P_1 almost as large as in the Arabian specimen, but the holotype (Guérin 1980: pl. 6) has a smaller P_1.

D. steinheimensis is a smaller species. According to Guérin (1980: table 47), the smaller Arabian upper teeth (M.36895–901) would match *D. steinheimensis* in size and the larger ones (M.36891–4) *D. sansaniensis*. I shall not, however, split the Arabian material at species level.

D. schleiermacheri is a later form. Its upper molars contrast with the Arabian form in their weaker paracone rib but stronger mesostyle rib. The closure of the postfossette by flanges from hypocone and ectoloph is also more apparent. Its upper premolars show fusion between the protocone and hypocone in middle and late wear and a stronger metacone rib. The lower molars have more of a central indentation on their labial walls and the P_1 is smaller or absent.

The lower incisors from Arabia, M.36907–8, are smaller than the large ones assigned to *Aceratherium* in the Eppelsheim collection but larger than BM(NH) 21490 in the same collection assigned to *D. schleiermacheri*. The more or less straight roots of the more worn pair make them more akin to *Dicerorhinus* according to Hooijer (1966: pl. 4, figs 2–5). Guérin (1980: 218), following Heissig (1972), points out that incisors of *Dicerorhinus* differ from those of *Aceratherium* in possessing a neck. The worn pair from Saudi Arabia do not have such a neck whereas the unworn one does. It may also be noted that the mandible M.35076 shows alveoli for two small I_1s, thereby agreeing with *D. leakeyi* (Hooijer 1966: 123) and *D. schleiermacheri* (M.2781).

The posterior projection of the angle of the lower jaws differs from *Aceratherium*, in which the back of the vertical ramus descends in more of a straight line. The Arabian mandibles resemble two casts of *Dicerorhinus schleiermacheri* from Eppelsheim, *Dicerorhinus sansaniensis* (Guérin 1980: pls 5, 6), *D. leakeyi* (Hooijer 1966: pl. 2, fig. 4) and *Brachypotherium* (Mayet 1908: pl. 2, figs 1, 2; Roman 1912: pl. 8, figs 1, 3). The lower edge of the horizontal ramus in M.36902 does not curve upwards anteriorly so much as in *Diceratherium pleuroceros* (Roman 1912: pl. 6, fig. 4) or as in *Aceratherium* or *Dicerorhinus schleiermacheri*. Like *D. sansaniensis* and *D. leakeyi*, in *Brachypotherium* it looks curved but less so than in *Aceratherium*. Heissig (1972: 21) gives a forwardly-directed mandibular symphysis as a character of the subfamily Rhinocerotinae.

The nasal fragment M.36890, with its small horn base, is unlike *Aceratherium* and most *Brachypotherium* which are hornless. It is also unlike the twin-horned *Diceratherium* or some early *Brachypotherium* with vestiges (?) of paired horns (Osborn 1900: 253, figs 12B, D; Dietrich 1931: 210, figs 10, 11). The smallness and absence of surface rugosity could suggest that the bone is from a female, juvenile, primitive or geologically old animal. The absence of down-turning anteriorly is unlike *Dicerorhinus sansaniensis* or *D. leakeyi* but like *D. schleiermacheri* and *Rhinoceros browni*. Whether or not there was a frontal horn in the Arabian species is not known.

Fig. 41   Anterolateral view of left femur of ?*Brachypotherium*, M.36305. × 0·4.

Fig. 42   Anterior view of left tibia of *Diceror-hinus*, M.36784. × 0·33.

POSTCRANIAL BONES. The ventral part of a damaged right scapula, M.35075, could belong to a rhinoceros but the glenoid facet is very narrow transversely. It is probably too small to fit a mastodon.

The well-preserved right humerus, M.36909, is about the size of those of *Dicerorhinus leakeyi*, *schleiermacheri* and *orientalis* (Schlosser) listed in Hooijer (1966: 160, table 28). It is about as wide at the proximal as at the distal end. The olecranon fossa is deep at the distal end. Compared with the humeri of Pikermi rhinoceroses, the shaft looks longer between the base of the deltoid crest and the supinator ridge distally. The humerus of *Ronzotherium filholi* (Osborn), as figured by Brunet (1979: pl. 20b, c), is a slighter bone and that part of the distal end lateral to the condyles is narrower. It agrees well with M.2783, the cast of a specimen from Eppelsheim labelled as *D. schleiermacheri*.

The right ulna, M.36912, is again complete; even the top of the olecranon is present in its entirety. The process at the top of the olecranon projects strongly medially and the mid-shaft diameter from front to back is considerably less than in Pikermi examples of *Diceros pachygnathus*.

Fig. 43 Anterior view of left astragalus of *Dicerorhinus*, M.36785. × 0·5.

The right metacarpal IV, M.36913, is as curved and less thickset than M.18814 from Rusinga (perhaps belonging to *D. leakeyi*; Hooijer 1966: pl. 12, figs 2, 3); the latter is itself less thickset than Pikermi examples probably belonging to *Diceros pachygnathus*. M.36913 has no facet for articulation with a metacarpal V.

The two right scaphoids, M.36915–6, are less thickset than examples from Pikermi probably belonging to *Diceros pachygnathus*. There is only poor development of a downwards projection posteroventrally and this may be a resemblance to *Dicerorhinus* rather than to *Aceratherium* (see Bonis 1973: fig. 36).

The complete left femur, M.36783, is about the size of Pikermi examples but more gracile especially at the distal end. The third trochanter is smaller and higher on the shaft and in lateral view the top of the great trochanter slopes downwards anteriorly. These are additional differences from the Pikermi bones and the downward slope of the great trochanter may be linked with the third trochanter appearing to be higher on the shaft. The Arabian femur is not quite so long as a cast of an Eppelsheim femur (M.1283, labelled *D. schleiermacheri*), on which the great trochanter has a similar slope and the third trochanter is about the same size as the Arabian one.

The left tibia, M.36784, is the size of the *Dicerorhinus leakeyi* and *D. orientalis* listed in Hooijer (1966: 171, table 40) but a bit longer than the *D. schleiermacheri*. It is about the size of a rhinoceros tibia 27458 from Sansan, but less gracile as shown by the wider distal part of the shaft and distal articular surface. Compared with Pikermi rhinoceros tibiae it is slightly more gracile, the tibial tuberosity at the proximal end is less massive in proximal view and in anterior view there is less of a deep groove at the proximal end.

The left astragalus, M.36785, matches M.2786 from Eppelsheim which is labelled as *D. schleiermacheri* and is unlike 1290 and M.2785 labelled as *Aceratherium incisivum* from the same locality. The agreement with M.2786 lies in the prominent overhang of the lateral parts of the proximal trochleae and in the top edge of the front of the cuboid facet being widely separated from the base of the more proximal trochlear facets on the anterior surface, but it must be stated that Pikermi examples of astragali of *D. schleiermacheri* or *Diceros pachygnathus* do not match the Eppelsheim bone in these respects. M.36785 is taller than the Pikermi astragali and its proximal lateral trochlea is less bulbous. M.36785 is larger than most of the east African *Dicerorhinus* and *Aceratherium* listed by Hooijer (1966: table 42) but is not as large as the only one listed as definitely *Dicerorhinus*—that which belongs to the associated skeleton no. 2.

The left calcaneum, M.36788, has its tuber less thick, front to back, than in Pikermi examples.

The left metatarsal III, M.36299, is more slender than Pikermi ones.

The first and second phalanges of the median digit, M.35077 and M.36911, by comparison with Hooijer (1966: pl. 10, figs 4–7) are seen to match *Dicerorhinus* rather than *Brachypotherium*. There is also another, more damaged, median second phalanx and a number of phalanges of the side toes.
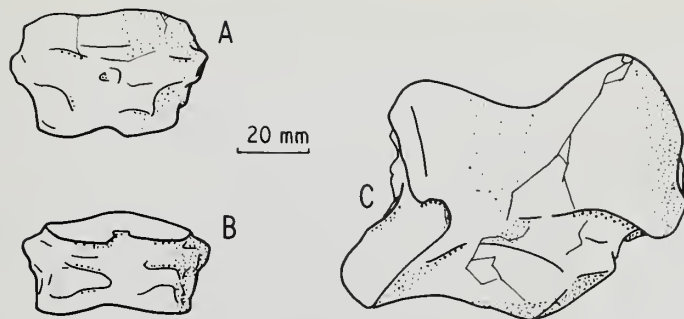
Fig. 44 Rhinoceros bones from Ad Dabtiyah. A, *Dicerorhinus*, median 1st phalanx in anterior view, M.35077. B, *Dicerorhinus*, median 2nd phalanx in anterior view, M.36911. C, *Brachypotherium*, left astragalus in anterior view, M.36306.

DISCUSSION. Early *Dicerorhinus* species and *Rhinoceros browni* emerge as close to the Arabian material. The *Dicerorhinus* species with which comparisons have been made come from continentally-separated localities and the one which differs least could be *D. sansaniensis*. It has to be noted, however, that the characters of the latter were available to me only from plates in Guérin (1980) and Filhol (1891). Many characters in this assessment would also probably turn out to be variable in large samples in spite of their long-standing use in rhinoceros taxonomy. Furthermore, on dental morphology alone the Arabian species could only be distinguished from *Diceratherium pleuroceros* by its greater size.

The Arabian species can be named as *Dicerorhinus* sp. aff. *sansaniensis*, but this may reflect no more than the attainment of a similar evolutionary level of tooth morphology. In particular it need not imply zoogeographical relationship with Europe. A skull from Ad Dabtiyah would be needed to make a reliable identification. As far as geological age is concerned, Sansan itself is of Astaracian age but *D. sansaniensis* is known back to the Orleanian as noted previously. In Africa *D. leakeyi* is best known from the time range 20–16·5 Ma, which probably corresponds to the Orleanian in Europe, and Hooijer (1978: 374) regards Alengerr, Kenya (12–14 Ma?) as the latest reasonable record. The preorbital part of its skull is longer than in *D. sansaniensis* (Hooijer 1966: pl. 1; Guérin 1980: pls 5, 6) which would fit with the suggestion of an earlier age than Sansan. The Dera Bugti *D. abeli* could well date from the basal Miocene (Eames 1950, Khan 1968), i.e. have an age equivalent to the Agenian in Europe. Some of the other Dera Bugti mammals support this assessment, for example the mandibular piece (M.12339) of '*Amphicyon*' *shahbazi* (Pilgrim), which looks like *Pseudocyonopsis* Kuss, a genus extinct in Europe after the Agenian (Springhorn 1977: 37). All this suggests that the rather primitive *Dicerorhinus* of Ad Dabtiyah could be of an age equivalent to the Orleanian land mammal age in Europe. The rather large size of the dP^1 (M.35012) could also support an early date for Ad Dabtiyah. It appears to be about 10% longer relative to M^2 than in *D. primaevus* or Astaracian *D. sansaniensis* (Guérin 1980: 233), and thereby in closer agreement with *D. leakeyi* and *D. abeli*.

NUMERICAL APPROACHES. As an alternative to the above comparisons a matrix was drawn up of 25 cranial and dental character differences in 18 taxa of Oligocene and Miocene rhinoceroses. The characters used were:

SKULL:

    1. Paired horn bases present or absent at front of nasals.
    2. Horn bases present or absent posteriorly on nasals.
    3. Lower incisors directed forwards or upwards.
    4. Lower edge of mandible convex or straight.
    5. Premolar row short or long compared with molar row.
    6. Cheek teeth higher- or lower-crowned.

UPPER MOLARS:

    7. Paracone rib prominent or weak.
    8. Trace of mesostyle absent or present.

9. Protocone partially constricted or not.
10. Hypocone partially constricted or not.
11. Antecrochet present or absent.
12. Crochet present or absent.
13. Hypocone flange closing postfossette or not.
14. M^3 ectometaloph straight or curved.
15. Lingual cingula absent or present.

UPPER PREMOLARS: 16. Lingual cingula absent or present.
17. P^3 and P^4 with hypocone and protocone unfused or fused.
18. Metacone rib absent or present on labial wall.
19. Crenulations present or absent on front of metaloph.

LOWER MOLARS: 20. Antero- or posterolabial cingula absent or present.
21. Central labial indentation deep or shallow.

LOWER PREMOLARS: 22. Anterolingual cingula absent or present.
23. Concavity on anterolabial wall of P_2 absent or present.
24. Central labial indentation shallow or deep.
25. P_1 absent or present.

In the above list the first mentioned alternative was considered advanced.

The state of all characters was ascertainable in the Arabian material, but not invariably in the other taxa. Every character state existed in more than one taxon so there were no unique occurrences. Two dendrograms were constructed from this matrix. The first was a phenetic dendrogram (Gentry 1974: 184, based on a method of Corbet & Hanks), for which one counts the differences of the taxa from one another, standardizes the totals as percentages of the number of characters compared, and associates on the dendrogram those forms which are least different. The second dendrogram associates forms sharing the largest numbers of supposedly advanced similarities. Neither dendrogram allows for parallel evolution or displays the contribution of individual characters but each has a percentage scale of difference or similarity.

There were difficulties in constructing these dendrograms. Once a character difference had been spotted between two taxa it was often hard to assign other taxa to one or other state and adoption of intermediate categories was not always satisfactory. Secondly, consistency of assessment was hard when using photographic illustrations, despite the excellent reproduction in many older publications. And finally, on the second dendrogram some character polarities were in doubt. As noted earlier, several early *Brachypotherium* specimens have traces of bipartite horn bases and this could imply descent of hornless rhinoceroses from ancestors with *Diceratherium*-like horns. Again, if Radinsky (1966: 636) is right that procumbency of I_2s is part of the initial family-level specialization of rhinocerotids, then the more upright I_2s of *Aceratherium* should be counted as secondary despite their unspecialized appearance. Alternatively *Aceratherium* could be removed from the Rhinocerotidae. The following comments can be made on the two dendrograms (Fig. 45).

1. The Arabian rhinoceros forms part of a grouping of *Dicerorhinus* species and *Rhinoceros browni* on both dendrograms and within that grouping it associates with early or primitive *Dicerorhinus* rather than with *D. schleiermacheri*.

2. The phenetic dendrogram presents comprehensible major groupings of the rhinoceroses despite the limitations on its construction. One sees on it the three clusters of (A) the mid-Tertiary hornless rhinoceroses plus the primitive *Ronzotherium* and *Diceratherium*; (B) horned rhinoceroses centred upon *Dicerorhinus*; (C) the *Hispanotherium* group. The last two groups are also recognizable on the second dendrogram but here advanced *Brachypotherium* and *Aceratherium* attach themselves to *Hispanotherium* presumably because of parallel advances. The closeness of many of the horizontal linking lines on the chart suggests that repeats of the same exercise would be unlikely to produce the same result.

3. The association of *Chilotherium*, *Chilotheridium* and *Hispanotherium* on both dendrograms supports the view of their similarities taken above. If they should be a natural group, the early Miocene irruption of *Hispanotherium* into Iberia may have come from an African origin close

Ronzotherium
Diceratherium pleuroceros
Aceratherium (Oligocene)
Aceratherium (later spp.)
"Dicerorhinus" tagicus
Brachypotherium (Agenian)
Brachypotherium (later spp.)
Paradiceros mukirii
Dicerorhinus schleiermacheri
Diceros pachygnathus
Dicerorhinus sansaniensis
Dicerorhinus leakeyi
Rhinoceros browni
Dicerorhinus abeli
Arabian Dicerorhinus
Chilotherium blanfordi
Chilotheridium pattersoni
Hispanotherium

Ronzotherium
Diceratherium pleuroceros
"Dicerorhinus" tagicus
Aceratherium (Oligocene)
Rhinoceros browni
Dicerorhinus leakeyi
Dicerorhinus sansaniensis
Arabian Dicerorhinus
Dicerorhinus abeli
Dicerorhinus schleiermacheri
Diceros pachygnathus
Brachypotherium (Agenian)
Paradiceros mukirii
Brachypotherium (later spp.)
Aceratherium (later spp.)
Chilotherium blanfordi
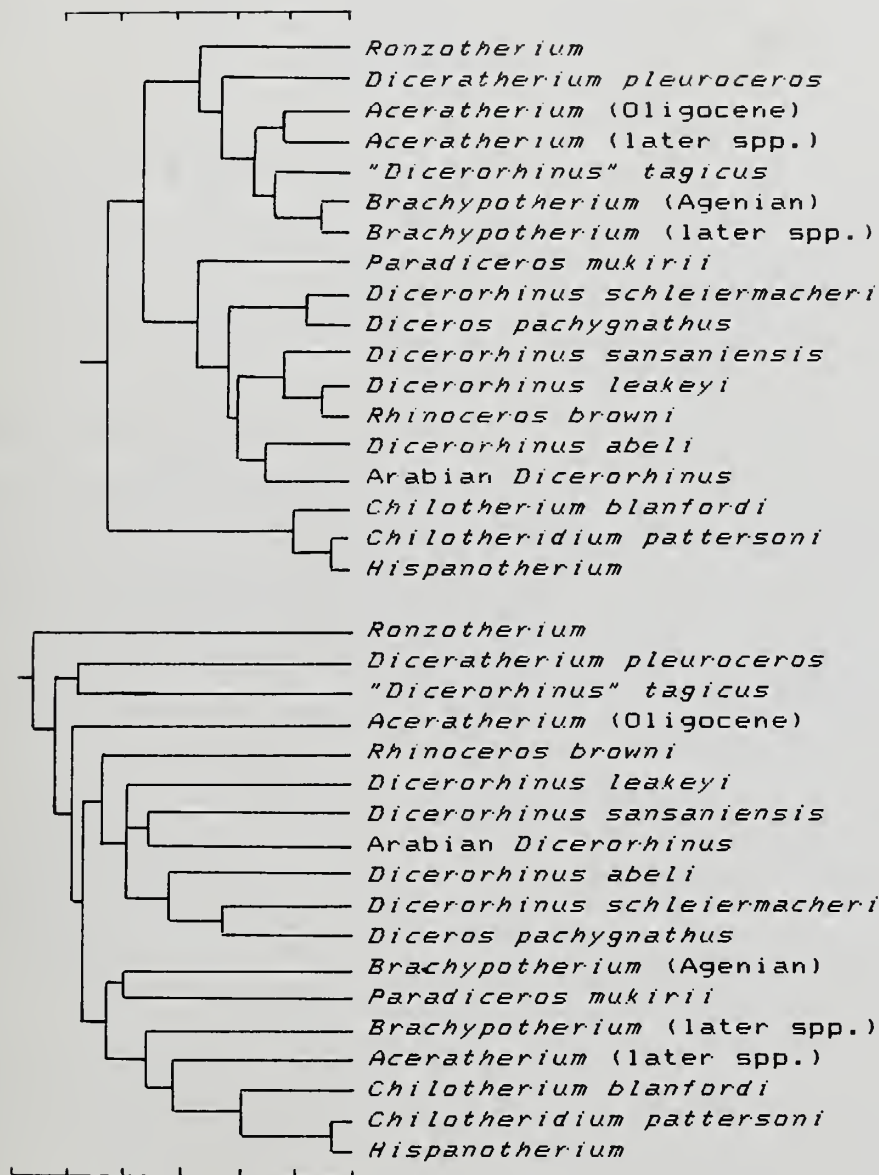Chilotheridium pattersoni
Hispanotherium

Fig. 45 Above, phenetic dendrogram of relationships among some Oligocene and Miocene rhino-
ceroses. The scale runs from 10% nearest the names to 60% nearest to the base of the tree. Below,
advanced characters dendrogram for the same rhinoceroses. The scale runs from 0% nearest the
base of the tree to 60% nearest the names.

to *Chilotheridium* instead of from east to west dispersal along the northern side of Tethys (cf. Antunes 1979).

Genus *BRACHYPOTHERIUM* Roger, 1904

Brachypotherium sp.
Figs 33B, 38B, 39C, 41?, 44C

MATERIAL. Measurements in mm.

M.36300   Tooth fragments including a reassembled labial wall of a left upper molar in middle wear. Occlusal length 56·5. Fig. 33B.

M.36301   Right radius preserved over its complete length but without anterior parts. Overall length 308.

M.36302   Right scaphoid. Fig. 38B.

M.36303   Right metacarpal III, much damaged. Overall length *c.* 148.

M.36305   Left femur without posteroproximal part and with damage medially on patellar groove. Overall length 432. Fig. 41.

M.36306   Left astragalus, much damaged. Dimensions (after Guérin 1980: fig. 22): height 76, anteroposterior dimension (DAP int) 51, breadth (DT) 95. Fig. 44C.

M.36307   Right cuboid.

M.36308   Left metatarsal III, proximal posterior part damaged. Overall length 133; transverse width in middle of shaft 48·5. Fig. 39C.

DESCRIPTION. The large size of the labial wall of an upper molar (M.36300), its flatness and the small size of the paracone rib in comparison with the large flat area leave no doubt of the generic identity being with *Brachypotherium*.

The right radius M.36301 is a little shorter than rhinocerotid radii from Pikermi belonging to either *Diceros* or *Dicerorhinus*, but its shaft width is about the same. Its proportions match closely a radius from Rusinga, M.18908, identified by Hooijer (1966: 148; pl. 9, fig. 1) as *Brachypotherium heinzelini* Hooijer. It is too short to match the complete ulna M.36912.

The scaphoid M.36302 is less high in side view than the other two from Ad Dabtiyah.

Judged from the anterior facet at its distal end, the metacarpal III, M.36303, looks less wide than a corresponding metacarpal III, M.18813, from Rusinga identified by Hooijer (1966: pl. 10, fig. 2) as *Brachypotherium*.

The femur, M.36305, is appreciably smaller than the *Dicerorhinus* femur. Its third trochanter is smaller, it lacks a vertical ridge running down from its great trochanter anterolaterally, and the lateral and medial condyles are less widely separated in ventral view. The presence of any third trochanter at all shows that it must belong to a perissodactyl. If not of a rhinoceros it could perhaps be a chalicothere. Although not very like the femur of the middle Miocene *Chalicotherium grande* (Blainville) figured by Zapfe (1979: 184, fig. 107), it is like the North American *Moropus* Marsh of earlier geological age (Coombs 1978: fig. 13B). However, a right femur of a *Brachypotherium* (Mayet 1908: pl. 2, fig. 3) also looks as if it lacks the vertical ridge, so the present bone is tentatively placed in that genus.

The measurements of the astragalus M.36306 show that it is low and wide, as befits a *Brachypotherium* astragalus. In anterior view the lateral part of the proximal trochleae has quite an overhang. The process low on the medial side also projects well transversely. The top edge of the front of the cuboid facet is widely separated from the base of the more proximal trochlear facets on the anterior surface. The ventral facet for the navicular has a very concave profile in anterior view.

The right cuboid, M.36307, is less deep than that in the associated skeleton of *Dicerorhinus leakeyi* figured by Hooijer (1966: pl. 13, fig. 4) but not quite as shallow as the *Brachypotherium* figured by Guérin (1980: fig. 48G).

The left metatarsal III, M.36308, is shorter and has a wider shaft than the left metatarsal III referred to *Dicerorhinus*. It is longer than the upper Miocene examples of *Brachypotherium* measured by Guérin (1980: 342), but Hooijer (1966: table 17) quoted *Brachypotherium* measurements which match it.

Table 3 *Brachypotherium* species from Europe and Turkey: proportions of astragali (height × 100/breadth) and third metatarsals (breadth × 100/length).

Bone	Proportion	Likely age	Source
Astragalus	89%	Agenian	Measured from Bonis (1973: fig. 32).
	77%	Late Orleanian	Ginsburg & Bulot (1984: 358).
	74%	Late Orleanian	BM(NH) M.7760 from Thenay, France.
	76%	Middle Ataracian	Steinheim (Hooijer 1966: 148, quoting Roger).
	72%	Middle Astaracian	BM(NH) 33529 from Villefranche d'Astarac.
	72%	Late 'Astaracian'	Heissig (1976: 88).
	64%	Late Astaracian	Guérin (1980: 311).
Metatarsal III	31%	Agenian	Mean of three readings from Repelin (1917: 35, 36); Viret (1929: 267).
	37%	Orleanian	*B. stehlini* (Hooijer 1966: 147).
	37%	Middle Astaracian	*B. brachypus* (Lartet) (Hooijer 1966: 147, quoting Roger).
	37%	Late Astaracian	Heissig (1976: 89).
	41%	Late Astaracian	Guérin (1980: 342).

DISCUSSION. A distinctive feature of *Brachypotherium* is the progressive shortening and widening of its limb bones. If this evolved in a straightforward manner during the course of the Miocene it ought to be possible to see how far along the line the Arabian species fits in. Unfortunately there is a shortage of specimens with recorded measurements, but some data for European and Turkish astragali and metatarsals is assembled in Table 3.

The Arabian species has these astragalus and metatarsal ratios at 80% and 36% respectively, which show that it is fairly primitive for a *Brachypotherium* and is likely to date from the Lower or lowest Middle Miocene. One would not expect it to postdate the early Astaracian. However, it should be noted that a Rusinga astragalus measured by Hooijer (1966: 148) has a ratio of 70% yet would probably date in European terms from the earlier Orleanian.

Palaeoecology of Arabian rhinoceroses

Guérin (1980: 380) and many others have commented on the 'hippopotamid' aspect of *Brachypotherium* as manifested by its large skull, barrel-like body and short, stubby limbs. The usual and reasonable conclusion from this is that it was an animal of aquatic habitats. A wooded environment is also often mentioned, which would be a point of difference from *Hippopotamus amphibius*. However, Webb (1983: 289) quotes taphonomic evidence that the north American *Teleoceras* Hatcher, very like *Brachypotherium*, 'lived in the water but grazed on adjacent dense grasslands' exactly as does the modern hippopotamus (Kingdon 1979: 250)—an amazing parallelism for two mammals in different orders and with different digestive strategies.

Miocene *Dicerorhinus* stands close to the ancestry of the extant horned rhinoceroses and what is known of their ecology can be used as a guide to that of the fossil form. The somewhat specialized African rhinoceroses live in lightly wooded areas, preferably with thickets (*Diceros bicornis*) or in more open environments with grasses (*Ceratotherium simum*); both species need access to water (Kingdon 1979: 80–119). *Rhinoceros unicornis* was in historic times an inhabitant of the grassed and wooded Indian alluvial plains and it feeds mainly on grasses (Laurie 1982: table 2). *Dicerorhinus sumatrensis* inhabits densely wooded areas but prefers their margins and disturbed areas. It can ascend and descend steep slopes with agility and, a century or two ago, may have been found in hillier country than the sympatric *R. sondaicus* (Groves & Kurt 1972; van Strien 1975: 37).

One can therefore conclude that the Arabian *Dicerorhinus* is likely to have fed by browsing in wooded habitats with easily available water.

Zoogeography of Arabian rhinoceroses

If the Arabian *Brachypotherium* really is of Lower Miocene age, as implied by the proportions of its astragalus and metatarsal, it could be conspecific with *B. snowi* (Fourtau 1918) from Moghara, Egypt. The occurrence of *Brachypotherium* at this period as far east as Ad Dabtiyah would be interesting inasmuch as Guérin (*in* Pilbeam *et al.* 1979: 36) does not find it in the Siwaliks sequence until after *Hipparion* is present. However, Heissig (1972: 103) claimed to have identified *Brachypotherium* as far back as in the Kamlial Formation.

A comment may also be made here on the question of the occurrence of *Aceratherium* in Africa. The holotype skull of *Turkanatherium acutirostratus* Deraniyagala 1951 from the Middle Miocene of Moruorot, Kenya, was subsequently referred to *Aceratherium* by Arambourg (1959: 74). This fossil was the first described from Africa adequate to sustain an identification as either *Aceratherium* or something else. Its upper cheek teeth are large and wide by comparison with European *Aceratherium*. They do show moderate or strong antecrochets, but in this, as in the two preceding characters, they agree well with the later Miocene *Brachypotherium lewisi* Hooijer & Patterson from Lothagam (Hooijer & Patterson 1972: 2). It is possible that Deraniyagala's skull is the same species or lineage as the short metapodials, phalanges and other elements found in east Africa and referred to *Brachypotherium*, e.g. those of Hooijer (1966: pl. 10, figs 1–3, 6–8). The skull material of *Aceratherium campbelli* Hamilton (1973: table 3; pls 1, 3) from Zelten, Libya, may also have been incorrectly placed at generic level. Its teeth were large and appear to have been wide; it looks very like the Moruorot skull. The high occiput and concave profile of the cranial roof in both skulls is unlike European *Aceratherium* (Mermier 1896: pl. 2, fig. 2; Guérin 1980: pl. 3) but can be matched from within *Brachypotherium* (Mayet 1980: pl. 2, fig. 1). African *Brachypotherium*, as in Europe identified by its short limb extremities, may have been an entirely separate development and have evolved *Aceratherium*-like antecrochets on its upper molars. This idea needs further investigation. If it were correct, the absence of *Aceratherium* at Ad Dabtiyah could be held to align the fauna with Africa rather than with Europe. Unfortunately the concurrent absence of *Chilotheridium* could be held to indicate the reverse. Hence the rhinoceroses reported in this paper remain zoogeographically inconclusive.

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