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VERTEBRATE PALEONTOLOGY OF THE KOUM BASIN, NORTHERN CAMEROON, AND ARCHOSAURIAN PALEOBIOGEOGRAPHY IN THE EARLY CRETACEOUS

A Thesis Presented to the Graduate Faculty of
Dedman College

Southern Methodist University

in

Partial Fulfillment of the Requirements
for the degree of
Master of Science
with a
Major in Geology
by

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(B.S., Rutgers University, 1984)

August 10, 1990

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Vertebrate Paleontology of the Koum Basin, Northern Cameroon, and Archosaurian Paleobiogeography in the Early Cretaceous

Adviser: Associate Professor Louis L. Jacobs
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The Koum basin is located in West Africa and is a half-graben filled with Cretaceous and younger sediments. It formed in response to tectonic stresses that preceded the development of the Benue trough and the final connection of the North and South Atlantic Oceans. The Cretaceous sediments, up to 3000 meters thick, represent lacustrine, fluvial, and alluvial fan deposits, and suggest an axially-drained half-graben sedimentation model.

Archosaur fossils recovered from the eastern Koum basin include the teeth of two terrestrial crocodylians (cf. *Araripesuchus wegeneri* and cf. Sebecosuchia) teeth of sauropod and two kinds of theropod dinosaurs (cf. Spinosauridae and Theropoda indet.), and postcrania and teeth of the ornithopod dinosaur cf. *Ouranosaurus nigeriensis*. Archosaur trace fossils from the central Koum basin include the footprints of sauropod, two theropod, and an ornithopod dinosaur. The footprint assemblage is equivalent to the dinosaur osteological assemblage from the eastern basin in number and type of taxa represented.

The bone-bearing strata from the Koum basin are roughly correlative with the well-known Aptian Gadoufaoua fossil locality in Niger, based on the presence of *Araripesuchus*, cf. Spinosauridae, and *Ouranosaurus*; they are possibly younger than fossiliferous deposits from the Early Cretaceous of Malawi that contain similar faunal elements. Footprint-bearing strata from Koum are possibly correlative with pre-Gadoufaoua beds in Niger.

Araripesuchus is known from South America and two other African localities; it enjoyed a broad distribution across western Gondwana prior to the isolation of Africa from South America. The presence of sebecosuchians in Koum demonstrates their early, wide dispersal. The range of spinosaurids in Africa is extended to the southwest, and the range of *Ouranosaurus* is extended southward by the Koum basin occurrences. The appearance of *Ouranosaurus* in African fossil localities may be the result of faunal exchange with Laurasia in the Early Cretaceous.

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CHAPTER I

INTRODUCTION

The discovery of fossil-bearing deposits of Early Cretaceous age in the Koum basin in northern Cameroon (Flynn *et al.* 1987; Brunet, Jacobs, *et al.* 1988; Jacobs *et al.* 1988 and 1989; Congleton *et al.* in press), near the point where Africa was last connected with South America before the final opening of the South Atlantic Ocean, provides a window into the paleobiogeography of Gondwana immediately prior to its final disintegration. The opening of the South Atlantic is critical to the understanding of the vicariant origins of the major groups of Cretaceous archosaurs. Furthermore, paleontological work in this part of West Africa sheds light on the geology of a portion of an Early Cretaceous sedimentary basin in an area of the world in which Early Cretaceous terrestrial rocks are as yet very little known.

The Cretaceous Period was a time of worldwide change. Pangea split in the Jurassic into the northern and southern continents of Laurasia and Gondwana, and by the beginning of the Cretaceous Gondwana was disintegrating as well. By medial Cretaceous times, West Gondwana was breaking up as the proto-South Atlantic was opening. Africa was becoming established for the first time as a separate continent.

Amid this scenario of continental reconfiguration, terrestrial biotas were changing. Vicariant diversification of small vertebrates followed distinctly separate paths on the different continents. Salamanders underwent their major diversification in Laurasia (Naylor 1980; Estes 1982), and leptodactyloid and pipoid frogs diversified in Gondwana. Teiid lizards evolved endemically in the north; iguanid lizards and pelomedusid turtles evolved in Gondwana (Bonaparte 1986). Mammals followed new evolutionary paths as they diversified vicariantly in the Early Cretaceous, with advanced tribosphenic mammals evolving in the north and derived non-tribosphenic mammals occupying West Gondwana (Bonaparte 1986; Van Valen 1988; Jacobs *et al.* 1988). Monotremes, non-tribosphenic derivatives, were established on the Australian continent at this time as well, but the fossil record there, as in Africa, is poor (Archer *et al.* 1985; Jacobs *et al.* 1988).

Despite the endemic, vicariant nature of terrestrial small vertebrate faunas in the late Mesozoic, archosaurian faunas, especially dinosaurs, show broad similarities across the globe (Charig 1973), reflecting prior widespread distributions. The similarities between the dinosaur faunas of the Late Jurassic Morrison Formation of western North America and Tendaguru in East Africa are well known (Charig 1973; see also Galton 1977a, 1977b). Ornithopods of the family Hypsilophodontidae are found in Early Cretaceous localities in Australia, Africa, Europe, and North America (see, for example, Molnar and Galton 1986; Galton and Jensen 1975; Galton and Taquet 1982; Winkler *et al.* 1988). The ornithopod genus *Iguanodon* or its close allies are known from the Early Cretaceous of Europe, North America, and Africa (see Norman 1986; Weishampel and Bjork 1989; Taquet 1976). The paleoichnological record of the Cretaceous in general agrees with the osteological record. With the exception of Antarctica, Cretaceous dinosaur footprints have been found on all continents. Several works, including Ellenberger (1965), Ellenberger *et al.* (1969, 1970), Haubold (1986), Olsen and Baird (1986), and Dejax *et al.* (1989), make limited intercontinental comparisons.

Crocodiles also exhibit global similarities at the generic level in Early Cretaceous times, including *Bernissartia* and a "dwarf" crocodile (*Theriosuchus*) known from North America and Europe (Buffetaut and Ford 1979; Langston 1974), several genera which are known from both sides of the South Atlantic (Buffetaut and Taquet 1977, 1979), and an unusual Early Cretaceous form known from both North America and South America (Langston 1974). These similarities, if supported by detailed systematic studies, suggest that rates of evolution were less affected by continental reconfiguration in archosaurs than in mammals. By Late Cretaceous times, however, a new order was established and archosaur faunas were endemic to their respective regions.

Given these conditions, the goals of this thesis are: (1) to describe the Early Cretaceous archosaurs and archosaur ichnites from the Koum basin in northern Cameroon within the context of the global Early Cretaceous fauna; (2) to describe and interpret the identity, gait, and behavior of the archosaurian trackmakers responsible for the Koum basin ichnites; (3) to place fossil vertebrate localities within the relative stratigraphic context of the Benue trough and to apply the stratigraphic implications of Cretaceous archosaurs to the geological setting and evolution of the Benue trough; and (4) to compare the systematic and stratigraphic record of Cameroon archosaur fossils and ichnites to what is known of the terrestrial Lower Cretaceous within Africa.

CHAPTER II

GEOLOGICAL OVERVIEW OF THE KOUM BASIN

Tectonic and Paleogeographic Setting

General Remarks

The study area is in the Koum basin in northern Cameroon, West Africa (figure 1). The Koum basin is a relatively small half-graben geographically isolated from the Yola arm of the Benue trough (figure 4). The Yola arm is an elongate east-west trending sedimentary basin located to the west-northwest of the Koum basin, and is a continuous extension to the Benue trough. The Koum basin is located about 25 kilometers to the southeast of outcrops of Yola Arm sediments. The formation of the Koum Basin was probably related to the Early Cretaceous rifting event which was responsible for the formation of the Yola arm and the Benue trough, as well as the South Atlantic Ocean (Popoff 1988).

The major tectonic features dominating west-central Africa are the Pan-African mobile belt and the Benue trough. The Pan-African mobile belt represents the suture zone of three colliding continental cratons (Popoff 1988) dating from the late Precambrian. The Benue trough, extending northeast from the Gulf of Guinea, is a much younger feature

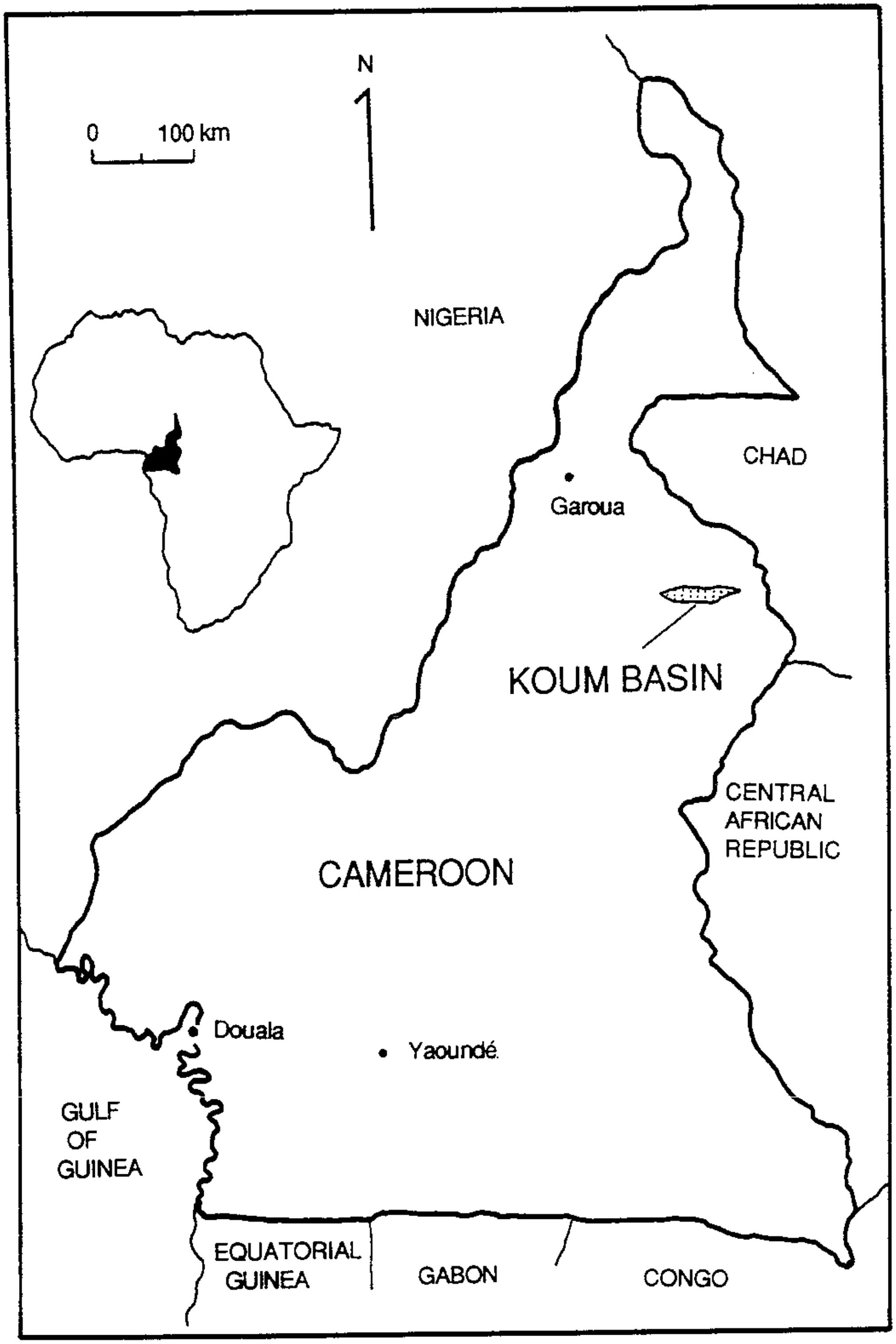


Figure 1. Location map of study area.

superimposed on the Precambrian craton. Its formation was in part governed by older lineaments inherited from the Pan-African event, and by regional stress regimes imposed by forces associated with the opening of the South Atlantic Ocean and Gulf of Guinea.

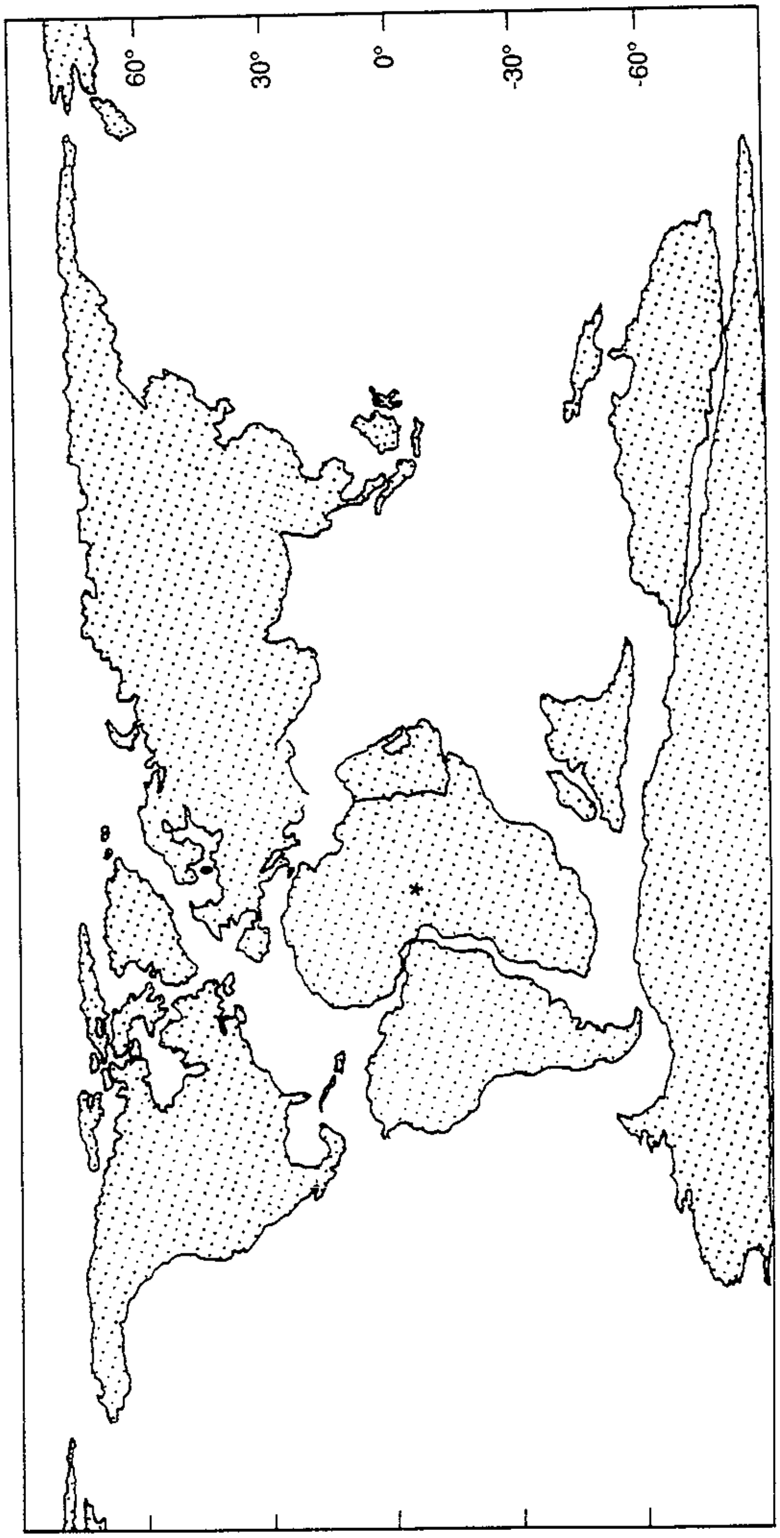
Early Cretaceous Global Paleogeography

One Early Cretaceous global paleogeographic reconstruction is shown in figure 2. Most reconstructions agree that by the earliest Cretaceous, the southern North Atlantic was open (Barron 1987; Scotese *et al.* 1988). India, Antarctica, and Madagascar had diverged from Africa. Africa and South America were contiguous. The incipient South Atlantic Ocean was opening at its southern end by the Valanginian (Scotese *et al.* 1988), as indicated by the oldest oceanic crust in the basin. Africa was slightly south of its present latitude, and its position changed little throughout the duration of the Cretaceous (Barron 1987). The Koum basin was between 5° and 10° south latitude in the Early Cretaceous.

Early Cretaceous Global Climates

Studies of global temperature distribution of the Cretaceous indicate that the world climate was appreciably more equable than today, with an absence of polar ice caps and broader tropical and temperate belts (Hallam 1984; but see Gregory *et al.* 1989). Rich and Rich (1989) describe a near-polar biota of dinosaurs and other reptiles from the

Figure 2. Plate tectonic reconstruction of the world during the Barremian (redrawn from Barron 1987).


60°
30°
0°
-30°
-60°

Aptian-Albian of Australia, indicating a cool, humid climate between 70° and 85° south latitude. Ziegler *et al.* (1987) note that for many parts of the world, rainfall patterns in the Early Cretaceous were probably strongly seasonal, and large tropical forests, particularly lowland rainforests, probably did not exist. Hallam (1984) concludes that following a period of widespread Jurassic aridity, the Early Cretaceous began a trend toward progressively more humid climates globally, culminating in humid conditions over much of the world after the end of the Early Cretaceous. Proposed causes for this global change in humidity include the progressive fragmentation of Pangea and high eustatic sea levels (Hallam 1984).

Africa and South Atlantic Region Paleoclimates

Early Cretaceous climates for Africa have been summarized by Ziegler *et al.* (1987), who concluded from study of the Nubian Sandstone, the Continental intercalaire, and their equivalents (the Messak and Cabao Sandstones of Libya, the Desert Rose Unit of Egypt, the Selima Formation in Sudan) that a savannah-like environment existed over much of Africa at the time, with seasonal change dominated by changes in moisture, not temperature. Chamley and Robert (1982) used detrital clay mineralogy from deep sea cores from the South Atlantic to make inferences regarding onshore climatic conditions during the Early Cretaceous. They found an abundance of smectitic clays, suggesting a somewhat hot climate with alternations (probably seasonal) in humidity. Similar conclusions were reached by Riccardi (1987) in a summary of South American Cretaceous climates. He defined an arid zone which existed north of present-day 43° south latitude (paleolatitude of about 30° south) which persisted through the Lower and much of the Upper Cretaceous, based on the presence of red beds, evaporites and eolianites throughout the region. From freshwater sponge and conchostracan fossils, he concluded that moisture availability was seasonal. Palynological studies of the Senegal basin in West Africa indicate that arid conditions predominated in the Barremian and lower Aptian (Michaud and Flicoteaux 1987). Plant macrofossils and pollen assemblages (dated as Barremian) from the Mayo Oulo and Babouri-Figuil basins of northern Cameroon (near the study area) indicate a hot, somewhat dry climate, but with enough moisture to support ferns and swamps which contained arborescent gymnosperms (*Brachyphyllum* and *Frenelopsis*) (Brunet *et al.* 1988; Dejax *et al.* 1989). This is consistent with a warm climate characterized by seasonal precipitation. In summary, it appears from a variety of sources (sedimentological, mineralogical, palynological, and paleontological) that a warm arid climate with seasonal moisture availability dominated in the tropical zone around the South Atlantic during Early Cretaceous times.

Origin of the South Atlantic Ocean

The opening of the South Atlantic Ocean began in the south during the Late Jurassic and propagated northward (figure 3). Stress regimes were tensional to the south and compressional in the north, around the Gulf of Guinea, during the initial stages of rifting (Reyment and Dingle 1987). The beginning rift phase in the southernmost South Atlantic was characterized by lacustrine sedimentation in the Late Jurassic, followed by marine deposition as rifting progressed. Unrestricted marine sedimentation occurred until Aptian time when a gulf extended to the present-day Niger delta. There was no marine connection with the North Atlantic at this time. Further to the south, the Walvis Ridge and Rio Grande Rise uplifted and blocked oceanic circulation, causing extensive salt deposition (Burke 1975).

The first communication of South Atlantic seawater with the North Atlantic occurred in the Upper Albian (Reyment 1969; Förster 1978), when a connection opened at the north coast of Brazil and the south shore of the Gulf of Guinea. The connection may have been the result of transgression of the continental margin (Reyment 1969), or by rifting, or a combination of rifting and coastal transgression (Förster 1978). This event has been documented by ammonite faunas, specifically elements from the Elobiceratan ammonite zone (Reyment 1969) including *Elobiceras*, *Angolaites*, and *Neokentroceras* (Förster 1978). Communication was intermittent throughout the remainder of the Albian and

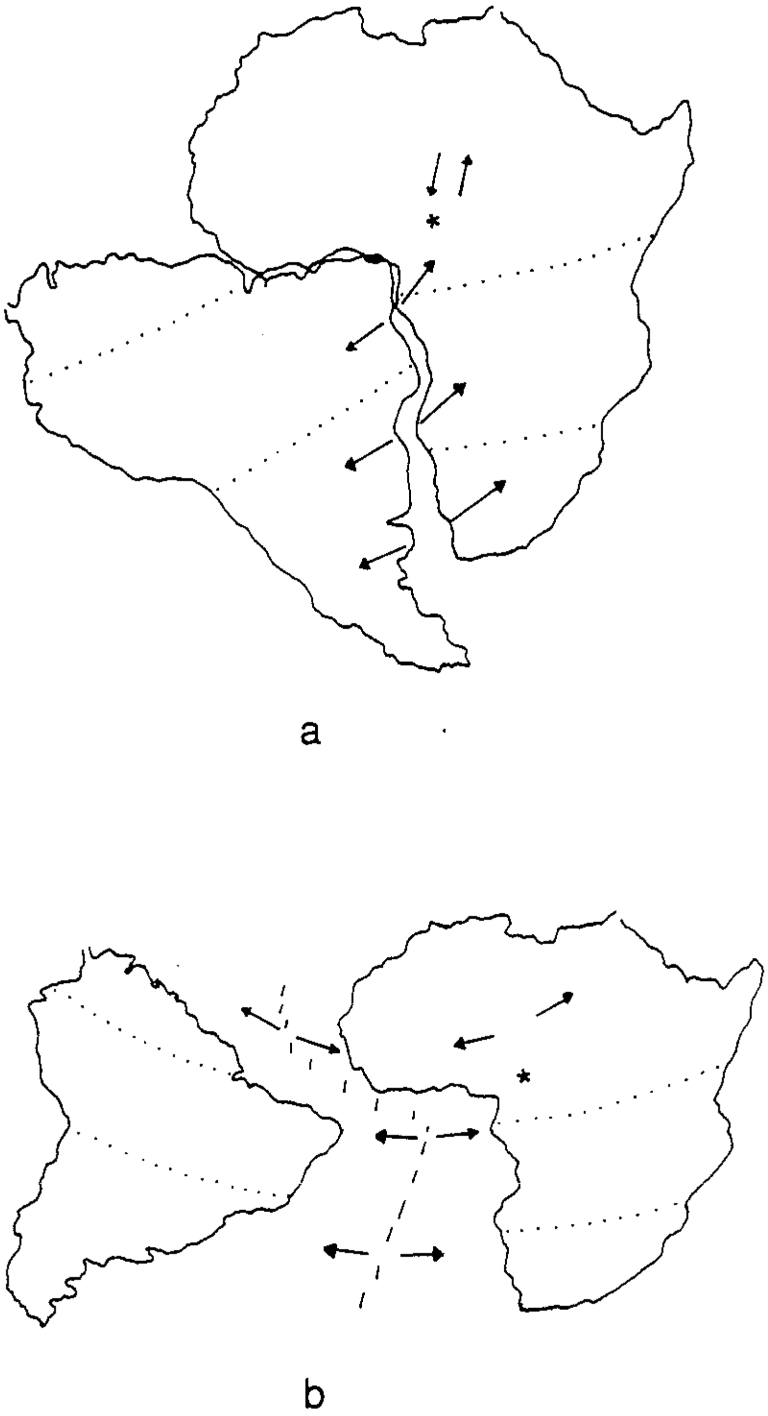


Figure 3. Stages of development of the South Atlantic Ocean. a - 130-119 Ma (Early Cretaceous). b - 67 Ma (end of the Cretaceous). Redrawn from Fairhead (1988). Location of Koum basin denoted by asterisk.

earliest Cenomanian (Reyment 1980; Reyment and Dingle 1987). By the Late Cenomanian-Early Turonian eustatic highstand, the North and South Atlantic Oceans were well connected, though the flow of middle and deep waters was still obstructed by submarine topography (Reyment and Dingle 1987). Africa and South America were separated to the south of the present-day Niger delta by oceanic crust. Along the northern coast of the Gulf of Guinea they were separated by a transform fault and en échelon pull-apart basins (Mascle *et al.* 1988) forming a narrow strait.

An alternative hypothesis for the early history of the South Atlantic was outlined by Rand and Mabesoone (1982), alleging the existence of a land bridge in the region of the present-day Niger delta between South America and Africa, persisting into the Maastrichtian. This model accounts for inconsistencies in the marine faunal record (the lack of exchange of planktonic foraminifera between the North and South Atlantic until the end of the Maastrichtian). This model also explains the existence of a regional gravity anomaly in the region. It does not account for the well documented ammonite faunal record discussed above. However, Rand and Mabesoone (1982) allow that possible "spillovers" occurred during periods of transgression in the Albian and Turonian.

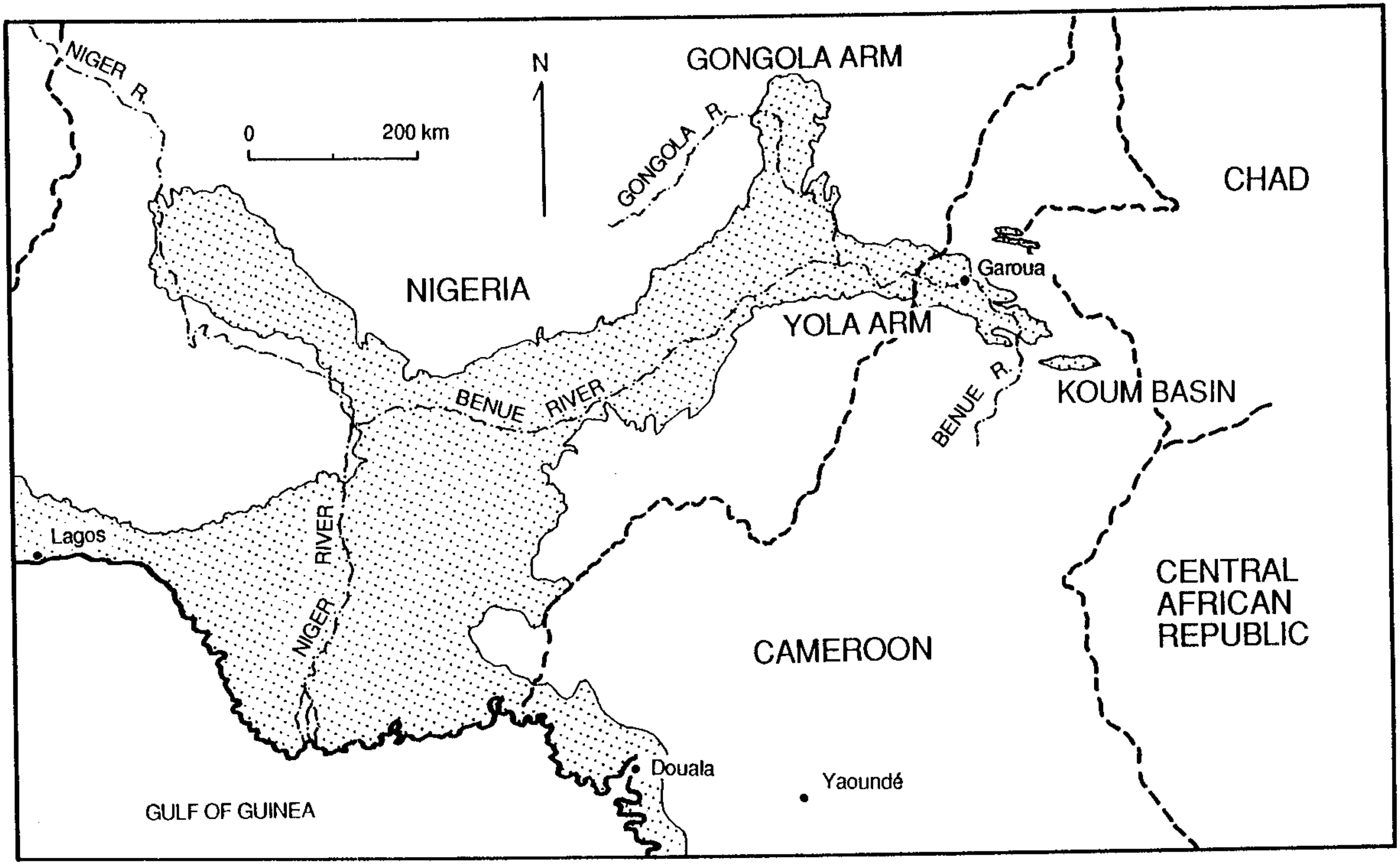
Tectonic and Depositional History of the Benue Trough

The Benue trough is a major tectonic feature in West Africa and forms the route for several major West African rivers. The upper trough is Y-shaped, stretching into east-central Nigeria in the north before forking into the northern (Gongola) and eastern (Yola) branches (figure 4). The Gongola arm trends north-south toward the west side of Lake Chad, where it becomes obscured by younger sediments; the Yola arm trends east-west into northern Cameroon, where it dissipates.

The Benue trough is a rift-like feature filled with Cretaceous and younger sediments. The main stages of the evolution of the Benue trough occurred during the opening of the South Atlantic (Grant 1971; Mascle 1976; Allix and Popoff 1983; Popoff *et al.* 1983; Benkhelil and Robineau 1983; Fairhead 1988; Popoff 1988).

The oldest intracontinental basins associated with the Benue trough are oriented in the E-W direction and are bounded by one or more normal faults (Allix and Popoff 1982, 1983; Popoff *et al.* 1983; Popoff 1988). These basins occur in two families, one group centered in the Yola arm and the other in the southern Gongola arm (Popoff 1988). The sediments in these basins have been considered Aptian, though more recent data give latest Jurassic to earliest Cretaceous ages in Nigeria (K-Ar age of 147 ± 7 MA)(Popoff *et al.* 1982) and Barremian (Popoff 1988; Brunet *et al.* 1988) in northern Cameroon. Following this early episode of basin

Figure 4. Distribution of Cretaceous and younger sediments (stippled pattern) in the Benue trough. Redrawn from Allix (1983).


NIGER R.
0
200 km
N
GONGOLA ARM
GONGOLA R.
CHAD
NIGERIA
Garoua
YOLA ARM
BENUE RIVER
BENUE R.
KOUM BASIN
Lagos
NIGER RIVER
CENTRAL AFRICAN REPUBLIC
CAMEROON
Douala
Yaoundé
GULF OF GUINEA

initiation, a second phase of crustal stretching, local block tilting, basin installation, and basaltic magmatism took place from the Barremian through the middle Albian (K-Ar age of 103 ± 5 MA)(Popoff *et al.* 1982; Popoff 1988). This second phase was dominated by NE-SW crustal motion (Popoff *et al.* 1983; Maurin *et al.* 1986; Allix and Popoff 1983), and was characterized by the installation of a system of down-dropped en échelon basins up the axis of the Benue trough, overprinting the earlier E-W features. A final compressional tectonic phase occurred in the Santonian, and resulted in broad NE-SW folding in the earlier Cretaceous sediments of the main trough axis.

The history of sedimentation in the Benue trough was in large part controlled by tectonic events. The earliest Mesozoic sediments known in the region are located near Burashika, Nigeria, less than 300 km from the Koum basin. The Barremian E-W extensional basins exposed in northern Cameroon were initially filled with conglomerates (Popoff 1988) and were later occupied by Barremian lakes and rivers. The conglomeratic sediments are thought to be thickest around basin margins, and display rapid lateral facies changes. The continental lake phase lasted from the Barremian into the mid Albian (Popoff 1988; Popoff *et al.* 1983), and corresponds to the lower Bima Formation in Nigeria. The lacustrine and fluvial sedimentation was discontinuous but widespread in the Benue trough to the west of Garoua in Cameroon, NE Brazil and as far north as Ténéré in Niger. This period of deposition has been referred to by Popoff (1988) as the medio-African and NE Brazilian Cretaceous Great Lakes. Sediments were characterized by Popoff (1988) as strongly reduced pyritic shales and arkosic pebble conglomerates and sandstones, representing low energy fresh water and higher energy fan-delta, deltaic, and fluviatile environments.

From the upper Albian to lower Cenomanian, a fluvial plain occupied the upper Benue trough, and was responsible for deposition of the upper Bima Sandstone (Popoff *et al.* 1983; Popoff 1988; Allix and Popoff 1983). A major marine transgression flooded the upper Benue trough in the Cenomanian and Turonian (Allix 1983) as far east as western Chad (Wacrenier 1953) and north into Niger (Reyment and Dingle 1987). Marine sediments are restricted to the chain of down-dropped basins of the Benue trough, as well as the Gongola and Yola arms. Alternating marine, marginal marine, and terrestrial conditions persisted in the Benue trough for the remainder of the Cretaceous (Petters 1983; Reyment and Dingle 1987).

The tectonic relationship of the Benue trough with the opening of the South Atlantic and Gulf of Guinea is complex. The initial phase of intracratonic N-S extension and the initiation of the E-W grabens has not been attributed to any single cause. The main chain of en échelon basins forming the axis of the Benue trough has been attributed to sinistral transcurrent shear motion along a landward prolongation of equatorial oceanic fracture zones (the present-day Romanche, Chain, and Charcot faults) (Benkhelil and Robineau 1982, 1983; Popoff 1988). Where this fault intersected preexisting N-S lineaments in the basement, down-dropped basins formed. Landward transport of transcurrent motion along a number of these oceanic fracture zones can explain many of the NE-SW Cretaceous structural features of the Benue trough. This mechanism is similar to the model proposed by Maurin *et al.* (1986), and requires a significant amount of intraplate deformation of Africa. In fact, it may explain areas of poor fit between Africa and South America in some plate tectonic reconstructions (*e.g.*, Bullard *et al.* 1965).

Geology of the Koum Basin

Previous work

Since the early part of the twentieth century, a number of geologists working in the region of northern Cameroon have described the geology and paleontology of the small Cretaceous basins of the area. The earliest work was carried out by Mann (1913), who described rocks from the Babouri-Figuil and Mayo Oulo-Léré basins. Hennig (1913) described the first vertebrate fossils from the region (fish scales and a crocodile tooth), recovered by Mann (1913). The Koum basin was the last Cretaceous basin to be identified. It has been poorly studied because of its relative inaccessibility, even though it is the largest of the isolated Cretaceous basins in the region.

The first specific report of Cretaceous sediments in the region east of Tchollíré (Koum basin) was Aubel (1938). He provided a terse account of the sediments he encountered while mapping the granitic and gneissic rocks of the area. Roch (1953) described the basins of Mayo Oulo-Léré, Hama Koussou, Babouri-Figuil, and Mbéré, but failed to mention Koum. A geologic sketch map of northern Cameroon and southwestern Chad, compiled by Aubel and presented in Roch (1953), shows an area of Cretaceous sediment outcropping east of Tchollíré, without discussion.

Schwoerer (1954a) mentions an unstudied suite of Cretaceous sediments east of Tchollíré; he provides a relatively accurate map of the extent of the Koum basin in a follow-up report (1954b) and mentions that fossil wood found there seems to relate the sediments to the "grès de la Bénoué," presumably a reference to the sandstones known from the Yola arm in the region of Garoua. He notes that the preponderance of finer-grained sediment and the persistent shallow north dip of the strata sets it apart from other rocks of the region. The geologic map of Schwoerer (1965) shows Yola arm sediments to be of similar age to those in the Koum basin. It contains terrestrial clastic debris distinct from the predominantly marine sediment which fill the Yola Arm. In the text accompanying the first detailed geologic map of northern Cameroon, Schwoerer (1965) gave a very brief description of the rocks of the Koum basin. He grouped the Koum basin rocks with those of the Logone and Bénoué basins, defining their age as "Crétacé moyen".

Tillement (1972) gave a detailed account of the geology of the Koum basin, in a larger work on regional hydrogeology. He sketched about 400 m of strata measured near the center of the basin, and estimated the thickness of the entire section (barring structural complexities) to be at least 3000 m.

Popoff (1988) mentions the Koum basin in the larger context of the opening of the South Atlantic Ocean and the Gulf of Guinea in the Early Cretaceous. He proposed that the Koum basin, along with other E-W oriented basins in the Yola and Gongola arms of the Benue trough, were part of an early episode of rifting associated with a N-S extensional regime which existed prior to inception of the Benue trough proper. Brunet *et al.* (1988) also implicate Koum (as well as other small isolated basins in northern Cameroon) in an early episode of rifting which preceded the formation of the main part of the Benue trough.

Pollen, invertebrates, dinosaur footprints, and osteological remains are known from the Koum basin (Flynn *et al.* 1987). Among the animals represented by fossils are conchostracans, fish, turtle, cf. thyreophoran, ornithopod, theropod, and sauropod dinosaurs, and mammal remains, all Cretaceous in age (see table 1). Jacobs *et al.* (1989) describe a dinosaur footprint locality near the village

Table 1.--Floral and faunal list for Lower Cretaceous fossil localities in the Koum basin, northern Cameroon.

Taxon	Locality
Palynomorphs	
Spermatophyta	
Gymnospermae	
Coniferales	
Cheirolepidaceae	
Classopollis sp.	KB-6
Body fossils	
Spermatophyta indet.	KB-11
Arthropoda	
Crustacea	
Conchostraca	
Cyzicus (Lioestheria) lamberti	KB-4 KB-17 KB-19 KB-22 KB-24
Conchostraca indet.	KB-15
Vertebrata	
Osteichthyes	
Semionotiformes	KB-6
Dipnoi	KB-6
Amphibia	
Anura	
Pipoidea	KB-6
Reptilia	
Chelonia	KB-6
Crocodylia	
Uruguaysuchidae	
cf. *Araripesuchus wegeneri*	KB-6 KB-8
cf. Sebecosuchia	KB-6
Saurischia	
Theropoda	
cf. Spinosauridae	KB-6

Table 1 (continued).--Floral and faunal list for Lower Cretaceous fossil localities in the Koum basin, northern Cameroon.

Taxon	Locality
Saurischia (continued)	
Theropoda indet. A	KB-6
Theropoda indet. B	KB-6
Sauropodomorpha indet.	KB-6 KB-13
Ornithischia	
cf. Thyreophora	KB-6
Iguanodontidae	
Ouranosaurus sp.	KB-6
Mammalia	
Theria indet. A	KB-6
Theria indet. B	KB-6
Ichnites	
Vertebrata	
Reptilia	
Saurischia	
Theropoda	KB-3 KB-17
Sauropodomorpha	KB-18
Ornithischia	
Ornithopoda	KB-17 KB-23

Koum. Congleton *et al.* (in press) provide a tentative correlation of the fossil-bearing beds near Mayo Djarendi in the eastern end of the Koum basin with the Aptian Gadoufaoua locality near Agadez, Niger, as well as a brief description of sediments in the basin.

Conchostracan fossils from several localities in the central part of the Koum basin (KB-4, KB-15, KB-19, KB-22, and KB-24b) have been identified as *Cyzicus (Lioestheria) lamberti* (P. Tasch, personal communication). This taxon is known from two localities near In Gall, on the road between In Gall and Agadès, Niger (Defretin 1956). The sediments at this locality belong to the argiles de l'Irhazer, and were considered by Taquet (1976) to underlie and predate the Tégama Series rocks which comprise the fossiliferous deposits of Gadoufaoua.

Two species of *Cyzicus (Lioestheria)* have been identified from the Babouri-Figuil basin in northern Cameroon (species 1 and species 2), among several other taxa of conchostracans (P. Tasch, personal communication; Defretin and Boureau 1952; Defretin 1953). Neither is conspecific with the Koum basin taxon. The differences between the conchostracan faunas of Koum and the other Early Cretaceous basins of northern Cameroon may be due to differences in age or ecological conditions.

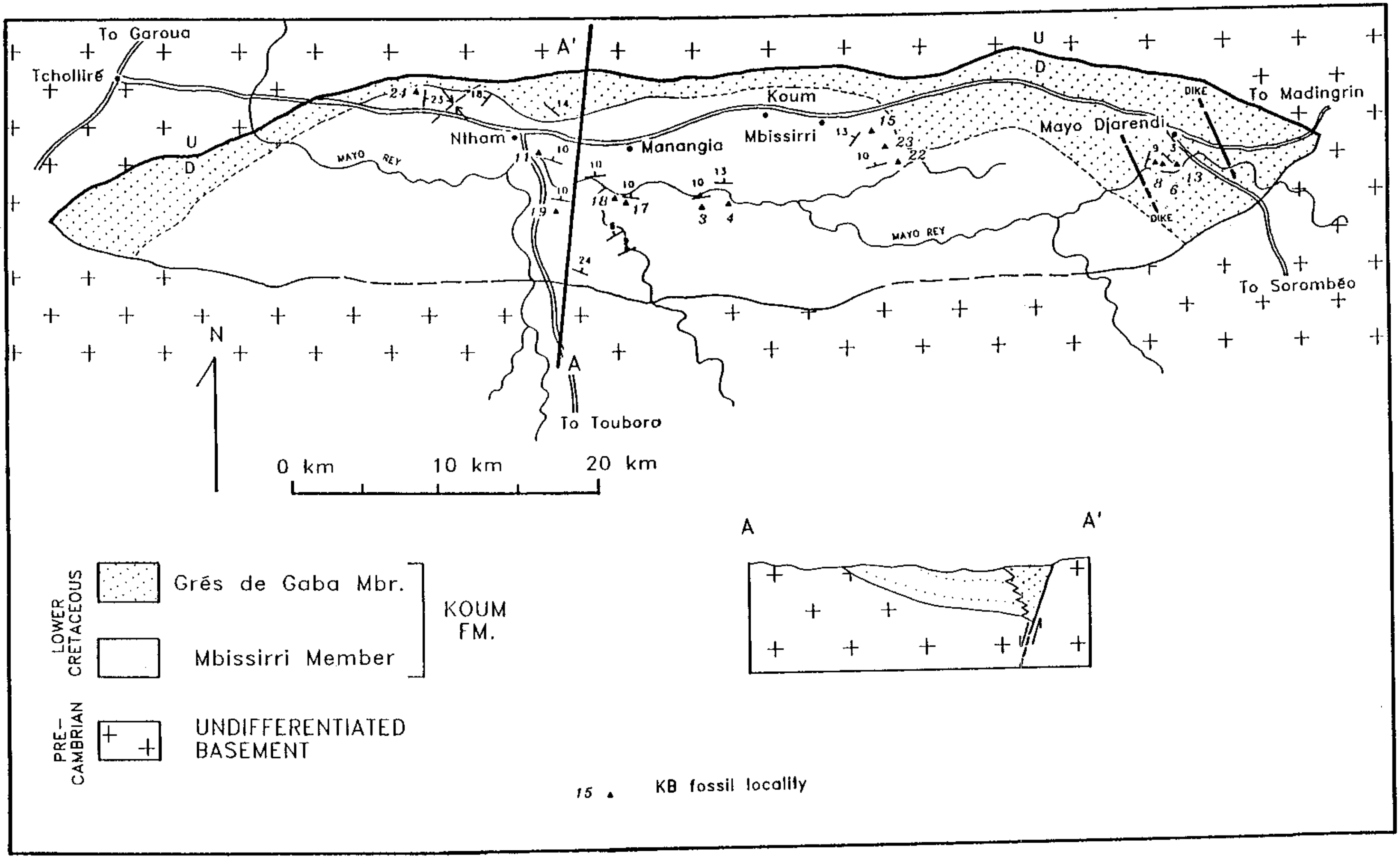
Physiography

The Koum basin is roughly elliptical in shape with its long axis oriented E-W (figure 5). Maximum length is approximately 80 km; maximum width about 16 km. It is about 1200 km^2 in areal extent. The basin is surrounded by relatively resistant Precambrian metamorphic rocks, and the basin itself is a topographic low. Occupying the center of the basin and flowing from east to west is the Mayo Rey, a perennial stream which is a tributary of the Benue River. The basin floor has been dissected by the Mayo Rey, and remnant lateritic soils cap the undissected terrace that forms a large portion of the basin surface. The greatest relief is found in the basin center and near the contact with the Precambrian basement.

Structure

The Koum basin is filled primarily by sediments of Cretaceous age. These are uniformly tilted to the north, with dips ranging between 5 and 15 degrees (figure 5). Younger sediments observed south of the village Ntham as well as in the eastern end of the basin, presumably of Late Tertiary or Quaternary age, rest horizontally on the Cretaceous sediments. The Koum basin is a half-graben, bounded to the north by a south-dipping normal fault, forming the contact between the Cretaceous and the Precambrian basement (Tillement 1972). This major tectonic feature is difficult to observe directly in the field because it is covered by colluvium and vegetation. North of the village Ntham a small, low amplitude syncline with an E-W axis was observed in close proximity to the northern fault. The wavelength of the structure is on the order of several hundred meters. Dips on the north limb of the structure are to the south, and are the last dips observed before the covered fault contact. Using aerial photos,

Figure 5. Geological sketch map of the Koum basin, northern Cameroon.


To Garoua
Tcholliré
A'
U
D
To Madingrin
DIKE
Koum
Mbissirri
Mayo Djarendi
Ntham
Manangia
MAYO REY
To Sorombéo
A
To Touboro
N
0 km
10 km
20 km
A
A'
LOWER CRETACEOUS
Grés de Gaba Mbr.
Mbissirri Member
KOUM FM.
PRE-CAMBRIAN
UNDIFFERENTIATED BASEMENT
15 ▲ KB fossil locality

Tillement (1972) interpreted several E-W linear features south of Ntham as small normal faults displacing Cretaceous sediment. The southernmost of these is in fact the Cretaceous-Precambrian contact. The sedimentary basin is consequently about 7 km narrower than Tillement (1972) assumed. Similarly, the eastern end of the basin is west of the position indicated by both Schwoerer (1965) and Tillement (1972). Geologic maps produced by both authors indicate that Cretaceous sediments extend about 17 km further east than ground reconnaisance can demonstrate. The Cretaceous sediments of the Koum basin cover only about 75% of the area indicated by published accounts.

In the vicinity of Mayo Djarendi in the eastern end of the basin, two volcanic dikes were observed. Both dikes strike NW-SE (at about 156°). The eastern dike is basalt, and the western is syenite. Sediments close to the dikes are thermally altered. The age of these features is uncertain, though they clearly cannot be older than the Cretaceous sediments they cut. Tillement (1972) mapped these features as faults, an apparent misinterpretation of aerial photographs.

Depositional units

Two clear sedimentary units have been observed in the Koum basin, each areally restricted and relatively well-defined. The Cretaceous sediments of the Koum basin will be referred to in entirety as the Koum formation. The following discussion describes the members of the Koum Formation observed in the field. Figure 5 is a geological sketch map and schematic N-S cross-section of the basin.

Mbissirri Member

The Mbissirri Member occupies the southern portion of the basin, and is composed of fine grained silty mudstones, clay shales, and rare thin limestones. Interbedded thin sandstones are common throughout the member and become coarser-grained near the top. The type section is located on Mayo Mbissirri (south of the village of Mbissirri), along which it is extensively exposed (figure 6). Here the sediments consist of cyclical repetitions of thin ripple and dune cross-bedded sandstones and thicker mudstones. The sandstone-mudstone couplets are typically about ten meters thick. Four thin sandy limestones or marls, one containing fossil conchostracans (locality KB-15; see figure 6; note that locality KB-15 is stratigraphically higher than the measured section) have been observed. Fossil root casts (macroscopic and microscopic) and possible mudcracks occur in the limestone at KB-15. The marls and limestones occur as laterally continuous, light colored beds in the mudstone sequences of the sandstone-mudstone couplets, and range from 5 cm to 40 cm thick.

Muddy sediments compose the majority of the Mbissirri Member at the type section (approximately 60 percent) and are commonly pinkish to dark red in color. In general the

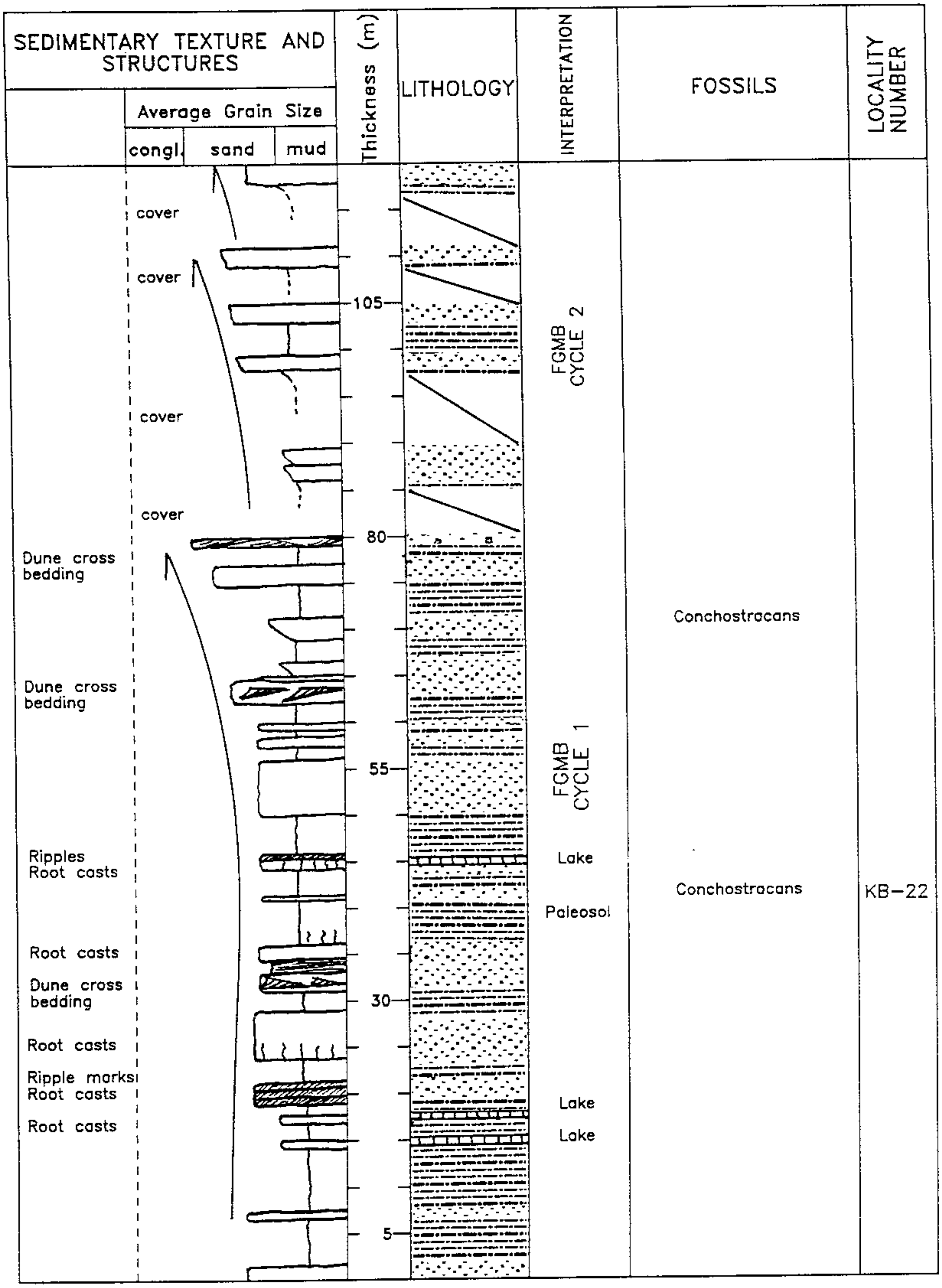


Figure 6. Stratigraphic column of sediments exposed along Mayo Mbissirri, Koum basin, northern Cameroon. Explanation below.

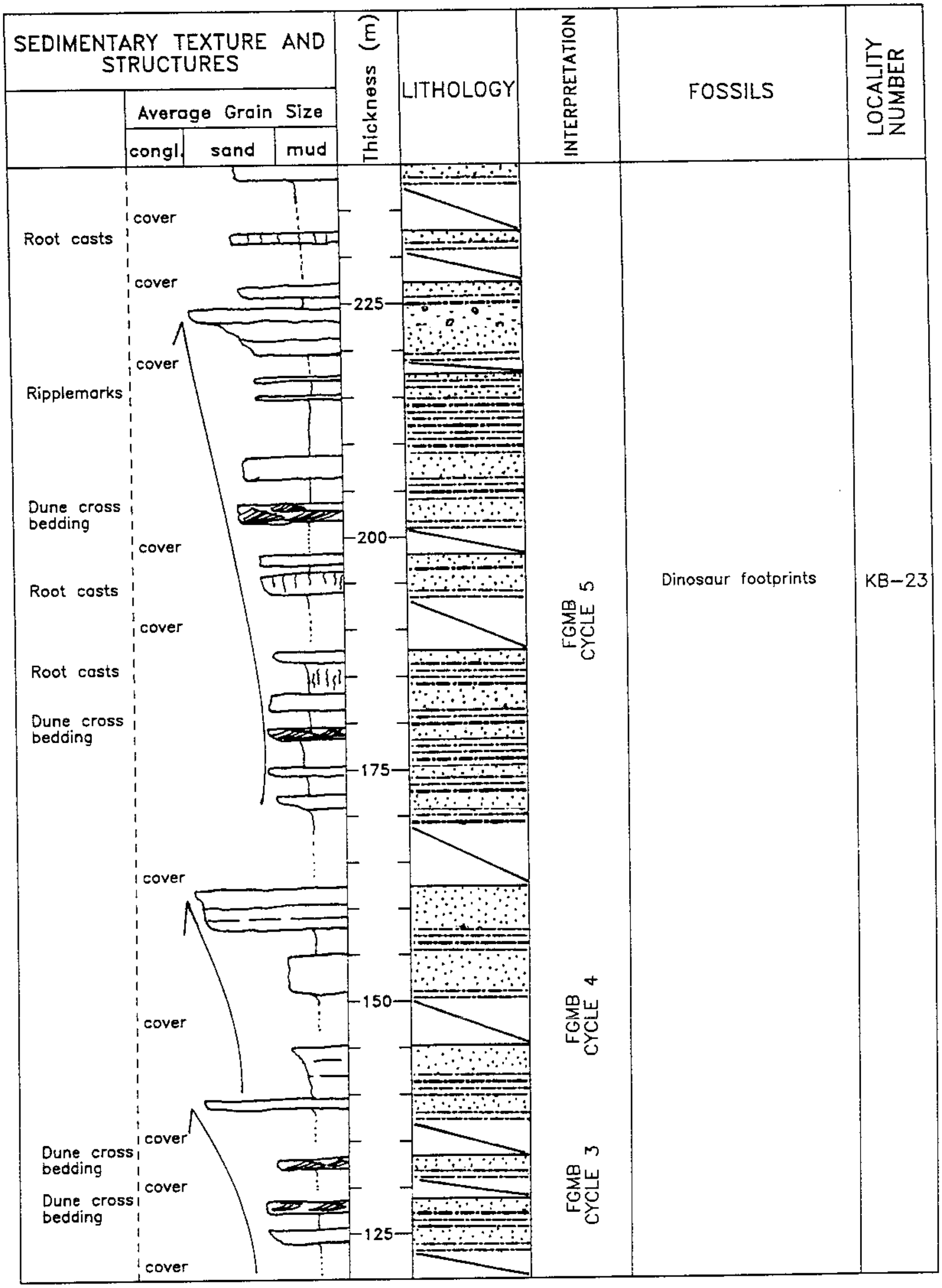


Figure 6 (continued). Stratigraphic column of sediments exposed along Mayo Mbissirri, Koum basin, northern Cameroon. Explanation below.

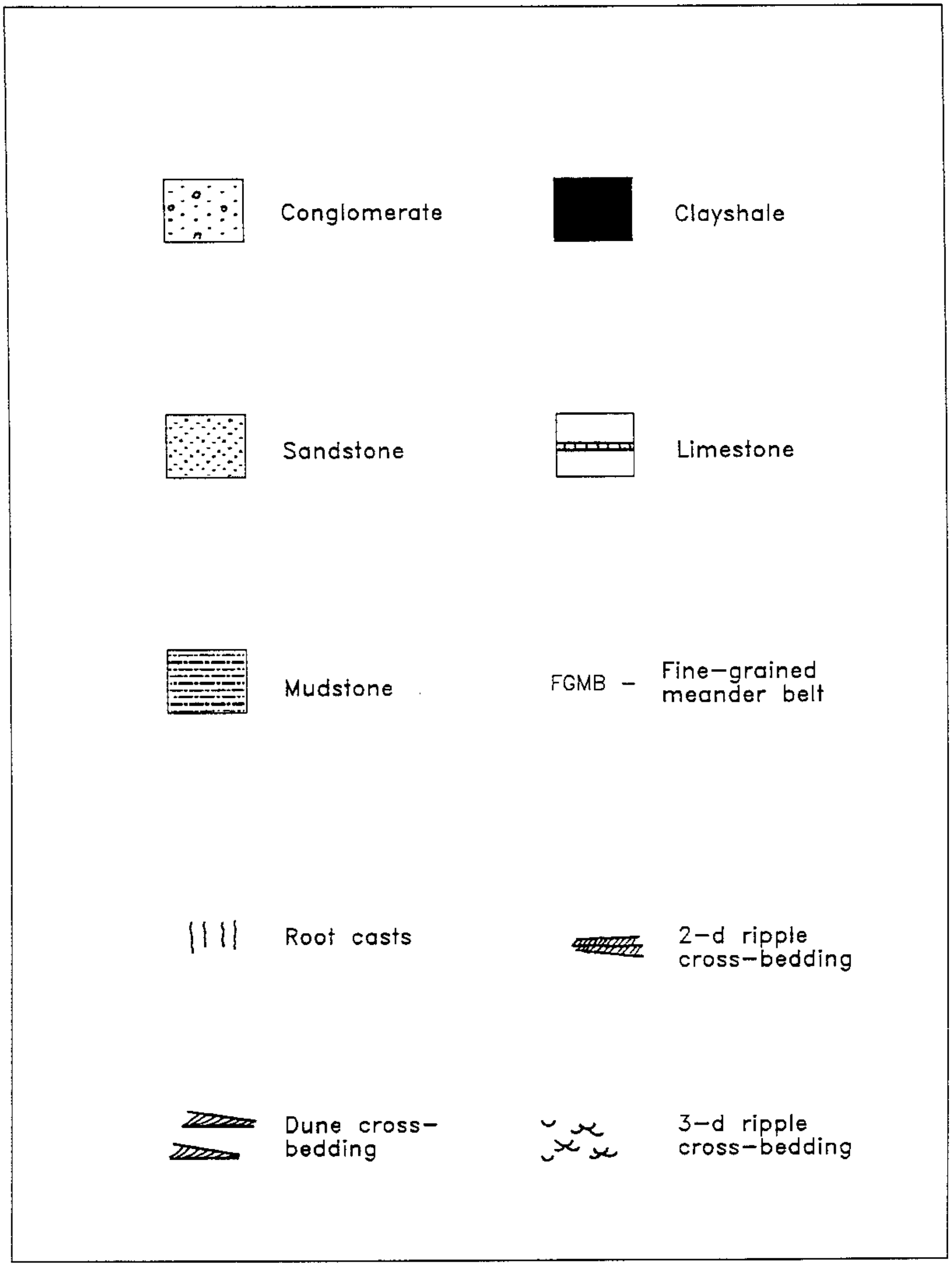


Figure 6 (continued). Explanation of patterns and symbols used in stratigraphic columns.

mudstones are poorly exposed, and when outcropping are deeply weathered.

Fossil root casts are common in the sandstone units; mudcracked surfaces are common in the mudstones and in the finer muddy sandstones; two carbonate-rich horizons containing nodular limestone concretions are present in the Mbissirri region, and are interpreted as possible paleosols. All the well-documented fossil footprint localities of the Koum basin occur in sandstones of the Mbissirri Member (KB-3, KB-17, KB-18, KB-23). Paleocurrents measured from ripples at KB-17 and KB-18 (18 km west of the type section) show a consistent southeasterly current direction.

Other good exposures of the Mbissirri Member are found in the bed of the parallel stream to the west of Mayo Mbissirri and to the south and west of Rhinoceros Camp (5 km south of the village of Koum). This member is also well exposed in the bed of the Mayo Rey south of Ntham, where the Ntham-Touboro road crosses the river (figure 8). Here the sediments are predominantly red silty mudstones with occasional laminated zones and mudcracked surfaces. Silica-cemented indurated horizons up to about 50 cm thick are common. Two thin (10-30 cm thick) parallel-laminated green clay shale horizons are found near the top of the outcrops near Ntham. The laminae are alternating light and dark layers less than 0.5 mm thick. They contain carbonized plant fragments and rare fragments of turtle carapace (locality KB-11).

The rocks of the Mbissirri member suggest a suite of lacustrine and aggraded meandering stream sediments that were part of a fine-grained meander belt. Possible lacustrine sediments found in the Ntham area (KB-11) consist of alternating light and dark thinly laminated clay shales containing plant and turtle fossils. Other possible lacustrine facies are seen in the Mayo Mbissirri section, and are represented by thin limestones, one of which contains fossil conchostracans. Deposits that can be attributed to meandering stream deposits are best developed in the Mbissirri area. Specific criteria that suggest a meandering stream origin for these include dune-size trough cross-bedded sandstones and occasional pebble conglomerates that may represent channel and point bar facies, overlain by finer-grained ripple laminated sandstones.

Sediments that possibly represent overbank silts overlie the sandstones and contain abundant rootlet structures and occasional paleosols as well as mudcracked surfaces. The paleosols contain carbonate nodules similar to modern caliche soils. Paleosols might be expected to develop during periods when the stream channel was on a distant part of the floodplain, when soil-formation processes could work uninterrupted for long periods. Within the overbank silts are occasional thin ripple laminated and occasional dune cross-bedded sandstones (generally about 30 cm thick) that possibly represent crevasse splays from a nearby stream channel.

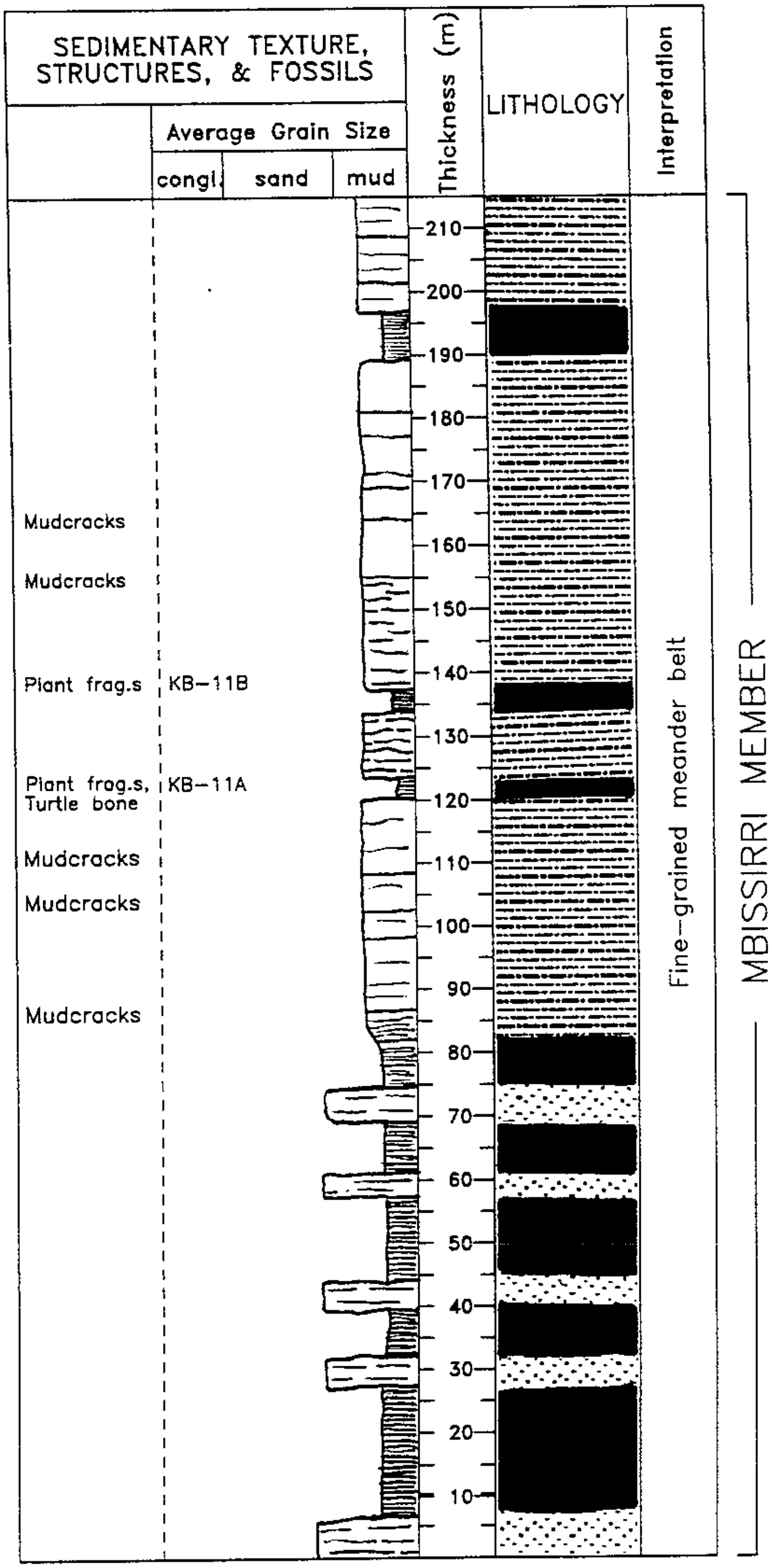


Figure 7. Stratigraphic column of sediments exposed near Ntham, Koum basin, northern Cameroon. Modified from Tillement (1972). See figure 6 for explanation.

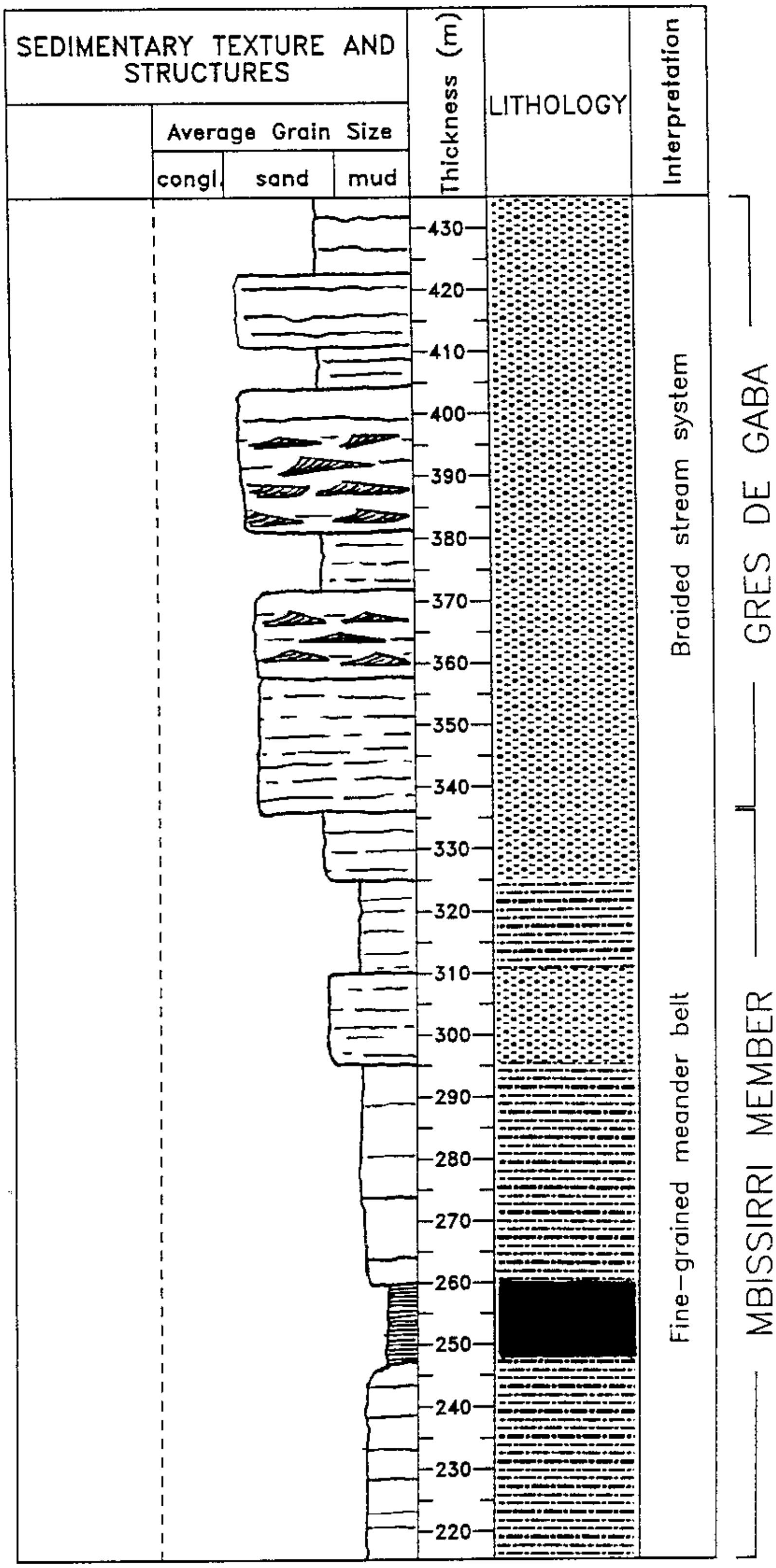


Figure 7 (continued). Stratigraphic column of sediments exposed near Ntham, Koum basin, northern Cameroon. Modified from Tillement (1972). See figure 6 for explanation.

Overall, the Mbissirri Member coarsens upward. Toward the top of the type section, coarser sandstones and pebble conglomerates are found, suggesting an increase in sediment transport energy. The upper contact of the Mbissirri Member is gradational with the overlying conglomeratic Grès de Gaba Member in the Mayo Mbissirri area (the contact zone is approximately 100 meters above the top of the type section).

Grès de Gaba Member

The Grès de Gaba (figure 8) is distributed along the northern margin of the basin, and was named and briefly described by Tillement (1972). It was named for exposures along the mayo near the village Gaba in the western end of the basin. No type section was designated by Tillement (1972). The Grès de Gaba is best exposed south of the village Mayo Djarendi near where the rivers Mayo Rey and Mayo Djarendi have their confluence, in the eastern end of the basin. These sediments are medium to coarse grained dune trough cross-bedded arkosic sandstones and pebble to cobble conglomerates (locally boulder conglomerate in the far northeast end of the basin) with interbedded occasionally mud-cracked thin siltstones, rare thin marly mudstones, and calcite-cemented mudstones that are possibly paleosols. They are considered pedogenic because of their nodular character, the presence of rootcasts, and the presence of trace fossils that resemble insect larval cases. Lithic clasts found in the conglomerates are commonly

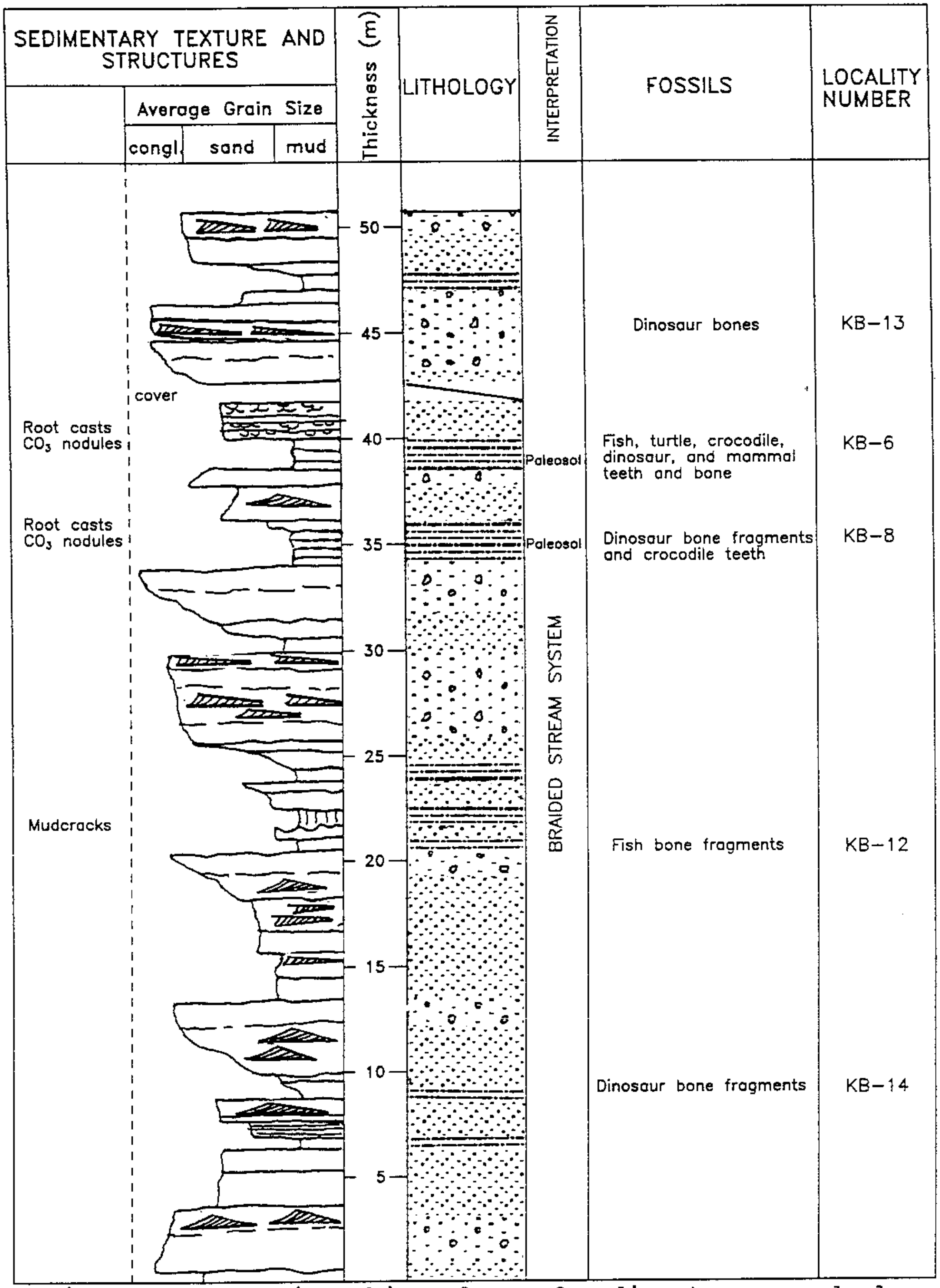


Figure 8. Stratigraphic column of sediments exposed along Mayo Djarendi, Koum basin, northern Cameroon. See figure 6 for explanation.

granitic, and probably were transported into the basin from the nearby Precambrian metamorphic terrain. Several bone-bearing fossil localities have been found in the Grès de Gaba in the vicinity of Mayo Djarendi, notably KB-6, KB-8, and KB-13. KB-6 and KB-8 are located immediately below paleosol horizons; KB-13 lies in a conglomerate characterized by imbricated clasts.

The Grès de Gaba possibly represents a coarse-grained, braided fluvial system in the vicinity of Mayo Djarendi, where it may have been part of the distal reaches of an alluvial fan. To the north of Mayo Djarendi, where the Mayo Djarendi-Madingrin road crosses the boundary fault, very poorly sorted accumulations of angular granitic clasts up to 40 cm in diameter were observed in the Grès de Gaba just south of the fault. It is unclear whether these sediments were deposited as colluvium along the fault scarp or whether they were transported by fluvial processes on an alluvial fan.

Geologic History and Interpretation

The Koum basin is a half-graben; motion on the major northern boundary normal fault allowed sediment to accumulate as the hanging wall block subsided. Coarse-grained sediments accumulated close to the fault as colluvium and braided stream deposits associated with alluvial fans (represented by the Grès de Gaba Member), while simultaneously, fine-grained sediments accumulated in the meander belt region nearer the center of the basin (represented by the Mbissirri Member).

The sequence of a minimum of about twenty fining-upward sediment packages in the Mbissirri Member along Mayo Mbissirri suggests that a vertically aggrading fine-grained meander belt system was responsible for their deposition. This fluvial system occupied the low-gradient region in the center of the Koum basin during the Early Cretaceous. The fining-upward packages appear to be grouped into five larger-scale coarsening-upward cycles on the order of 25 to 65 meters in thickness (see figure 7). These cycles may possibly be related to periods of activity on the northern normal boundary fault: As basin filling during periods of relative tectonic quiescence progressed, progradation of coarser sediments into the basin center proceeded without interruption; periods of activity on the fault that caused basin-floor subsidence then trapped coarser sediments close to the fault margin, "starving" the central basin of the coarser fraction and allowing a proportionately greater amount of finer sediments to accumulate in the basin center. At least five cycles of activity and quiescence are recorded in the Mbissirri Member. Similar trends are not as easily seen in the Grès de Gaba Member, partly because the measured section in this member is only 50 meters thick. However, the presence of two paleosols in the Mayo Djarendi section (immediatly overlying localities KB-6 and KB-8) possibly represent periods when the the braided stream channel was distant from those sites, allowing pedogenic processes to occur. Grain-size increases over the entire thickness of the Mbissirri Member. This gross coarsening-upward trend may represent progradation of the sediment source toward the basin center, an occurrence expected during the filling of the basin.

Leeder and Gawthorpe (1987) provide models for sedimentation in which facies distributions correspond to internal or axial drainage of half-grabens. In the internal drainage model (figure 9a), sedimentary facies are essentially limited to marginal alluvial fans and central playa lakes. Axially-drained half-grabens (figure 9b) show a broader range of facies, from marginal fans to axial meandering stream complexes (with channel, overbank, and pond sediments). The Koum basin, with its diversity of depositional facies, fits the latter model better.

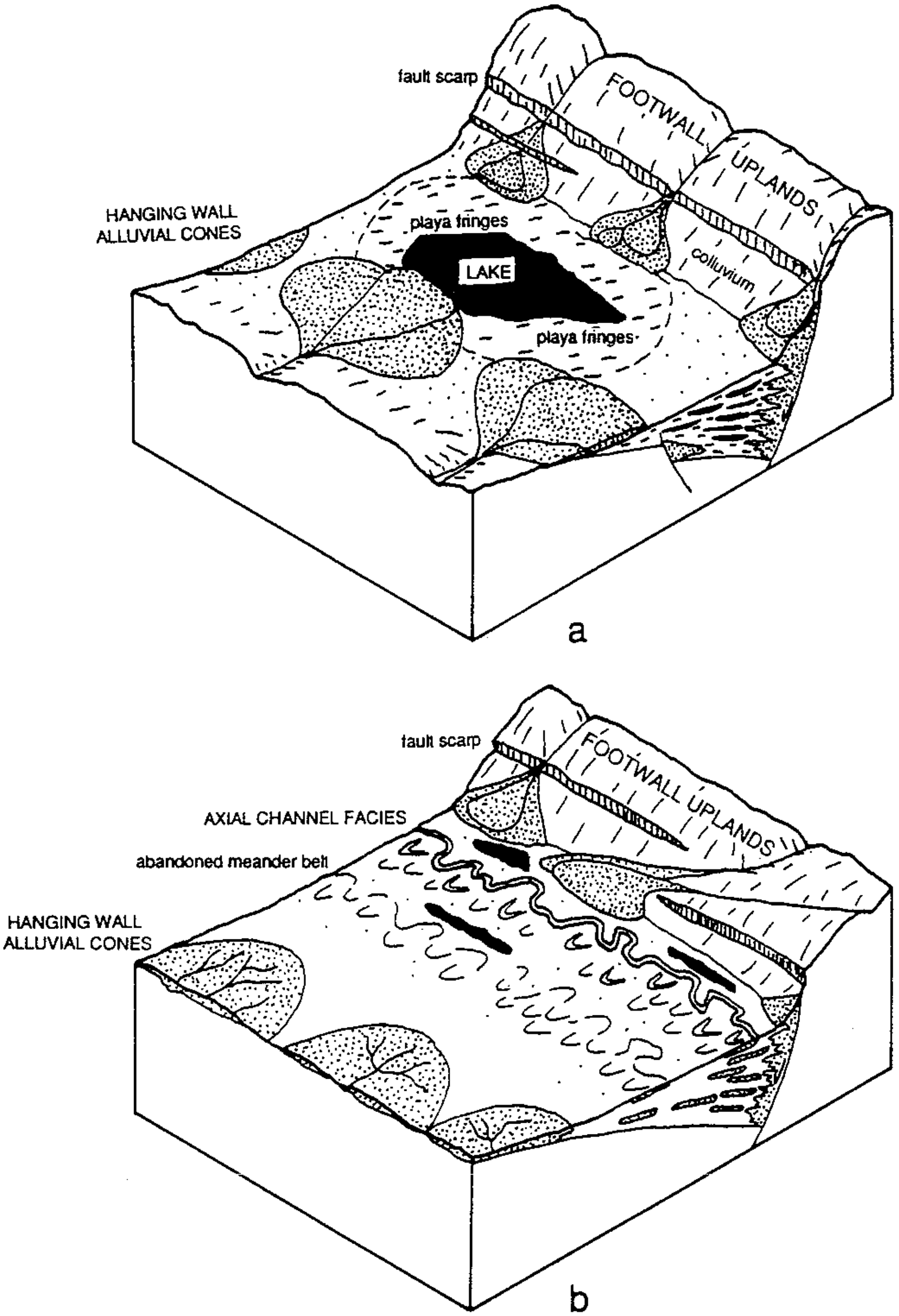


Figure 9. Block diagrams showing major sedimentologic features of half-graben continental basins. a - interior drainage model; b - axial-through drainage model (redrawn from Leeder and Gawthorpe [1987]).

CHAPTER III

SYSTEMATIC PALEONTOLOGY

General Remarks

Archosaurian reptiles from the Koum basin are described in this section. The anuran material from Mayo Djarendi will be described elsewhere. The mammalian material has been previously described by Brunet, Jacobs, *et al.* (1988) and Jacobs *et al.* (1988).

Koum basin specimen numbers have the prefix CAM. They will be permanently housed in Cameroon. Comparative specimens from northern Malawi have the prefix MAL, and will be housed in Lilongwe, Malawi. The following abbreviations are used for institutions where other comparative specimens utilized in this study are housed: AMNH - American Museum of Natural History (New York); MNHN - Muséum National d'Histoire Naturelle (Paris); SMU - Southern Methodist University, Shuler Museum of Paleontology (Dallas); UCMP - University of California, Museum of Paleontology (Berkeley); USNM - United States National Museum of Natural History (District of Columbia).

Phylum Vertebrata
Class Reptilia
Subclass Archosauria
Order Crocodylia
Suborder Mesosuchia
Infraorder Notosuchia
Family Uruguaysuchidae
Genus *Araripesuchus*, PRICE 1959
cf. *Araripesuchus wegeneri* BUFFETAUT 1981

Referred material: CAM 101-299, 321, 330-344 (isolated teeth).

Locality: KB-6 and KB-8, near Mayo Djarendi, Koum basin, northern Cameroon.

Description: Small symmetrical ovate-acuminate, asymmetrical ovate-lanceolate, lingulate to conical teeth ranging from 0.8 to 3.8 mm in mesiodistal length, 0.5 to 2.8 mm in labial-lingual length, and 0.8 to 5.5 mm in height (figures 10-12; appendix 1). Appressed margins with well developed carinae, commonly serrate (ziphodont). On serrated teeth, denticles number from 13 to 43 per tooth. Denticle number is dependent on tooth size, larger specimens having more denticles than smaller ones (figure 10b). A strong central "cusp" comprises the tip of the tooth, and is morphologically distinct from the marginal serrations. The lingual and labial faces of the teeth are rugose, characterized by irregular wavy longitudinal ridges and striae which terminate before reaching the tooth margin. The degree of rugosity is variable on serrated teeth, but all specimens have it. The conical teeth are without exception ridged; the lingulate morphology is smooth on the labial side, but bears two shallow grooves on the lingual face. The ridges and striae found on the serrated teeth are in all but a few cases developed independently from the marginal serrations, whose placement on the carina is unrelated to the terminations of the ridges and striae.

Four distinct morphologies of cf. *Araripesuchus* teeth are recognized in the Koum basin sample (figure 10a; figure 11a-d; table 2). These morphotypes originate from different parts of the jaw, and reflect heterodonty in the animal's dentition. *Araripesuchus* shows a range of blade-like leaf-shaped teeth through conical teeth. A similar range of morphological variation is seen in the maxilla of the type specimen of *Theriosuchus pusillus* (BMNH 48330), a brevirostrine crocodile from the uppermost Jurassic (Purbeck Formation) of Great Britain. *Theriosuchus* has teeth which are similar in overall form to those of cf. *Araripesuchus* (see discussion below).

Morphotype 1 (figure 12a) is symmetrical and ovate-acuminate in form. It is inferred to come from the posterior of the tooth row. Morphotype 2 (figure 11b) is clearly similar in form to morphotype 1, but is asymmetrical and in general more lanceolate than 1. It comes from a more anterior (proximal) part of the jaw. Morphotype 3 (figure

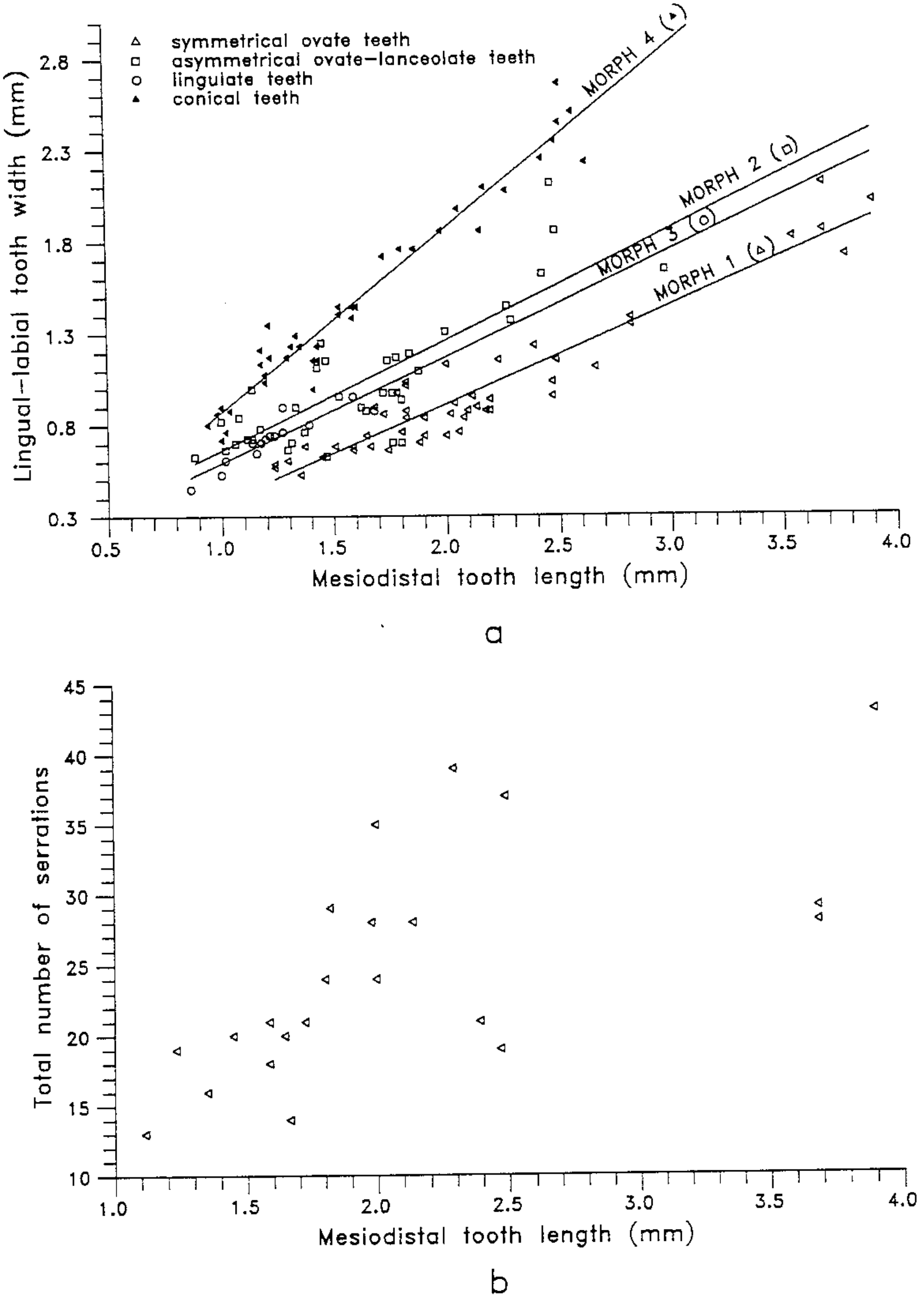


Figure 10. Scatter plots for teeth of cf. *Araripesuchus wegeneri* from Cameroon. See text for explanations.

11c) is lingulate and symmetrical, and is incisoriform. It is devoid of any marginal serrations. It is relatively rare, and its position may be at the very front of the snout. Morphotype 4 (figure 11d) is a conical morphology more typical of crocodilians. It is moderately compressed laterally. The lingual face is smaller than the labial face, because the carinate margin is lingual to the leading and trailing edges of the tooth. The equivalent morphotype is found immediately behind caniniform teeth in the type specimen of *Theriosuchus pusillus*, and directly in front of the morphotype 2 equivalent tooth type. These tooth morphotypes all have crowns which are incurved lingually; morphotype 2 shows the greatest degree of curvature, morphotype 3 the least.

Figure 10a is a bivariate plot of mesiodistal tooth length and lingual-labial tooth width for the four tooth morphotypes attributed to cf. *Araripesuchus*. Morphotypes 1, 2, and 3 cluster together into a distinct group. Morphotype 4 falls into a distinct cluster. The slopes of the regression lines defining the first three morphotypes (teeth which are strongly compressed laterally) fall between 0.5 and 0.6, indicating that mesiodistal tooth length increases at about twice the rate of lingual-labial tooth width; large teeth are relatively longer than small teeth. For the conical morphotype 4, the slope of the regression line approximates unity, meaning that for larger teeth, the mesiodistal and lingual-labial tooth proportions are maintained.

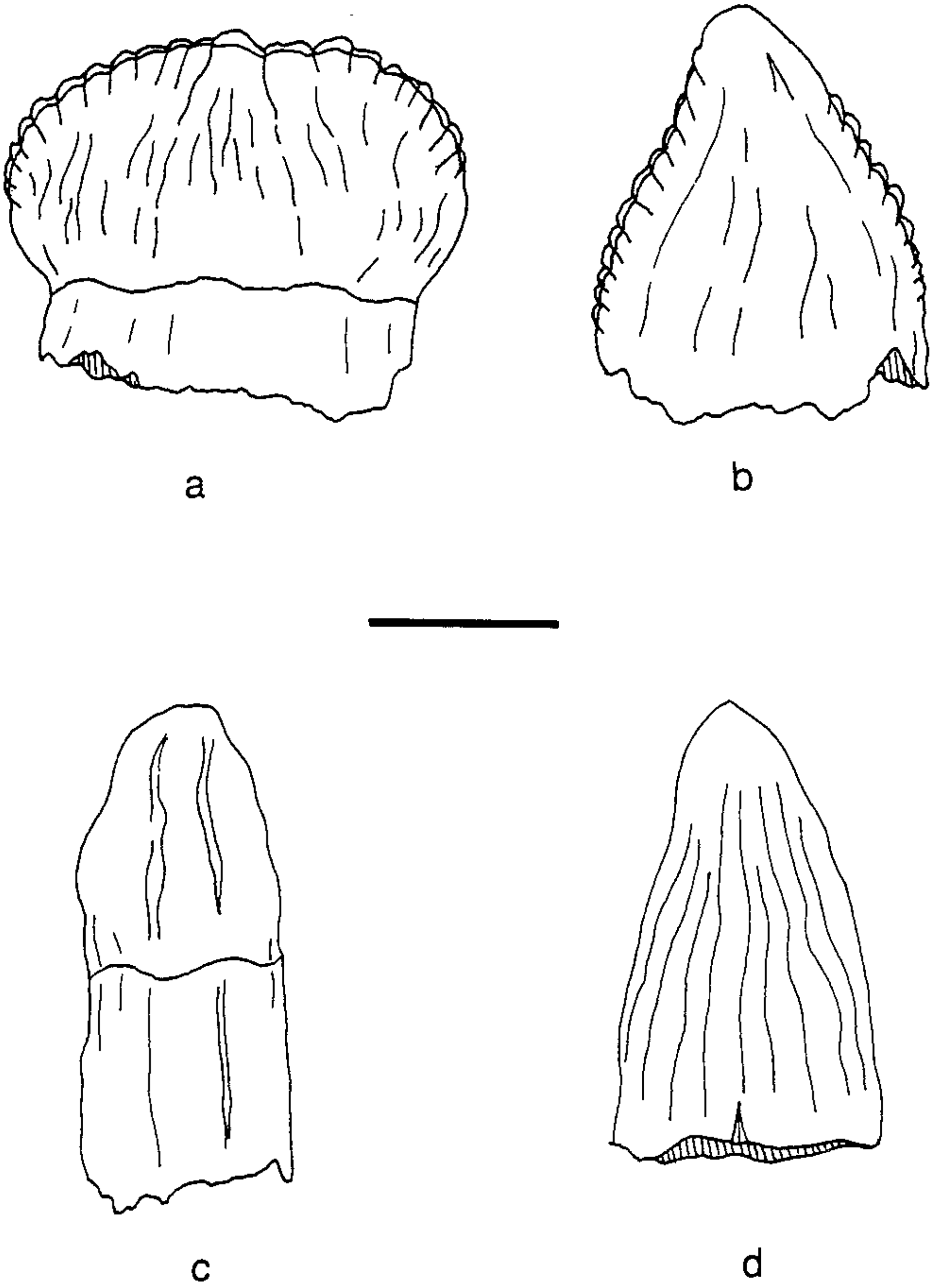


Figure 11. Teeth of cf. *Araripesuchus wegeneri* from locality KB-6, Koum basin, northern Cameroon, in lingual view: a - morphotype 1 (CAM 151); b - morphotype 2 (CAM 126); c - morphotype 3 (CAM 226); d - morphotype 4 (CAM 174). Scale bar = 1 mm.

Table 2.--Descriptive statistics for cf. *Araripesuchus wegeneri* teeth from localities KB-6 and KB-8, Koum basin, northern Cameroon.

Morphotype 1

Variable	N	$\bar{X}$	S	Min. Value	Max. Value	Range
Mesio-distal length	50	2.14	0.74	1.17	4.34	3.17
Lingual-labial width	62	1.00	0.36	0.53	2.11	1.58
Crown height	53	1.84	0.59	0.90	3.91	3.01
Denticle number	19	22.74	8.85	0.00	43.00	43.00

Morphotype 2

Variable	N	$\bar{X}$	S	Min. Value	Max. Value	Range
Mesio-distal length	35	1.65	0.49	0.88	2.97	2.09
Lingual-labial width	41	1.09	0.36	0.63	2.11	1.49
Crown height	19	2.44	0.79	1.15	4.46	3.31
Denticle number	22	5.00	11.85	0.00	39.00	39.00

Table 2 (continued).--Descriptive statistics for cf. *Araripesuchus* sp. teeth from localities KB-6 and KB-8, Koum basin, northern Cameroon.

Morphotype 3

Variable	N	$\overline{X}$	S	Min. Value	Max. Value	Range
Mesio-distal length	14	1.23	0.22	0.86	1.68	0.82
Lingual-labial width	16	0.75	0.15	0.45	0.98	0.53
Crown height	14	1.37	0.24	0.80	1.64	0.84
Denticle number	13	0.00	0.00	0.00	0.00	0.00

Morphotype 4

Variable	N	$\overline{X}$	S	Min. Value	Max. Value	Range
Mesio-distal length	38	1.66	0.52	0.94	2.62	1.68
Lingual-labial width	39	1.52	0.52	0.76	2.66	1.90
Crown height	20	2.79	1.09	1.13	5.52	4.38
Denticle number	44	0.00	0.00	0.00	0.00	0.00

Discussion: Isolated small crocodilian teeth which are laterally compressed and serrated are the most numerous dental remains found at the KB-6 site. These teeth are referred to cf. *Araripesuchus wegeneri* because of their close correspondence to the teeth in a small crocodilian skull recovered from the Aptian Gadoufaoua locality in Niger (*Araripesuchus wegeneri*) and described by Buffetaut and Taquet (1979) and Buffetaut (1981). The type locality for *Araripesuchus* is in the late Aptian Santana Formation in northeastern Brazil (Buffetaut and Taquet 1979; Buffetaut 1982a, 1985; see also Price 1959). The skull recovered from Niger resembles the specimens described by Price (1959) in being about the same size and having a short and broad snout as well as a flaring of the maxillae behind their junction with the premaxillae, among other characters (Buffetaut and Taquet 1979; Buffetaut 1981). The African specimen is distinct because of its differently shaped antorbital fenestra and because the third premaxillary and third maxillary teeth are enlarged (Buffetaut and Taquet 1979; Buffetaut 1981). Unfortunately, the dentition of the South American *Araripesuchus* material is undescribed.

The features that best serve to characterize the teeth of *Araripesuchus wegeneri* are seen on photographs of the type specimen, made before it was damaged by acid preparation (figure 12). The type specimen had three teeth prepared sufficiently to describe. Notable characters include: (1) the leaf-shape of the teeth, strongly

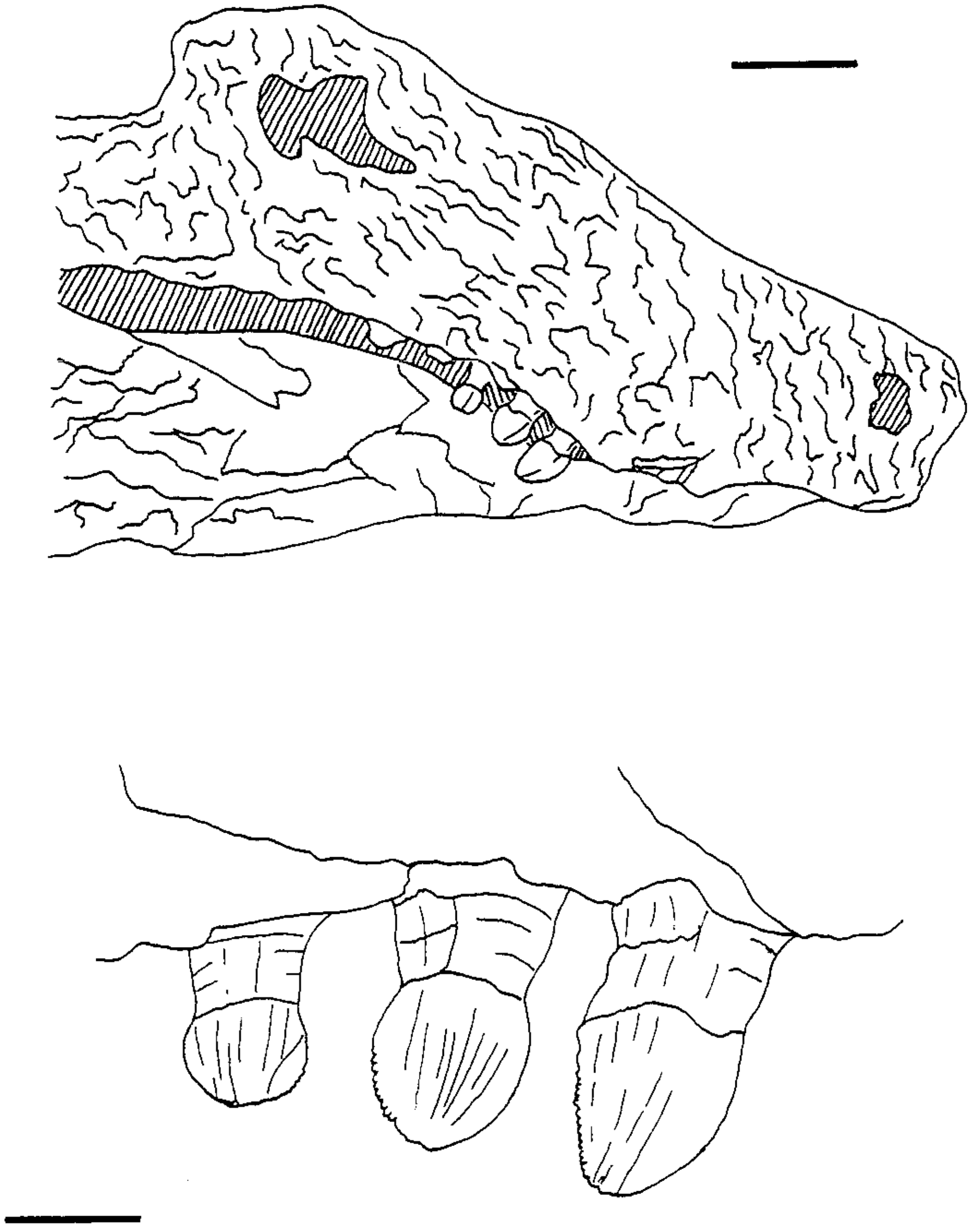


Figure 12. Type specimen of *Araripesuchus wegeneri* (MNHN GDF 700) from Gadoufaoua, Niger. a - lateral view of right side of skull. b - detail of right side maxillary dentition. Scale bar for a = 2 cm; b = 5 mm.

compressed in the lateral direction; (2) rugose labial faces of the teeth, causing them to appear to be striated; (3) strong serrated carinae along the margins of the teeth. The serrations are developed independently from striae found on the labial faces. These three characters as well as the size of the teeth serve to unite the isolated dental remains from KB-6 with the Gadoufaoua specimen.

The Gadoufaoua teeth are slightly larger than the majority of the teeth from Cameroon, but fall within the range. The posterior teeth of South American *Araripesuchus* that are preserved in an undescribed skull at the American Museum of Natural History are (like their African counterparts) laterally compressed, but do not have any striations on the labial face (Jacobs *et al.* 1990). Isolated laterally compressed crocodilian teeth from the Santana Formation and attributed to *Araripesuchus* lack marginal serrations (de Broin, oral communication). It is clear that, on the basis of dental remains, the *Araripesuchus* material from the African side of the Atlantic belong to (at least) a different species, and that the specimens from northern Cameroon are comparable to *Araripesuchus wegeneri*.

A crocodile tooth morphotype similar to the Koum basin cf. *Araripesuchus* is known from the Lower Cretaceous of Malawi in southeastern Africa (Jacobs *et al.* 1990). Like the Cameroon material, the teeth are laterally compressed and possess a carina with serrations. The size of the

Malawi material is comparable to the Cameroon teeth, though the sample mean is less than the sample mean for the Cameroon and Niger material (appendix 1; figure 13). Differences include a total lack of striations and ridges on the lingual and labial tooth faces. Except for the lack of striations, the sample from Malawi is indistinguishable from that of Cameroon.

The cf. *Araripesuchus* teeth from northern Cameroon also resemble small, laterally compressed atoposaurid crocodile teeth from the middle Purbeck of Durdleston Bay near Swanage, Great Britain, identified as *Theriosuchus pusillus* (Joffe 1967). Several specimens (BMNH 48251, 48328, and 48330) are leaf-shaped teeth with strong lateral compression and the development of a prominent serrated marginal carina. Unlike *Araripesuchus*, the serration of the carina results from ridges and striations on the lingual and labial tooth face extending to the margin of the tooth. The type specimen of *Theriosuchus pusillus* (BMNH 48330) is a skull with most of the dentition preserved. The morphology of the teeth changes from peg-like cones at the front of the jaw to slightly laterally compressed caniniforms further back; following the caniniform teeth are slightly curved conical teeth that closely resemble the morphotype 4 cf. *Araripesuchus* teeth described above; still further back the teeth become progressively more leaf-shaped, changing from laterally compressed pointed lanceolate teeth (morphotype 2) to laterally compressed teeth more squat and ovate in

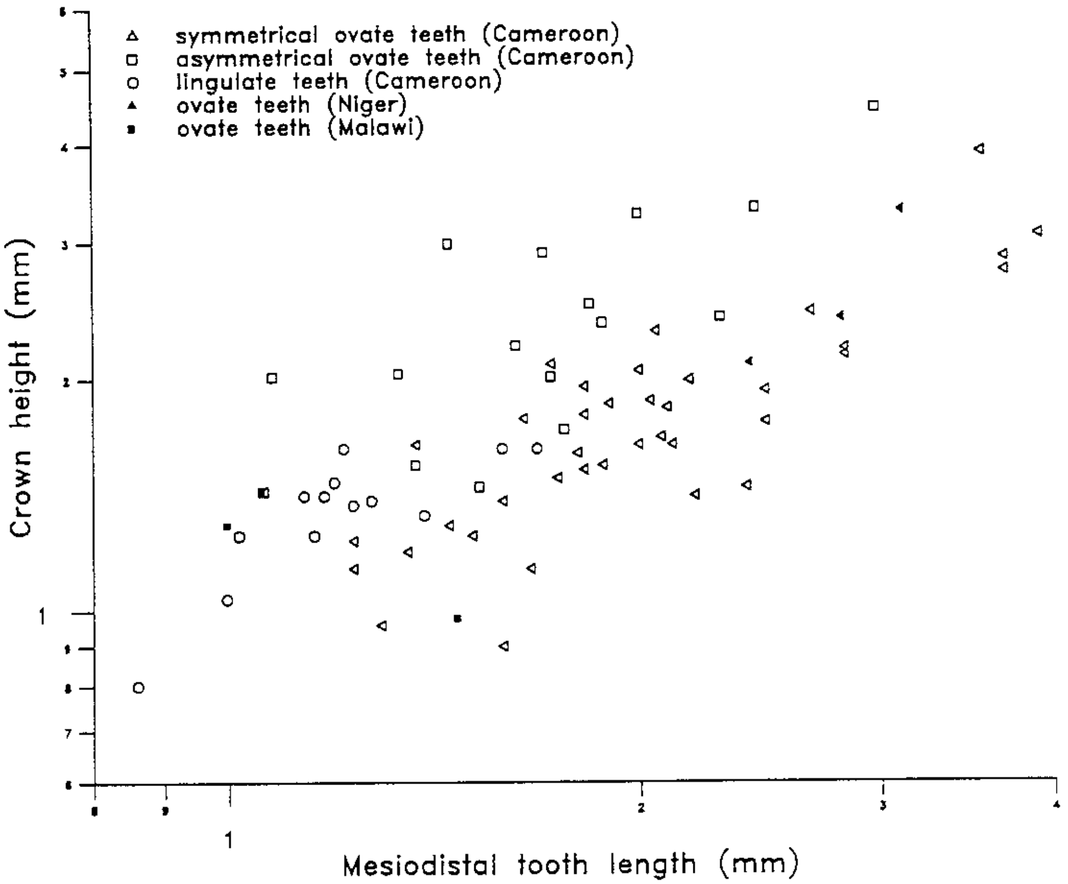


Figure 13. Scatter plot of teeth of cf. *Araripesuchus wegeneri* from Cameroon, Malawi, and Niger. See text for explanation.

outline (morphotype 1). The cf. *Araripesuchus* and *Theriosuchus* teeth are similar to those described by Buffetaut and Ford (1979) from the Wealden of the Isle of Wight and attributed to *Bernissartia*, though the teeth of *Bernissartia* are not strongly compressed in the lateral direction, and are tribodont (button-shaped). This difference distinguishes the teeth of *Bernissartia* from those of *Theriosuchus* and cf. *Araripesuchus* from Africa. The difference distinguishing the teeth of both *Bernissartia* and *Theriosuchus* from cf. *Araripesuchus* teeth is that they are not truly ziphodont; *i.e.*, the serrations arise from and are the continuation of surface striations that longitudinally cross the lingual and labial faces of the tooth. The serrations are not an independent feature found only in the carina, as they are in *Araripesuchus wegeneri* and cf. *Araripesuchus*.

Infraorder Sebecosuchia

cf. Sebecosuchia indet.

Referred material: CAM 313, 346-348 (isolated teeth).

Locality: KB-6, near Mayo Djarendi, Koum basin, northern Cameroon.

Description: Robust, symmetrical, short conical teeth, slightly compressed laterally, with finely serrated anterior and posterior carinae. The symmetry of the teeth makes orientation difficult. Serrations extending to the base of the crown on both anterior and posterior margins. Lingual face with subdued longitudinal fluting. All specimens are damaged, and one (CAM 348) has the enamel corroded off. CAM 346 has a small serrated ridge parallel to the normal anterior carina, which is probably an abnormal feature.

Discussion: Ziphodont crocodile teeth of the type described here are problematic in the Early Cretaceous of Africa. Similar teeth, attributed to a ziphodont mesosuchian, are known from the Eocene of Algeria (Buffetaut 1982b). Ziphodonty was used by Langston (1956) and Buffetaut (1982b, 1982c) to unite fossil crocodiles from spatially and temporally disparate localities, assuming that ziphodonty has evolved only once among the Crocodylia. However, it is clear that ziphodonty evolved within the Notosuchia, as seen in *Araripesuchus*, separate from sebecosuchians. The occurrence of conical ziphodont teeth in the Early Cretaceous of Cameroon constitutes the oldest record from Africa (see also Buffetaut 1982b, 1982c). Table 3 compares published sebecosuchian tooth measurements (Langston 1956) and measurements from photographs of ziphodont mesosuchian teeth (Buffetaut 1982b) with the Cameroon material.

Table 3.--Measurements of sebecosuchian crocodile teeth from South America, Europe, and Africa.

Specimen number	Mesio-distal length (mm)	Lingual-labial width (mm)	Maximum preserved height (mm)	Serra-tions/mm (anterior margin)	Serra-tions/mm (posterior margin)
Sebecus sp., (Tertiary, Colombia) (from Langston 1956)					
UCMP 40220	17.60	8.60	42.80	6.0	6.0
UCMP 44564	17.20	9.80	40.00	7.0	5.0
UCMP 44563	16.30	8.60	...	3.0	...
UCMP 44565	12.80	7.90	...	...	4.0
UCMP 41308	14.20	7.00	...	5.5	4.5
UCMP 37877	14.60	6.80	34.80	7.0	7.0
UCMP 44562	...	...	22.50	6.5	5.0
Sebecus icaeorhinus (Eocene, Argentina) (Langston 1956)					
AMNH 3160	8.20	6.90	20.10	8.0	...
AMNH 3160	12.60	6.90	23.70	6.0	5.0
AMNH 3160	9.50	4.70	11.50	5.0	5.0
Pristichampsus rollinati (Eocene, France) (Langston 1956)					
UCMP 43921	6.60	5.00	16.40	8.0	8.0
UCMP 43921	9.90	5.40	18.40	8.4	8.0
UCMP 43921	7.60	4.90	12.50	7.0	8.0
Ziphodont mesosuchian (Eocene, Algeria) (Buffetaut 1982b)					
Figure 1 c&d	12.2	8.8	16.0	...	...
Figure 1 e&f	12.0	9.0	10.0	...	...
cf. Sebecosuchia (Early Cretaceous, Cameroon)					
CAM 313	7.45	...	...	8.3	...
CAM 346	5.72	3.02	5.43	6.9	...
CAM 347	6.52	4.55	6.92	...	5.8
CAM 348	6.92	4.03	6.20	...	...

Order Saurischia

Suborder Sauropodomorpha

Sauropodomorpha indet.

Referred material: CAM 325-329 (isolated teeth).

Locality: KB-6, near Mayo Djarendi, Koum basin, northern Cameroon.

Description: Five isolated fragmentary sauropod teeth have been recovered by quarrying at KB-6. The teeth are elongate slightly curved cylinders. The teeth are curved lingually. Enamel is longitudinally ridged on the lingual side of the teeth; these ridges gradually diminish toward the labial surface, and appear to be better developed near the base of the teeth. One tooth (CAM 313) has most of the crown preserved intact; the top of the crown is compressed laterally, forming a slightly spatulate worn surface. The base of the tooth is cylindrical. The teeth range from 2.17 to 6.68 mm in maximum mesiodistal length, and from 1.77 to 5.07 mm in maximum lingual-labial width (table 4).

Discussion: The sauropod teeth recovered from KB-6 are isolated, fragmentary remains. The teeth have been compared with those from the Early Cretaceous of northern Malawi. They are of similar size, although two Cameroon specimens are smaller than the smallest Malawi tooth. The Cameroon sauropods are morphologically distinct from those of Malawi

Table 4.--Measurements of sauropod teeth from locality KB-6, Koum basin, northern Cameroon.

Specimen number (CAM)	Mesio-distal length (mm)	Lingual-labial width (mm)	Maximum preserved height (mm)
325	5.35	4.83	19.72
326	3.46	2.98	15.06
327	2.17	1.93	5.56
328	2.33	1.77	4.75
329	6.68	5.07	14.09

because they have well-defined longitudinal grooves and ridges on their lingual face, and are less spatulate; all Malawi teeth are slightly spatulate. The teeth of *Brachiosaurus* from the Upper Jurassic of Tendaguru, Tanzania, illustrated in Janensch (1935), are very rugose on all sides and strongly spatulate. The teeth of *Astrodon johnstoni* (usually considered a brachiosaurid) from the Early Cretaceous of Maryland and the District of Columbia (Lull 1911) and Cf. *Astrodon* sp. from the Late Jurassic or Early Cretaceous of South Africa (Rich *et al*. 1983) have roughly cylindrical teeth but with a flattened and spatulate crown. Aff. Camarasauridae material from South Africa is also strongly spatulate and rugose (Rich *et al*. 1983). The non-spatulate and non-rugose character of the Cameroon teeth exclude them from the *Brachiosaurus-Camarosaurus* group. Among diplodocids, *Apatosaurus* teeth figured in Marsh (1895) have extremely flattened and spatulate crowns. Photographs of the teeth of *Dicraeosaurus* from Tendaguru (also a diplodocid) show roughly cylindrical teeth, except for the tops of the crowns, which appear flattened out and spatulate, similar to but more pronounced than CAM 313. The teeth of *Pleurocoelus* (a genus considered by Norman [1985] to be of dubious affinity), figured by Lull (1911) and Rich *et al*. (1983), are similar to the Cameroon teeth by being weakly spatulate and non-rugose. *Pleurocoelus* teeth and the Cameroon material compare well with teeth figured by Janensch (1935, plate 12, figures 19-21 and 24) from Tendaguru, and considered by Janensch to be indeterminate. The Cameroon material is more similar to *Pleurocoelus* and the indeterminate teeth from Tendaguru than diplodocid, camarasaurid, or brachiosaurid teeth.

Suborder Theropoda

Family Spinosauridae

cf. Spinosauridae

Referred material: CAM 320, 322, 349-358, 360 and SMU 72033 (isolated teeth).

Locality: KB-6, near Mayo Djarendi, Koum basin, northern Cameroon.

Description: Longitudinally fluted teeth of small to moderate size with finely serrate posterior margins (figure

14a-c; figure 15). All teeth except CAM 322 and 354 are conical, but slightly compressed laterally, with deep fluting on both faces of the teeth; the crown recurves posteriorly. Mesiodistal length ranges from 4.35 to 7.51 mm, lingual-labial width from 2.23 to 5.59 mm; serration on the anterior carina is present as faint denticulation near the distal end of CAM 355. CAM 360 has a flattened lingual face, smaller than the rounded labial face because the marginal carinae are displaced lingually; it originates from the anterior part of the tooth row by analogy with other theropods. CAM 322 and 354 are smaller, more laterally compressed, and more recurved posteriorly. Mesiodistal length is 5.71 and 2.13 mm, lingual-labial width 1.24 and 1.60 mm in CAM 322 and 354, respectively. Subdued longitudinal fluting is present on the lingual face of CAM 322, and is best developed near the base. CAM 354 displays prominent fluting on the lingual face, less on the labial face. Serrations on the anterior carina in both teeth are absent; posterior margin serrations are fine and weakly developed.

Discussion: These teeth resemble serrated (ziphodont) crocodilian teeth; however, a suite of characters (Langston 1956) discriminate ziphodont crocodile teeth from dinosaur teeth. The dinosaurian characters include: Strongly developed anterior and posterior carinae; better development of serrations on the posterior carina than on the anterior;

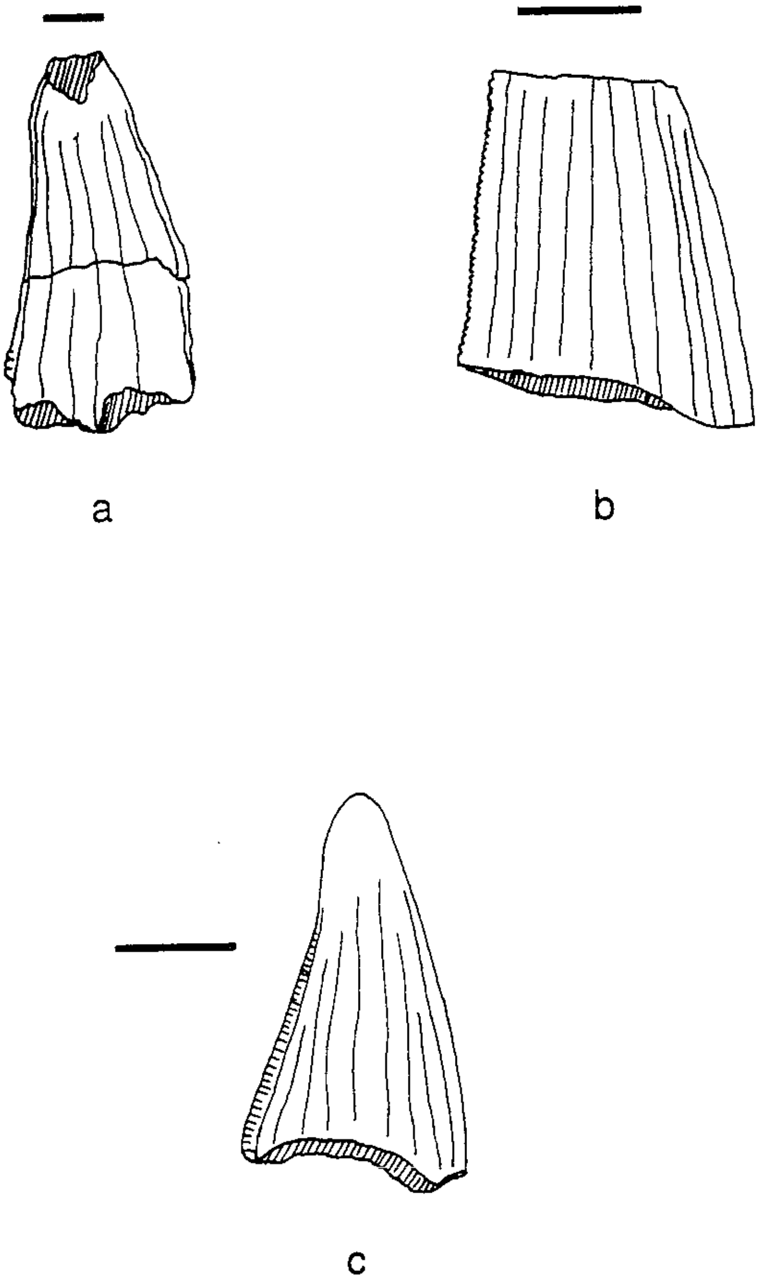


Figure 14. Teeth of cf. Spinosauridae in lingual view from locality KB-6, near Mayo Djarendi, Koum basin, northern Cameroon. a - CAM 162; b - CAM 320; c - CAM 322. Scale bars = 2 mm.

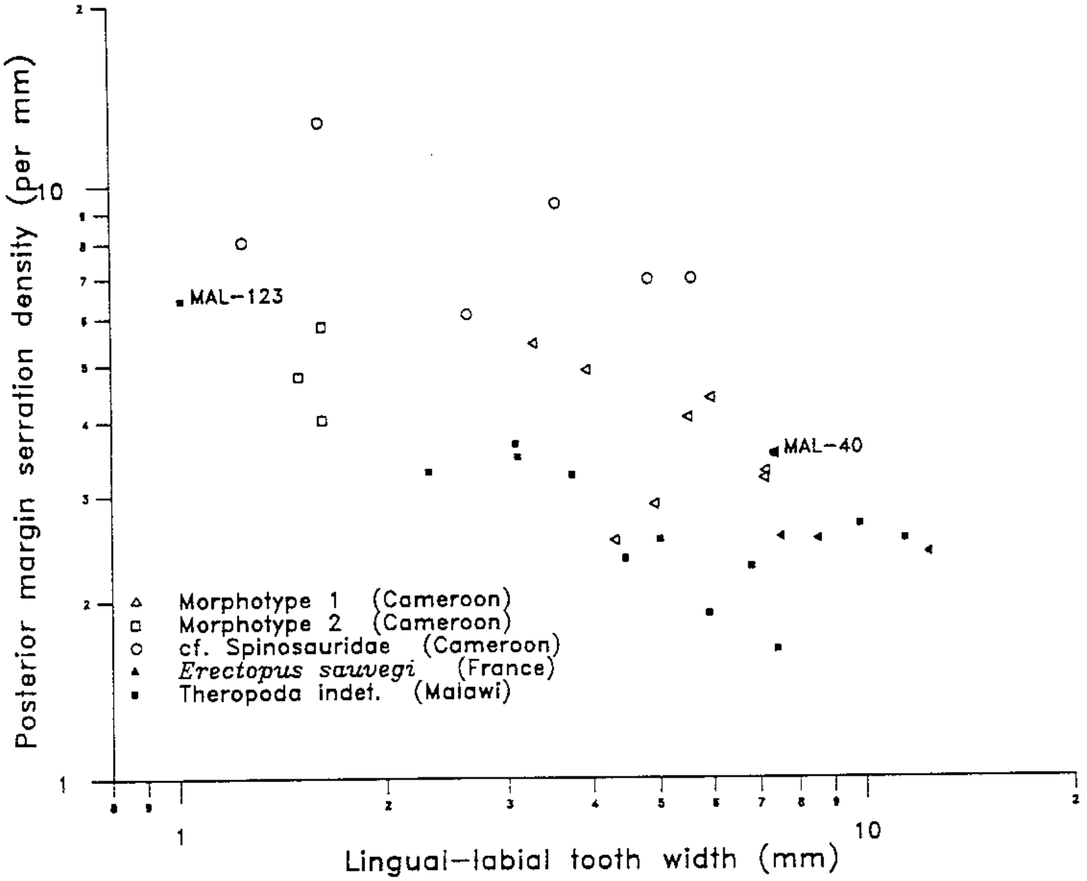


Figure 15. Lingual-labial tooth width versus posterior margin serration density for theropod dinosaur teeth from Cameroon, Malawi, and France.

Table 5.--Measurements of cf. Spinosauridae teeth from locality KB-6, Koum basin, northern Cameroon.

Specimen number	Mesio-distal length (mm)	Lingual-labial width (mm)	Maximum preserved height (mm)	Serra-tions/mm (anterior margin)	Serra-tions/mm (posterior margin)
320	7.51	5.59	8.07	....	6.98
322	5.71	1.24	8.94	....	8.05
350	5.31	4.31	7.73	....	....
351	6.20	4.83	12.32	....	6.97
354	2.13	1.60	3.33	....	12.78
355	4.35	3.54	11.27	....	9.33
356	....	....	....	....	....
357	....	....	....	....	....
358	2.80	2.23	4.11	....	....
360	5.07	2.62	8.21	....	6.08

leading margin of tooth longer than trailing margin, resulting in posterior curvature of the crown; greater lateral compression of the tooth; leading edge thicker than trailing edge in cross section; anterior teeth with marginal carinae displaced lingually. The Cameroon material has these characters and is referred to the Theropoda. It is referred to the Spinosauridae as outlined below.

Buffetaut (1989) notes that Stromer's (1915) original description of the type material indicates no serrations on the teeth, which bear well-developed longitudinal ribs and anterior and posterior carinae. The teeth are less compressed than the teeth of other theropods. The material described by Buffetaut (1989) includes a maxillary fragment with one functional tooth and several replacement teeth, all of which are poorly preserved. The functional tooth bears anterior and posterior carinae, but no evidence of serrations; it therefore agrees with the type material described by Stromer (Buffetaut 1989).

Spinosaurus material from Gadoufaoua, Niger, was described in detail by Taquet (1984). Two functional teeth preserved in a lower jaw are slightly compressed, smooth, and have serrate carinae. Despite the difference in the teeth, Taquet (1984) considered the Gadoufaoua material as probably closely related to Egyptian *Spinosaurus*. One of the Cameroon teeth (CAM 321) compares well to this description, but has subdued ribbing on the lingual face. A second specimen (CAM 320) has well developed ribbing on both the lingual and labial surfaces, and except for its serrate carina, more closely agrees with the *Spinosaurus* material described by Buffetaut (1989).

Buffetaut (1989) noted that *Baryonyx*, a theropod from the Wealden of Great Britain, is probably a close relative of *Spinosaurus*, based on characters of the teeth and jaws. *Baryonyx* has teeth only slightly compressed laterally, and with anterior and posterior carinae finely serrated. These features recall those described in the *Spinosaurus* material from Gadoufaoua, as well as the Cameroon teeth.

Isolated slightly compressed elongate fluted teeth without serrations and attributed to the Spinosauridae have been described from the Albian of Tunisia (Bouaziz *et al.* 1988) and the Late Jurassic of Thailand (Buffetaut and Ingavat 1986). If the Thai fossils are truly spinosaurid, the family Spinosauridae was widely distributed in both space and time.

A single isolated tooth from the Dinosaur Beds of northern Malawi (MAL-40) and assigned by Jacobs *et al.* (1990) to the order Crocodylia closely resembles cf. Spinosauridae material from the Koum basin. Similarities include broad fluting of the lingual and labial tooth surfaces as well as serrations on the posterior carina (the anterior carina is damaged). The tooth is only slightly compressed laterally, and is conical in overall shape. It differs from the Cameroon material by being larger and having a lesser posterior margin serration density. It also is slightly more hooked lingually, though this is not strongly pronounced.

Isolated theropod teeth from Tendaguru, Tanzania, attributed to *Labrosaurus stechowi* (Janensch 1925, plate 10, figures 1-6), have well developed fluting on their lingual faces. One tooth (type C) is conical and reminiscent of a crocodilian; the other teeth are compressed laterally and more closely resemble 'typical' theropod teeth. These teeth have posterior margin serrations better developed than on the anterior margins. Isolated teeth from the Upper Jurassic-Early Cretaceous "Continental intercalaire," assigned by Lapparent (1960) to *Elaphrosaurus iguidiensis* (a coelurid), bear fine longitudinal striations. These teeth are larger and more robust than the Cameroon cf. Spinosauridae material and are not as broadly grooved.

Teeth of *L. sulcatus* illustrated in Marsh (1895, plate 13), are strongly serrate and have broad fluting on their labial faces. Fluting of the lingual face is not noticeable. The genus *Labrosaurus* is considered by Norman (1985) to be synonymous with *Allosaurus*. Illustrations of the teeth of *Ceratosaurus* sp. (a genus allied with *Allosaurus* [Norman 1985]) from the Upper Jurassic of Utah (Madsen 1976), have deeply fluted lingual faces, serrate posterior margins and non-serrate anterior margins. Like *Labrosaurus* teeth, they are laterally compressed and blade-like. They differ by being sharply recurved posteriorly about halfway up the crown. The teeth of spinosaurids resemble those of *Labrosaurus* and *Ceratosaurus* by having longitudinal fluting; though there are exceptions, spinosaurid teeth are more conical. The Cameroon cf. Spinosauridae teeth more closely resemble those of *L. stechowi* than *L. sulcatus*, and are distinct from those of *Ceratosaurus* because they are not sharply recurved.

It is apparent from the literature that referred spinosaurid teeth display a variety of morphologies, from laterally compressed, smooth, and weakly serrate, to conical, ribbed, and non-serrate. There are also several non-spinosaurid theropods of Late Jurassic age that have fluted teeth, but these are mostly compressed laterally and have well-developed serrations. Intuitively, one would expect to find serrations on the teeth of all spinosaurids, since this feature is nearly ubiquitous within the

Theropoda; unfortunately, the lack of well preserved spinosaurid material has made it impossible to speculate on the degree of variability in tooth morphology within a single species, or even within an individual. The Cameroon material is assigned to cf. Spinosauridae because the teeth are conical, fluted, and serrate.

Theropoda indet.

Morphotype A

Referred material: CAM 25-27, 311, 312, 316, 318, 319, 359 and SMU 72038 (isolated teeth).

Locality: KB-6, near Mayo Djarendi, Koum basin, northern Cameroon.

Description: Relatively large elongate blade-like teeth, strongly compressed laterally, with conical serrations developed on anterior and posterior carinae and smooth lingual and labial faces (figure 16a). Overall height of crown up to 54.25 mm; mesiodistal length ranges from 5.94 to 16.24 mm; lingual-labial width ranges from 3.27 to 7.34 mm (table 6).

Discussion: Morphotype A is a relatively common morphology found in Cretaceous rocks at a number of widely distributed localities. Comparisons were made to similarly-shaped isolated theropod teeth from Malawi and to *Erectopus sauvegi* from the Early Cretaceous of France, and are graphically

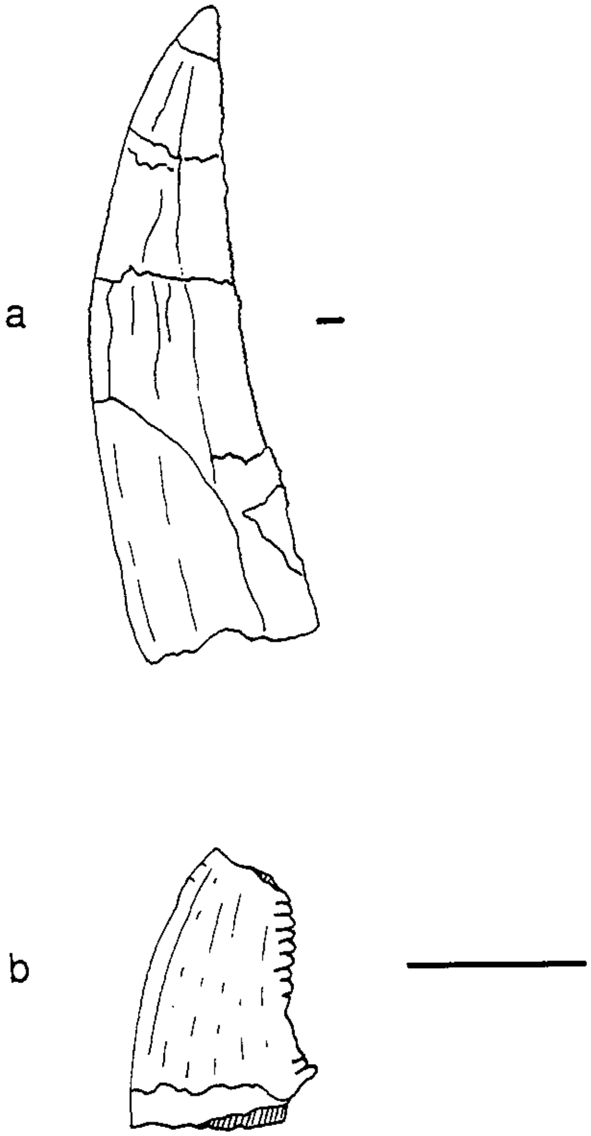


Figure 16. Teeth of theropod dinosaurs from locality KB-6, near Mayo Djarendi, Koum basin, northern Cameroon. a - morphotype A theropod (CAM 25); b - morphotype B theropod (CAM 317). Scale bars = 2 mm.

presented in figure 15. Teeth of *Erectopus* closely match Cameroon morphotype A teeth in overall shape, and aff. *Erectopus* is known from the Cenomanian of Baharije, Egypt (Stromer [1936], cited in Molnar [1980]). Serration densities as a function of lingual-labial tooth width distinguishes the Cameroon teeth. Whether these features are systematically meaningful remains to be demonstrated.

Morphotype A teeth do not resemble theropod teeth figured by Lapparent (1960) from the Late Jurassic-Early Cretaceous "Continental intercalaire" of the central Sahara. The Cameroon material is smaller and less robust than the Saharan material. Mateer (1987) describes two theropod teeth from the Late Jurassic or Early Cretaceous Enon Conglomerate of South Africa. The teeth fall within the size range and posterior margin serration density of the Cameroon material. They differ from the Cameroon teeth by having sharply recurved crowns. The Cameroon teeth more closely resemble those of *Erectopus sauvegi* and the Malawi material than that described by Lapparent (1960) or Mateer (1987).

Theropoda indet.

Morphotype B

Referred material: CAM 314, 315, 317 (isolated teeth).

Locality: KB-6, near Mayo Djarendi, Koum basin, northern Cameroon.

Description: Small strongly compressed teeth with smooth lingual and labial faces and significant posterior curvature of the crown (figure 16b). Serrate on only the posterior margin. Mesiodistal length from 2.98 to 3.23 mm; lingual-labial length from 1.49 to 1.61 mm (table 6).

Table 6.--Measurements of theropod teeth from locality KB-6, Koum basin, northern Cameroon, Mwakasyunguti, northern Malawi, and Bois de Penthièure, France.

Specimen number	Mesio-distal length (mm)	Lingual-labial width (mm)	Maximum preserved height (mm)	Serra-tions/mm (anterior margin)	Serra-tions/mm (posterior margin)
Theropoda indet. Morphotype A (Cameroon)					
25	14.90	7.12	54.25	4.12	2.50
26	16.24	7.34	22.39	....	3.52
27	8.90	7.09	21.10	....	3.20
311	9.23	5.93	12.56	4.84	4.38
312	6.65	3.91	8.69	....	3.25
316	....	....	....	....	....
318	6.11	4.30	13.86	3.10	2.61
319	5.94	3.27	9.62	7.67	5.42
359	11.44	4.91	20.92	2.88	2.90
SMU 72038	13.40	5.50	35.25	....	4.06
Theropoda indet. Morphotype B (Cameroon)					
314	3.11	1.61	3.85	....	4.03
315	3.23	1.61	4.47	....	5.80
317	2.98	1.49	4.35	....	4.77

Table 6 (continued).--Measurements of theropod teeth from locality KB-6, Koum basin, northern Cameroon, Mwakasyunguti, northern Malawi, and Bois de Penthièure, France.

Specimen number	Mesio-distal length (mm)	Lingual-labial width (mm)	Maximum preserved height (mm)	Serra-tions/mm (anterior margin)	Serra-tions/mm (posterior margin)
Theropoda indet. (Malawi)					
MAL-17	7.45	3.10	9.66	3.65	3.48
MAL-18	14.50	9.80	22.80	4.18	2.68
MAL-19	12.68	6.80	32.45	2.49	2.28
MAL-20	....	4.45	14.15	2.43	2.35
MAL-21	9.38	5.20	14.90	....	....
MAL-22	11.40	5.90	22.00	1.96	1.90
MAL-23	....	7.60	17.28	....	....
MAL-24	7.70	3.15	22.20	....	....
MAL-25	....	3.70	12.40	....	....
MAL-26	8.65	7.40	18.35	1.98	1.65
MAL-27	11.05	7.10	11.26	....	....
MAL-28	6.05	2.30	10.12	3.85	3.29
MAL-29	10.43	5.01	26.00	....	2.53
MAL-30	6.95	3.08	13.74	4.68	3.66
MAL-31	20.96	11.38	54.65	2.23	2.53
MAL-32	8.40	3.73	6.70	3.70	3.25
MAL-40	9.33	7.33	14.00	....	3.52
MAL-77	4.43	3.54	5.72	6.41	....
MAL-123	2.29	1.05	4.95	8.28	6.35
MAL-154	....	....	....	....	....
Erectopus sauvegi (MNHN lou-1) (France)					
(a)	16.00	8.50	53.00	2.60	2.53
(b)	18.20	7.50	60.50	2.85	2.55
(c)	21.00	12.30	61.40	2.87	2.40

Discussion: These small theropod teeth are distinct from Morphotype A described above by virtue of their small size and lack of anterior margin serrations. On the basis of size, they may represent a different taxon of theropod or a juvenile of Morphotype A. A single tooth from Malawi (MAL-

123) closely corresponds to this morphotype in size, serration density, and shape. Rich *et al.* (1983) figure two teeth from the Late Jurassic or Early Cretaceous Kirkwood Formation of South Africa which are approximately the same size and shape as the Cameroon teeth. At least one tooth has serrations on the posterior margin. It is not known whether serrations were present on the anterior margins, due to poor preservation. Rich *et al.* (1983) attribute the teeth to a theropod similar to *Compsognathus*, *Dromaeosaurus*, or *Ornitholestes*. Teeth attributed to *Coelurus*, approximately 6 mm in mesiodistal length, with well developed posterior margin serrations but absent or reduced anterior margin serrations, are known from the Early Cretaceous of Maryland (Lull 1911). The curvature of the crown is similar to the Cameroon teeth. The Cameroon morphotype B material is separated from morphotype A because it forms a distinct and coherent group (see figure 15).

Order Ornithischia

Suborder Thyreophora

Thyreophora indet.

Referred specimen: CAM 324 (isolated tooth)

Locality: KB-6, near Mayo Djarendi, Koum basin, northern Cameroon.

Description: CAM 324 is an abraded specimen with almost no enamel remaining. It is squat and mesiodistally elongate, and is a relatively small tooth, 3.22 mm in mesiodistal length, 1.85 mm in lingual-labial length, and with a crown height of 2.66 mm. The crown is slightly hooked in the lingual direction, and remnants of 3 or 4 denticles remain on the trailing margin of the tooth.

Discussion: This specimen is the only one of its kind recovered from quarrying and sediment washing in the Koum basin, and little can be said about its affinity except that it is a relatively primitive tooth of an ornithischian dinosaur. It is too squat to assign to the Hypsilophodontidae. It more closely resembles nodosaurid teeth such as *those of Priconodon crassus* from the Lower Cretaceous of Maryland and the District of Columbia (USNM 8440), or stegosaurid teeth such as *Kentrosaurus aethiopicus*, illustrated by Janensch (1935).

Suborder Ornithopoda

Family Iguanodontidae

Genus *Ouranosaurus* TAQUET 1976

cf. *Ouranosaurus nigeriensis,* TAQUET 1976

Referred material: CAM 310 (neural spine and neural arch of dorsal vertebra); CAM 1, 3-16, 303-309, 323, 361, and SMU 72025, 72032, and 72077 (isolated teeth).

Locality: KB-6 (isolated teeth) and KB-13 (isolated postcrania).

Description: The most diagnostic specimen is the neural arch and spine of a vertebra (figure 17). Both prezygapophyses and the most of the right postzygapophysis are preserved. The entire right side and most of the left side of the neural arch is preserved. Both sides of the neural arch were separated from the centrum along the suture boundary. The left transverse process is missing and was broken off at its base. The posterior proximal portion of the right transverse process is preserved in its entirety; the anterior and distal parts are missing. No parapophysis is preserved; since this feature is restricted to the distal portion of the transverse process in the posteriormost dorsal vertebrae, it may have been lost along with the left transverse process and the distal right transverse process. The anterior edge of the neural spine is well preserved, but part of the posterior edge as well as the distal portion of the neural spine is incomplete.

Discussion: As in *Ouranosaurus*, the prezygapophyses are flat and oval and are tilted medially and anteriorly. The transverse process is relatively broad and originates high on the neural arch; its anterior edge is directed ventrally about 30°. The neural spine is extremely elongated dorsally. These features are characteristic of the posterior dorsal vertebrae in *Ouranosaurus* (see Taquet 1976). The length of the neural spine in the dorsal vertebrae is diagnostic for *Ouranosaurus* as well. Taquet (1976) notes that the ratio between dorsal process length

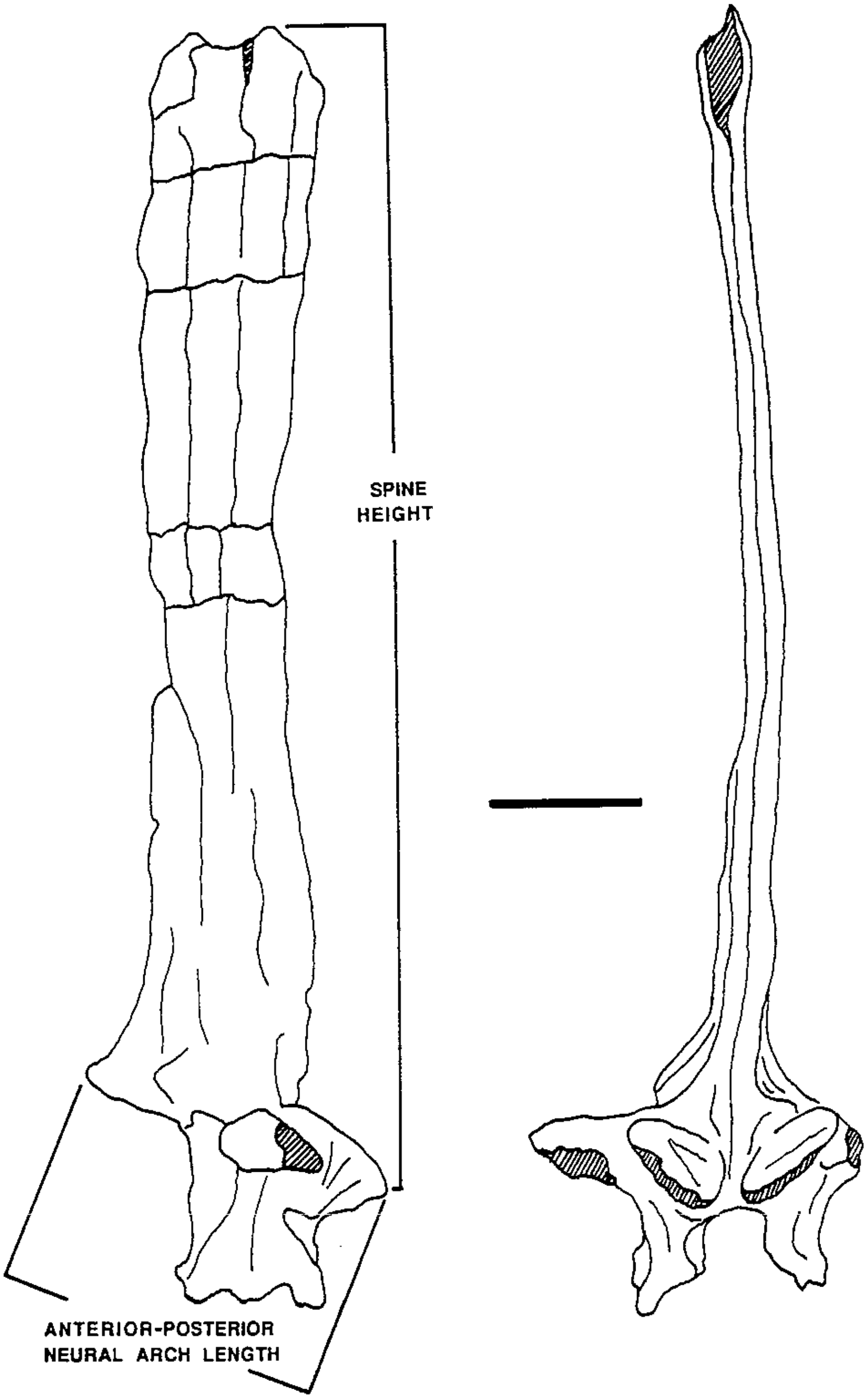


Figure 17. Neural arch and spine of posterior dorsal vertebra of *Ouranosaurus* sp. from locality KB-13, near Mayo Djarendi, Koum basin, northern Cameroon. a - lateral view of left side. b - anterior view. Scale bar = 5 cm.

and centrum height for dorsal vertebrae of *Ouranosaurus* is 3.9, whereas it is about 2.7 in *Iguanodon mantelli* and less in other iguanodontids. Since no centrum exists for the Cameroon specimen, a different but relevant ratio is compared. The ratio of maximum distance between the anterior end of the prezygapophysis to the posterior end of the postzygapophysis (anterior-posterior neural arch length), and the length of the neural spine from the anterior-most point of the prezygapophysis to the anterior distal end of the neural spine was calculated for the Cameroon specimen. For *Ouranosaurus nigeriensis* it was calculated from illustrations in Taquet (1976), *Iguanodon atherfieldensis* from illustrations in Norman (1986), and *I. bernissartensis* from illustrations in Norman (1980) (see Table 7). For the Cameroon specimen, the ratio is 3.56; for the illustrations of *Ouranosaurus* in Taquet (1976), the ratio ranges from 3.30-4.18 for posterior dorsal vertebrae; for *I. atherfieldensis* the range is 2.00-3.13; and for *I. bernissartensis* it ranges from 1.60-2.02. Although the Cameroon specimen is smaller than *Ouranosaurus nigeriensis*, its neural spine height/neural arch length ratio clearly lies in the range of that for posterior dorsal vertebrae of *Ouranosaurus nigeriensis,* and outside the range for both *I. atherfieldensis* and *I. bernissartensis*. In morphology, as well as the ratio of neural spine height/neural arch length, it most closely resembles the 27th (16th dorsal) vertebra in the spinal column of *Ouranosaurus*.

Table 7.-- Neural spine height and anterior-posterior neural arch length for dorsal vertebrae in iguanodontids and CAM 310.

Vertebra number	Neural spine height (cm)	Ant.-Post. neural arch length (cm)	Spine height/ neural arch length ratio
CAM 310 (this study)			
27?	40.1	11.3	3.56
Ouranosaurus nigeriensis (from Taquet 1976)			
20	64.4	15.9	4.05
21	62.9	17.0	3.69
22	61.7	16.3	3.79
23	63.7	16.0	3.98
24	62.1	14.8	4.18
25	...	...	...
26	61.7	...	...
27	56.6	16.0	3.54
28	55.5	16.8	3.30
Average	61.1	16.1	3.80
Iguanodon atherfieldensis (from Norman 1986)			
20	23.0	11.5	2.00
21	25.0	8.0	3.13
22	24.5	10.5	2.33
23	23.0	11.3	2.04
24	19.8	...	...
25	18.5	...	...
26	...	...	...
27	27.3	...	...
28	...	...	...
Average	23.0	10.3	2.38

Table 7 (continued).--Neural spine height and anterior-posterior neural arch length for dorsal vertebrae in CAM 310 and iguanodontids.

Vertebra number	Neural spine height (cm)	Ant.-Post. neural arch length (cm)	Spine height/ neural arch length ratio
Iguanodon bernissartensis (from Norman 1980)			
20	30.3	18.9	1.60
21	30.8	17.5	1.76
22	31.1	17.2	1.81
23	30.0	16.1	1.86
24	29.7	16.1	1.84
25	29.4	15.0	1.96
26	29.7	14.7	2.02
27	29.4	16.9	1.74
28	...	...	...
Average	30.1	16.6	1.82

Twenty-three reasonably complete iguanodontid teeth (figure 18) have been recovered from KB-6. Almost all specimens are deeply worn and are resorbed at their bases, suggesting they were lost by living animals and were not derived from skulls. Deep facets just below the crown, caused by chafing against the subjacent replacement tooth, are apparent on most of the KB-6 teeth. Using criteria listed by Taquet (1976), upper and lower as well as left and right was determined for each tooth, where possible (table 8; figure 19). Measurements of the teeth are also listed in table 8. The better-preserved specimens display several characteristic features, including enamel on only one side

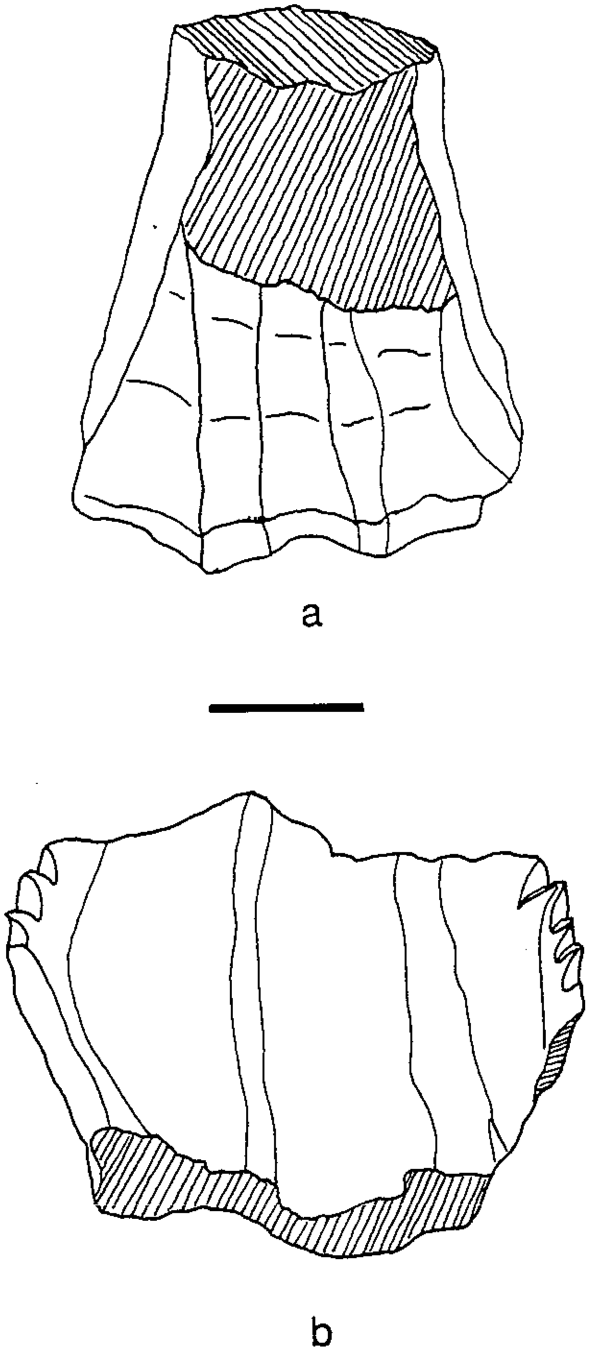


Figure 18. Teeth of *Ouranosaurus* sp. from locality KB-6, near Mayo Djarendi, Koum basin, northern Cameroon. a - maxillary tooth (SMU 72032), lateral view. b - dentary tooth (CAM 5), lingual view. Scale bar = 5 mm.

of the tooth crown, denticulations on the anterior and posterior edges of the crown, and the presence of a dominant longitudinal crest on the enameled tooth face as well as only one secondary crest paralleling the dominant one. The dominant longitudinal crest is displaced toward the rear of the tooth.

Taquet (1976 and references therein) argues that the teeth of *Ouranosaurus* are not generically diagnostic, and are indistinguishable from those of Early Cretaceous *Iguanodon atherfieldensis*, *I. bernissartensis*, and *I. mantelli*. Norman (1986) notes that the teeth of *I. atherfieldensis* and *I. bernissartensis* are virtually indistinguishable, and that both species possess teeth with a dominant longitudinal ridge displaced posteriorly from the midline of the tooth. Like *Iguanodon*, the teeth of *Ouranosaurus* share this feature. They are distinct from the teeth of "primitive" iguanodontids such as *Camptosaurus*, *Dryosaurus*, and *Tenontosaurus*, which have a dominant longitudinal ridge in the midline of the crown and numerous secondary and tertiary ridges to either side (Taquet 1976; p. 101). The teeth from KB-6 belong to the *Iguanodon-Ouranosaurus* morphotype. Iguanodontid teeth from KB-6 fall in the size range for teeth of *Ouranosaurus nigeriensis*, *I. atherfieldensis*, and *I. bernissartensis* (Taquet 1976; Norman 1980, 1986). Since diagnostic material for *Ouranosaurus* was found near KB-6 (KB-13), I conclude that the isolated teeth from KB-6 can be assigned to *Ouranosaurus*.

Table 8.--Measurements of Ouranosaurus teeth from locality KB-6, Koum basin, northern Cameroon.

Specimen number (CAM)	Upper/ lower	Left/ right	Anterior/ posterior length (mm)	Medial/ lateral width (mm)	Crown height (mm)	Total height (mm)
1	l	...	10.4	7.0	4.2	11.8
3	l	r	19.2	8.2	10.2	15.8
4	u	...	...	...	...	15.2
5	l	r	18.0	8.2	>15.0	15.0
6	l	r	12.2	7.2	2.6	12.0
7	u	...	11.8	12.2	6.0	18.0
8	u	...	16.4	13.8	...	8.0
9	l	...	12.8	5.8	...	9.8
10	u	l	12.6	8.8	3.4	14.2
11	l	r	23.2	11.2	...	28.2
12	l	...	18.8	9.6	...	9.0
13	u	r	14.0	10.2	...	15.4
14	l	r	13.8	8.0	2.8	16.4
15	u	...	...	12.6	...	5.4
16	u	l	14.8	10.2	7.8	18.2
303	u	...	...	16.0	...	8.0
304	l	r	26.2	11.8	16.0	30.2
305	u	...	13.2	13.0	7.0	11.2
306	u	l	10.8	8.2	5.6	13.0
307	l	...	14.0	8.2	> 6.8	16.0
308	l	r	12.2	7.2	13.0	17.8
309	u	l	16.0	11.0	15.2	18.4
323	l	r	8.9	5.6	7.5	11.4
361	u	...	10.5	8.1	6.1	10.7
SMU-72025	u	l	19.2	15.2	10.8	26.8
SMU-72032	u	l	14.5	9.5	...	15.1
SMU-72077	u	l	15.2	10.1	1.5	12.5

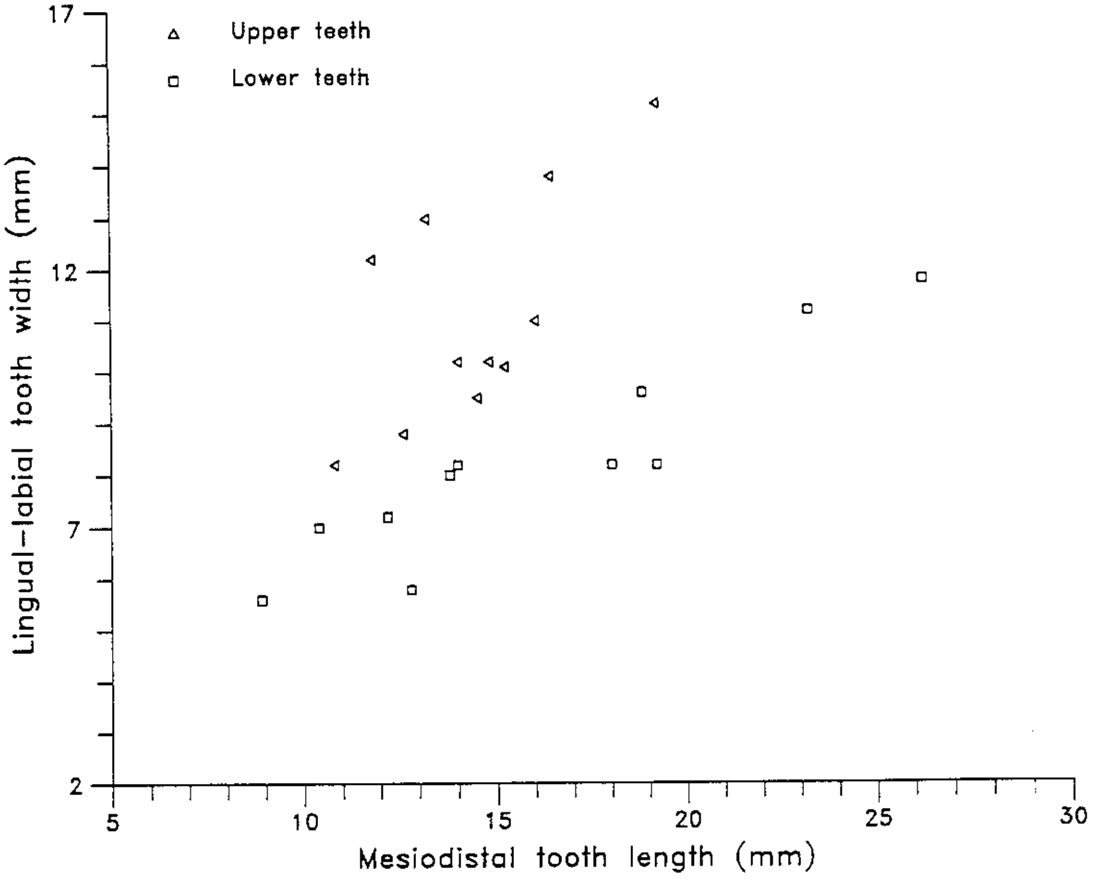


Figure 19. Mesiodistal length versus lingual-labial width for teeth of Ouranosaurus sp. from locality KB-6, near Mayo Djarendi, Koum basin, northern Cameroon.

PART IV

PALEOICHNOLOGY

The study of fossil footprints is undergoing a renaissance. The prolific ichnological record, long underutilized as a source of paleontological information, is now being used to document dinosaur behavior, paleoecology, population structure, and sedimentary environments to a much greater extent. The nature of the information available from fossil footprints augments the osteological record and provides insights into facets of ancient life unavailable from "bare bones" osteological data.

Quantitative studies of vertebrate paleoichnology are few. The majority of studies are site reports or taxonomic treatments of trackways. Taxonomic interpretation in some cases is inconsistent or questionable, and footprints may be subjectively assigned to taxonomic groups with inadequate justification (see Farlow 1987, for a discussion). The effect of behavior and gait on variability in footprint morphology requires further specific consideration.

The goal of this section is to quantitatively describe and interpret the identity, gait, and behavior of the archosaurian reptiles that produced the large number of footprints and trackways in the Koum basin by using morphometric methods. The Koum basin ichnological sample will then be compared with other dinosaur footprint localities in Africa.

Limitations of Ichnological Studies

A difficulty encountered by all workers studying fossil footprints is the association of the preserved trace with an appropriate osteologically-based taxon. Ichnites are sedimentologic structures recording a morphological structure (the foot) in dynamic contact with a plastic substrate, they are not organic remains of the trackmaker (Baird 1957). Olsen and Galton (1984) observe that

> The track is a shadow of the form of the organism, viewed in the dim light of behaviour, substrate nature, and diagenesis. The track never had most of the properties of an organism. Without the body-fossil dead in its tracks we can at best imagine the Platonic ideal of which the tracks are shadows - i.e., the foot. (Olsen and Galton 1984, 94)

Ichnological remains are classified into ichnotaxa, which are similar to form taxa, but which disassociates the trace from a specific animal (see Basan [1979] and Sarjeant [1989] for suggested rules governing the naming of fossil traces, and Faul [1951] for an alternative system of classification). An ichnotaxon consists of an ichnogenus and an ichnospecies, analogous to the Linnean genus and species of biological taxa. Ichnotaxa are distinct from the

Linnean system used in zoology. Several common ichnogenera used for dinosaur footprints probably represent the ordinal or subordinal level within the Archosauria, making them much more general than Linnean genera (Olsen and Galton 1984).

The effect of substrate on the morphology of the foot impression is widely observed (for examples, see Tucker and Burchette 1977; Lockley *et al.* 1986; Farlow 1987), and has led to problems of classification of dinosaurian trackmakers. According to Olsen and Galton (1984), Ellenberger (1972, 1974) oversplit the ichnotaxonomy of trackways from the Stormberg Group, southern Africa, because substrate variability had affected the morphology of the footprints. Similar problems arise with studies by Avnimelech (1966) and Gurich (1926).

Trackmaker behavior is a variable that influences footprint morphology. Examples of diverse behaviors exhibited by dinosaurian trackmakers are given by Coombs (1980), Thulborn and Russell (1981), and Ishigaki (1989). Weems (1987) used inferred behavioral differences to discriminate trackmakers in a large sample of dinosaur footprints from the Triassic of northern Virginia. Among the best studies of behavior and footprint morphology are those of Thulborn and Wade (1984, 1989), based on a large sample from a single locality from the Early Cretaceous of Queensland, Australia.

In a group of footprints similar in shape but dissimilar in size, two conclusions regarding their relationship can be made; either all belong to a growth series, or the different size classes represent different taxa with similar foot morphology but different in size. Olsen and Galton (1984) synonymized several ichnogenera attributable to theropod dinosaurs (*Grallator*, *Eubrontes*, and *Anchisauripus*) because several components of foot morphology varied between them in an allometric fashion. The classic criteria used to distinguish these taxa were relative length of digit III to overall footprint length, and absolute size of the footprint; *i.e.*, the smaller the footprint, the greater the digit III/footprint length ratio. Because the ichnogenera were established on the basis of this proportion and absolute size, and not on unique aspects of the pes impressions, their validity could not be objectively supported, and they were combined into a single ichnogenus (*Grallator*).

The stratigraphic distribution of ichnotaxa has been successfully used to define zones within continental sediments where osteological data are scarce or lacking (for examples, see Ellenberger 1970, 1972, 1974; Ellenberger *et al*. 1969; Olsen and Galton 1984; Haubold 1986).

Methodology

The methods and terminology used in this study are those outlined in Leonardi *et al*. (1987). Linear measurements were made in metric units to the nearest centimeter (except footprint depth and digit1-digit4 lengths, which were measured to the nearest millimeter); angular measurements were made with a Brunton compass or protractor (for angle of divarication) to the nearest degree.

Data were entered into a spreadsheet program on an IBM-compatible XT desktop computer to create a data matrix. Secondarily derived variables were calculated using spreadsheet functions. These prepared data were uploaded to an IBM 3081 mainframe computer for statistical analysis using SAS release 5.18 in a VM/CMS environment. Sheared principal component analysis was performed on the PC using fortran-compiled code written by N. Mcleod (University of Michigan). Correlation of variables was made using the Pearson product-moment correlation statistic. Appendix 3 contains a correlation matrix (table 30) for the Koum basin sample.

Trackway and Footprint Variables

A number of trackway and footprint variables at the KB-17 locality were measured *in situ* and recorded. Many of the same variables were recorded at the other Koum basin trackway localities, although in most cases other localities had fewer measurable variables due to poor preservation. The variables, as well as a number of secondarily derived values, are presented in appendix 2, tables 28-29. Capitalized abbreviations following the variable name are the column and row headings in summary statistical tables and in appendix 2.

Measurements can be assigned to two groups: morphological measurements characterize the size and shape of the footprint; trackway measurements are associated with the passage of the trackmaker over the substrate, and quantify the behavior of the individual.

Morphological Variables

Footprint length (FL) - Footprint length is the linear measure of the length of a complete footprint, from the base of the "heel" or most proximal point of the footprint to the distal end of digit III (figure 20a). In instances where the entire length of the footprint is incomplete due to factors of either preservation or trackmaker behavior, the footprint length measurement was not made. Footprint length is given in centimeters.

Footprint width (FW) - This variable is the linear measure of the width of a footprint, from the distal end of digit II to the distal end of digit IV (figure 20a). If either digit II or digit IV was missing, the footprint width measurement was not made. Footprint width is given in centimeters.

Since footprint width correlates strongly with length ($r=0.94$), and was more often preserved and measurable, it was the variable preferred for plots and analyses involving a quantification of size of the footprint.

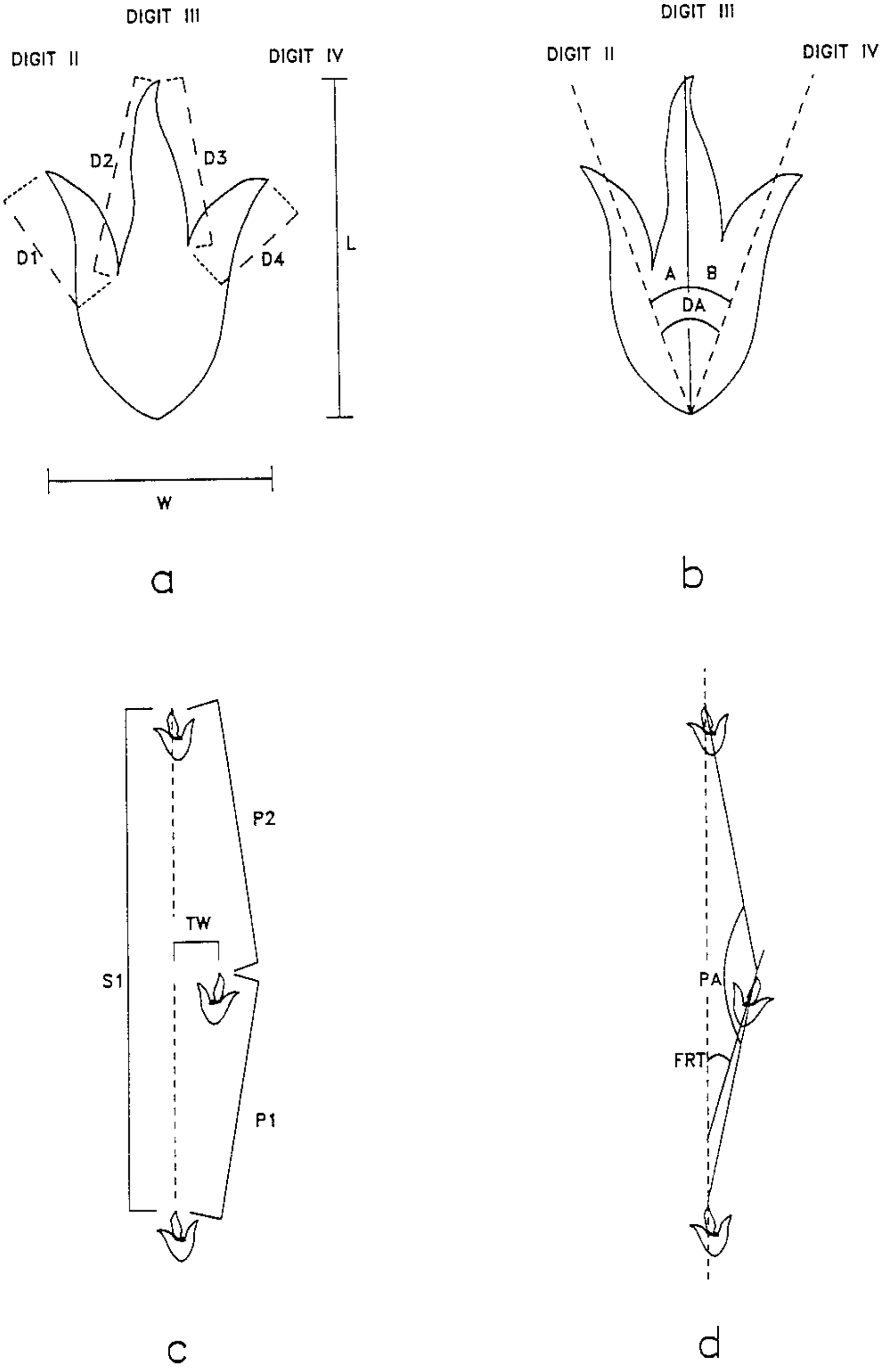


Figure 20. Footprint and trackway variables. a, b - footprint (morphological) variables. c, d - trackway (behavioral) variables. Symbols used are explained in text.

Footprint area (ARA) - The footprint area approximation was obtained by calculating the area of the segment of a circle whose arc angle equals angle of divarication (see below) and whose chord length equals footprint width. The relationship for footprint area is

(1)

$$ARA = DA*\left[\frac{FW}{2*\left[\operatorname{Sin}\frac{DA}{2}\right]}\right]^2$$

where DA is angle of divarication and FW is footprint width. Values of footprint area are given in square centimeters in appendix 2.

Size index (SI) - Size index is the normalized measure of the size of the footprint of an animal expressed as the base 2 logarithm of the footprint length multiplied by the footprint width, or

(2)

$$SI = \frac{\log_{10}\left[ARA\right]}{\log_{10}2}$$

where ARA is footprint area. This variable is similar to one used by Thulborn and Wade (1984), except that their size index is the square root of footprint length times footprint width. The size index employed here is expressed as a base 2 logarithm of the area approximation because it is easy to interpret; an increase of one unit is equivalent to a doubling of size.

Length/width (LW) - This variable is the dimensionless ratio of footprint length divided by footprint width, and is a gauge of gross footprint shape. For example, a value of 1.0 describes a footprint that is equally as long as it is wide; a value of 2.0 describes a footprint that is twice as long as it is wide.

Digit1 length-Digit4 length (D1, D2, D3, D4) - Digit1 length is the linear measurement taken from the distal end of the digit II impression to the point where the digit II impression meets the impression of digit III. Digit2 length is the linear measurement taken from the distal end of the digit III impression to the point where the digit III impression meets the impression of digit II. Digit3 length is the linear measurement taken from the distal end of the digit III impression to the point where the digit III impression meets the impression of digit IV. Digit4 length is the measurement taken from the distal end of the digit IV impression to the point where the digit IV impression meets the impression of digit III. Digit1, digit2, digit3 and digit4 lengths are diagrammed in figure 20a.

These variables are not standard footprint measurements, and have yet to be reported in the literature. They are useful for quantifying relationships among the digit impressions of tridactyl footprints. Ratios generated from them are useful size-independent variables valuable in multivariate statistical analyses.

Digit1 proportion - Digit4 proportion (D1P, D2P, D3P, D4P) - These are ratios of each of the digit lengths described above to footprint length.

Digit1 proportion2 - Digit4 proportion2 (D1P2, D2P2, D3P2, D4P2) - These four variables are ratios of each digit length (described above) to the sum of the remaining digit lengths, *e.g.*:

$$D1P2 = D1/(D2+D3+D4) \tag{3}$$

where D1 is digit1 length, D2 is digit2 length, etc.

Digit III skewness (SKEW) - This variable is the ratio of digit3 length to digit2 length, and quantifies asymmetry or skewness of the middle toe impression in tridactyl footprints.

Angle of divarication (DA) - The angle of divarication is formed between the midline axis of the digit II impression and the midline axis of the digit IV impression (figure 20b). This angle, measured in degrees, subtends the footprint width measurement.

The angle of divarication does not correlate strongly with any primary variables other than its own two components, alpha and beta (described below). However, it does have a strong negative correlation with the ratio of footprint length/footprint width (r=-0.66; see figure 21a), indicating that relatively narrow footprints have large values of the divarication angle.

Alpha (A) and Beta (B)- These variables are components of the angle of divarication. Alpha is the internal angle formed by the intersection of the midline axis of the digit II impression and the midline axis of the digit III impression and beta is the internal angle formed by the intersection of the midline axis of the digit III impression and the midline axis of the digit IV impression (figure 20b). These variables were measured from photographs of each footprint. To allow for variation between photograph measurements and actual field measurements, alpha and beta were computed as two proportions of the angle of divarication measurement. Therefore, the sum of alpha and beta always equals the angle of divarication. Alpha and beta are given in degrees.

Alpha does not correlate strongly with any variable except length/width (r=-0.57), which is the case for divarication angle. Beta also correlates with length/width (r=-0.59), and correlates with footprint width as well (r=0.47; figure 21b). This suggests that variance in footprint width can be at least partially explained by varying the angle of the lateral or outside digit (digit IV) relative to digit III, whereas the angle between the medial digit (digit II) and digit III is statistically independent

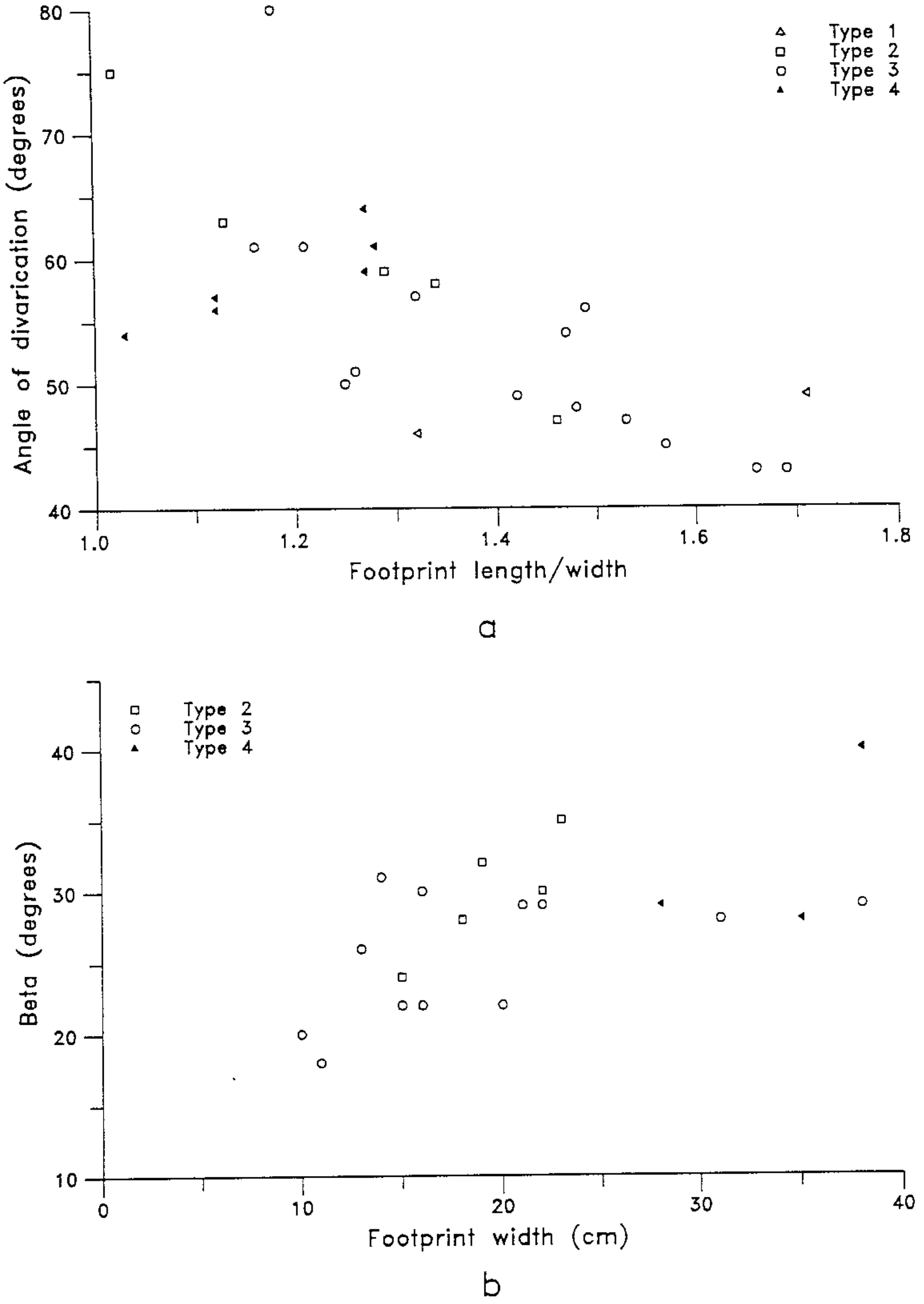


Figure 21. Scatter plots of footprint data from the Koum basin. Data averaged by trackway. Footprint types explained in the following section.

of the width of the foot.

Footprint depth (FD) - Footprint depth is the linear measurement in centimeters of relief of a footprint; it was measured normal to the substrate at the point of maximum relief in each footprint. The point of maximum relief does not necessarily coincide at analogous points from footprint to footprint, but was frequently found to lie at the base of the digit III impression. Footprint depth is given in centimeters.

Footprint depth is a variable dependent on substrate character (softer substrates should result in deeper footprints) as well as trackmaker mass. Footprint depth correlates well with footprint length, width, and area ($r=0.62$, 0.64, and 0.77, respectively), indicating that trackmaker size has a strong influence on the depth of the footprint.

Footprint rotation (FRT) - Footprint rotation is the measure of alignment of the footprint long axis with the direction of the corresponding stride, and is given in degrees (figure 20d). A "pigeon-toed" gait is indicated by negative values of footprint rotation; the opposite is indicated by positive values. An angle of zero demonstrates alignment of the footprint long axis with the stride. Values for this variable were obtained by subtracting the footprint long axis orientation (FO described above) from the direction of the stride opposite the footprint.

Hip height (HH) - This variable quantifies the height in centimeters of the acetabulum above the ground in a normal standing position; it is important for calculating derived variables, such as speed. Thulborn (1989) provides ratios of hip height to footprint length for small and large ornithischian and theropod dinosaurs. For small bipedal ornithischians and theropods (FL<25 cm) this ratio is 4.6; for large bipedal ornithischians and theropods (FL>25cm) the ratio is 5.7. For type 1 and type 2 footprints in this study, whose members generally fall below the 25 cm footprint length, the ratio for small dinosaurs was used. For type 4 footprints whose members are all longer than 25 cm, the larger value was used. For type 3 footprints, hip height was calculated from the mean of the two ratios (=5.15) because the size range includes 25 cm.

Body volume (VOL) - Body volume of the individual trackmakers was calculated using the relationship established by Thulborn (1989) between footprint length and the height of the hip above the ground (HH, described above), and data derived by Colbert (1962) from scale models of dinosaurs (figure 22). From Colbert's data for bipedal dinosaurs, the following relationship exists:

$$\text{VOL} \approx .000429h^{2.82} \tag{4}$$

where h is the height of the crest of the ilium above the ground. Since the method used in this paper relies on

Thulborn's method of calculating the height of the acetabulum above the ground and does not estimate the height of the ilial crest above the ground, an error is introduced into the body volume calculation. The nature of this error consistently underestimates the body volume of the trackmaker, and is relatively small. Values for body volume are given in liters.

Body Mass (MASS) - Estimates of trackmaker body mass were made directly from body volume calculations using the relationship supplied by Alexander (1989):

$$\text{MASS (kg)} \approx \text{VOL (l)} \tag{5}$$

where VOL is body volume as defined above. Body mass values are given in kilograms.

Trackway Variables

Trackway orientation (TO) - Trackway orientation is the compass bearing of the trackway. A minimum of three successive footprints was needed to obtain a trackway orientation measurement.

Stride length (S) - Stride is the distance between the distal end of the digit III impression of two successive centimeters. Stride length quantifies the complete cycle of locomotion from one limb to the other and back.

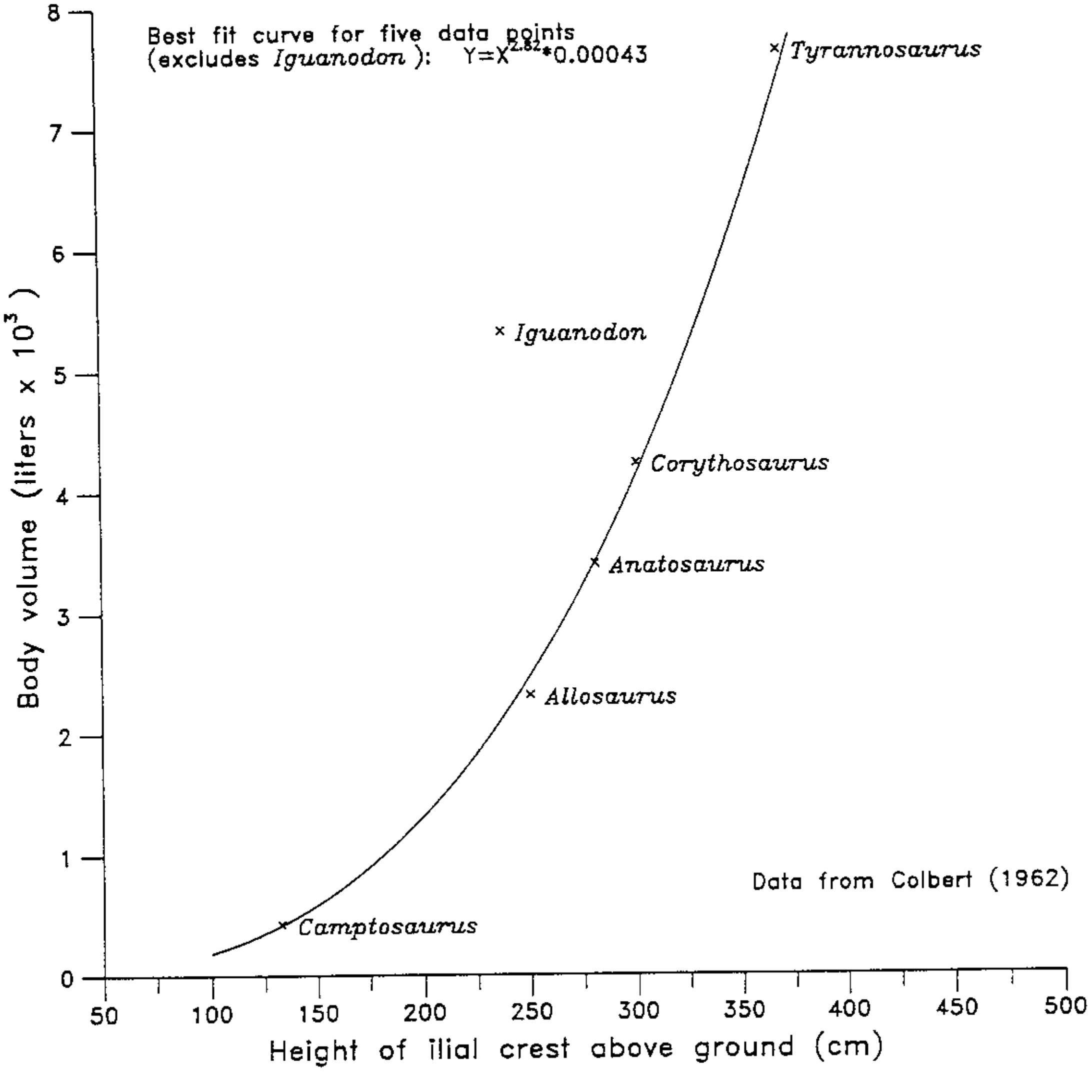


Figure 22. Relationship of body volume to height of ilial crest for selected bipedal dinosaurs.

Pace length (P) - Pace is the distance between the distal end of the digit III impression of two successive footprints of the opposite foot, *i.e.*, between successive right and left footprints (figure 20c). Pace length quantifies half of the stride cycle, and in most cases equals approximately half of the stride length. Values for pace length are given in centimeters.

Pace has a strong correlation with stride (r=0.97) and has a larger sample size, since only two consecutive footprints are needed for a measurement instead of three needed for stride. For these reasons, pace was used instead of stride whenever possible in bivariate plots and statistical analyses.

In general, pace correlates well with size-related morphological variables such as footprint length and digit1-4 lengths. This is not surprising, since larger animals take larger paces; the correlation is imperfect, however, because a small running animal will have a pace as long as a large walking animal, which is the case with several trackways in the Koum basin sample.

Trackway width (TW) - Trackway width is defined here as the length of the perpendicular bisector of a stride that originates at the junction of the two subtending paces footprints of the same foot, *i.e.*, between successive right or successive left footprints (figure 20c). It is calculated using the trigonometric relationship

$$TW = \frac{(P1*P2)\mathrm{Sin}(PA)}{S1} \qquad (6)$$

where P1 and P2 are the initial and second pace lengths and S1 is the associated stride measurement, as defined above, and pace angle is as defined below.

Trackway width correlates in general with morphological variables related to size, such as footprint length (r=0.66) and size index (r=0.62). This reflects the dependence of trackway width on the girth of the dinosaur's pelvis, and not on behavior.

Pace angle (PA) - Pace angle is the angle defined by the intersection of two successive pace measurements and subtends the corresponding stride measurement (figure 20d). It was obtained by subtracting the smaller of two successive pace directions from the larger and subtracting the difference from 180. The same angle may be obtained by using the law of cosines and the same pace and stride measurements. Differences in pace angles obtained by the two methods are insignificant.

Pace index (PI) - Pace index is the ratio of the length of the first portion of the stride length measurement to the second portion of the stride length measurement. The lengths of the first and second portions were obtained by determining the point at which the trackway width measurement (a perpendicular bisector) intersects the stride measurement. The first portion was calculated using the relationship

(7) $$\text{first portion of stride length} = (P1^2+TW^2)^{0.5}$$

where P1 is the first pace measurement associated with the stride measurement of interest and TW is trackway width. The second portion of the stride length was obtained by subtracting the first portion from total stride length.

Pace index quantifies the asymmetry of a trackmaker's gait. A value of 1.0 indicates a perfectly symmetrical gait; departure from unity indicates an uneven or asymmetrical gait, caused by a change in direction or velocity of the trackmaker or an unexpected quality of the animal's motion, such as a limp or a staggering gait.

Relative stride length (RSL) - This variable is related to the stride/length and pace/length variables described above but uses hip height as the normalizing factor to remove the effects of size from the length of stride. It is a dimensionless ratio that follows the formula

(8) $$RSL = S/HH$$

where S is stride length and HH is hip height (defined above). Relative stride length is the standard measure used by other authors to describe the gaits of dinosaurs and mammals in terms of walking, running, or trotting (see for example Alexander *et al.* 1977; Thulborn and Wade 1974; and

Weems 1987). Values below 2.0 indicate a walking gait; values between 2.0 and 2.9 indicate trotting; and values above 2.9 indicate a gallop or sprint (see Alexander 1977; Thulborn and Wade 1984).

Speed (m/s and km/h) (SMS and SKH) - Trackmaker speed is calculated from the stride and hip height variables following the equation proposed by Alexander (1976)

$$\text{(9)} \qquad SMS \approx 0.25g^{0.5}S^{1.67}(HH)^{-1.17}$$

where g is the gravitational acceleration constant, S is stride length, and HH is hip height (defined above). Speed is given in meters per second in appendix 2, as well as kilometers per hour.

Since Alexander first proposed the calculation of speed from trackway data (1976), a number of studies of dinosaur trackways have involved the estimation of trackmaker speeds (see for example Coombs 1978; Demathieu 1984; Farlow 1981, 1987; Kool 1981; Russell and Beland 1976; Thulborn 1982, 1984; Thulborn and Russell 1981; Thulborn and Wade 1984, 1989; Weems 1987). With the exception of the work of Thulborn, these studies have utilized the hip height estimation method of Alexander (1976), who suggested that hip height was approximately four times footprint length (based on osteometric data). Thulborn and Wade (1984, 1989) revised this ratio from their own osteometric data (discussed above), and found Alexander's (1976) method consistently underestimates hip height, thereby overestimating trackmaker speed. It is important to keep this in mind when comparing the results of these various studies.

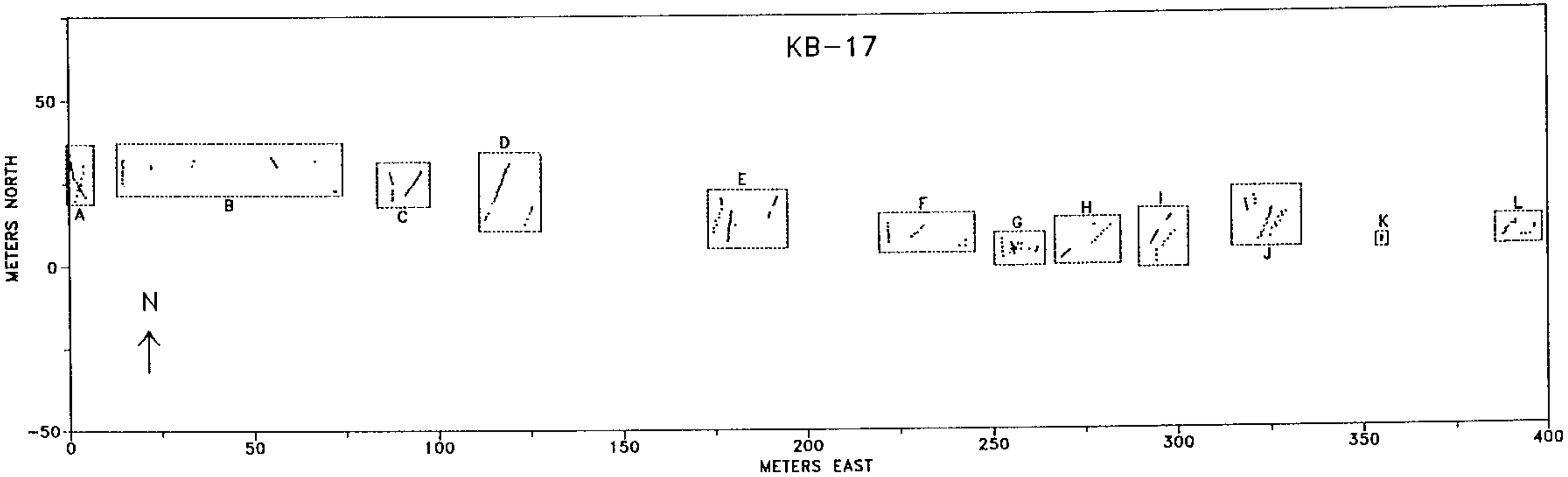
Striding rate (STRT) - Striding rate is the measure of how many strides the trackmaker took in a given span of time; it is given as the number of strides made by the trackmaker per second. It is calculated by multiplying the speed of the trackmaker in meters per second by the number of strides the trackmaker executed per linear meter.

Distribution of trackways and site stratigraphy

In addition to the variables measured and described above, all trackway localities were mapped and individual footprints and trackways were placed in areal context (figures 23-25). As with the length and angular data described above, the measurements were taken with a Brunton compass and non-metallic measuring tape. Mapping was executed in 'pace and compass' fashion. A field version of the map was compiled to provide a rough check on the results while still at the locality. Trackways were numbered sequentially, and each footprint is designated by a trackway number, followed by a hyphen, and an integer representing the position of the footprint in the trackway.

Stratigraphic level was determined for each trackway, and indicates which of four primary depositional bedding planes the trackway is preserved upon within the KB-17 locality (figure 26). Each of the four levels represents a

Figure 23. Base map of trackway locality KB-17, south of Manangia, Koum basin, northern Cameroon. Boxed-in areas are shown in detail in figure 24.


KB-17
N
A
B
C
D
E
F
G
H
I
J
K
L
METERS NORTH
50
0
-50
METERS EAST
0
50
100
150
200
250
300
350
400

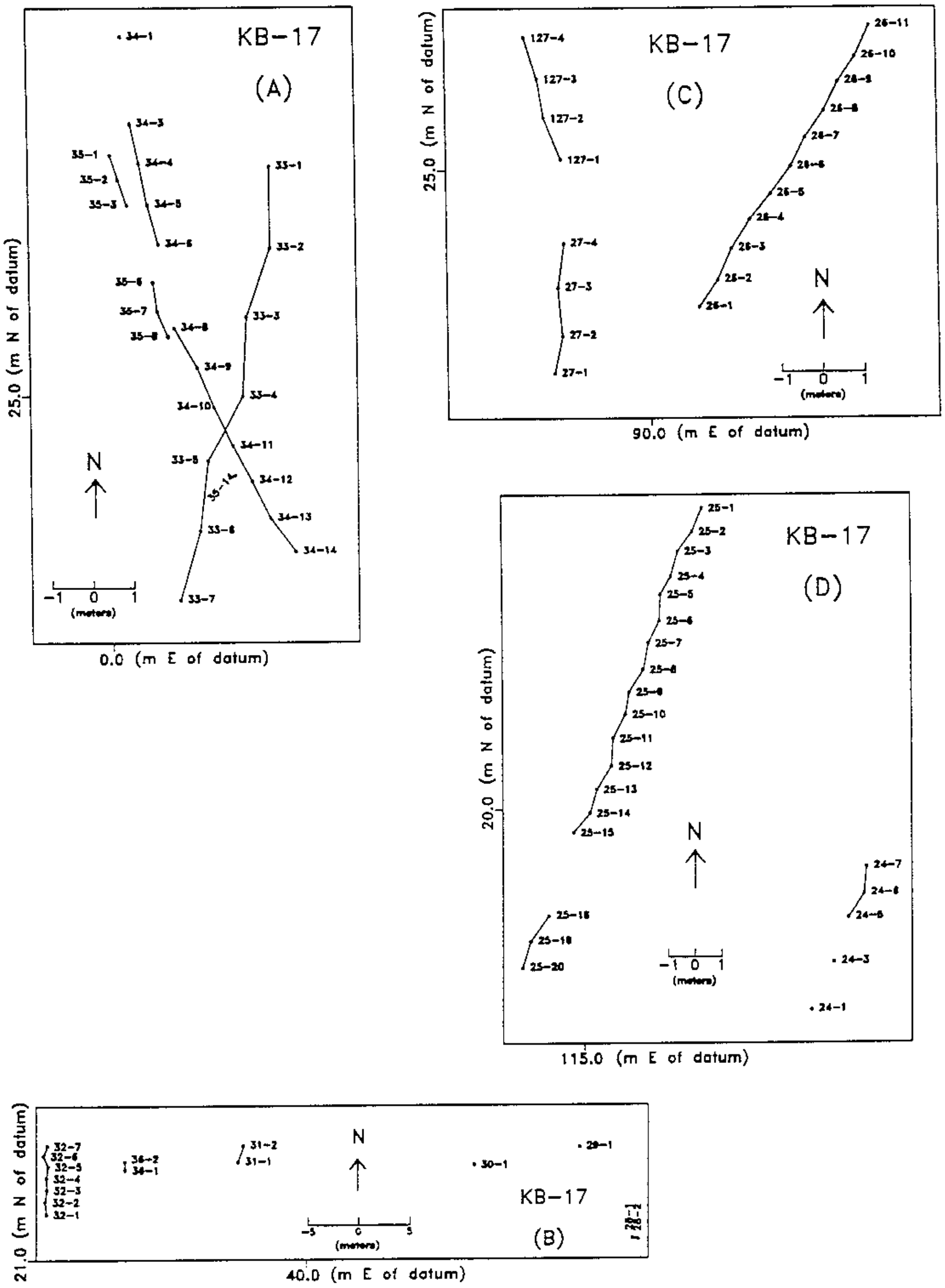


Figure 24. Detail of trackway concentrations at locality KB-17, south of Manangia, Koum basin, northern Cameroon.

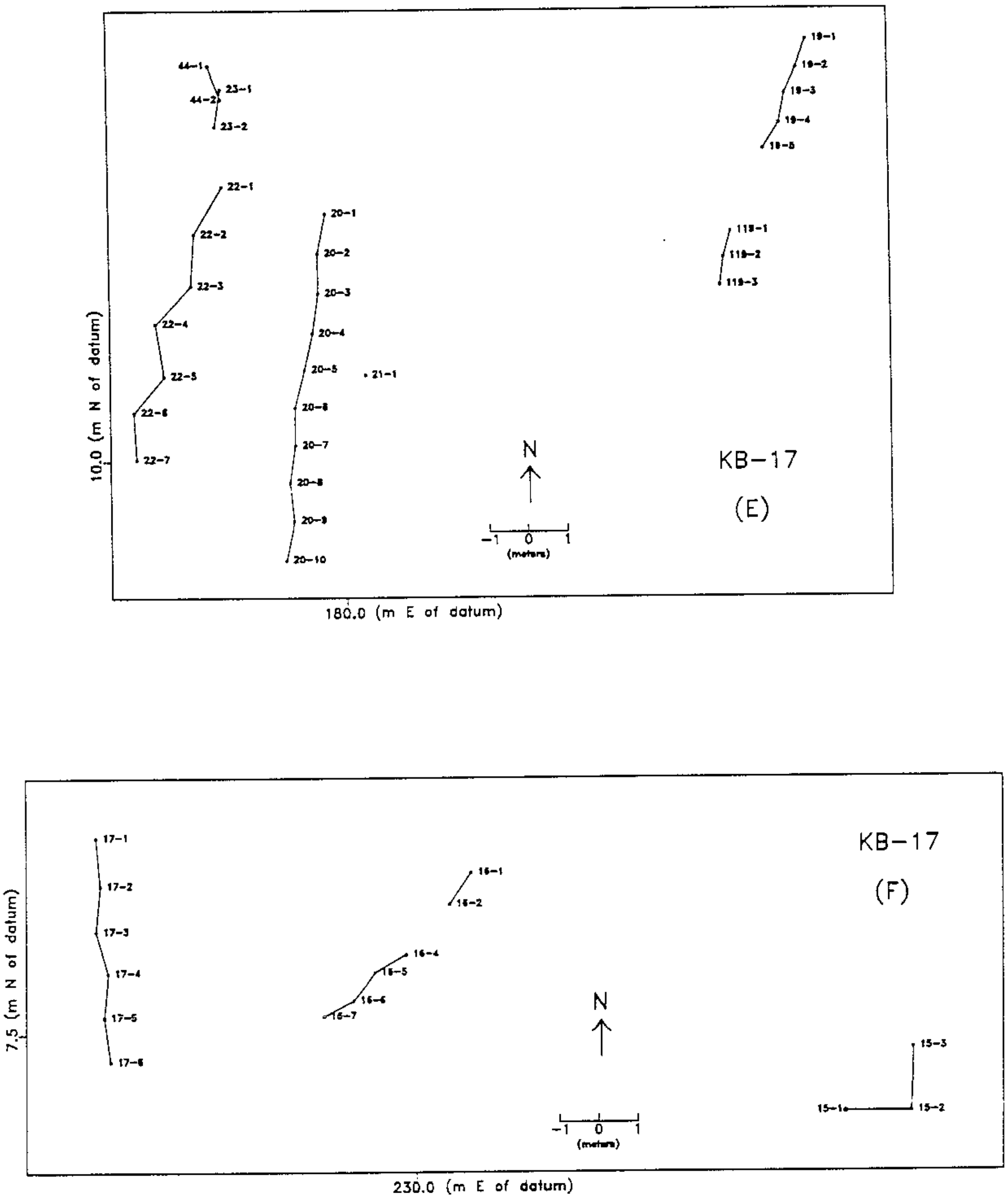


Figure 24 (continued). Detail of trackway concentrations at locality KB-17, south of Manangia, Koum basin, northern Cameroon.

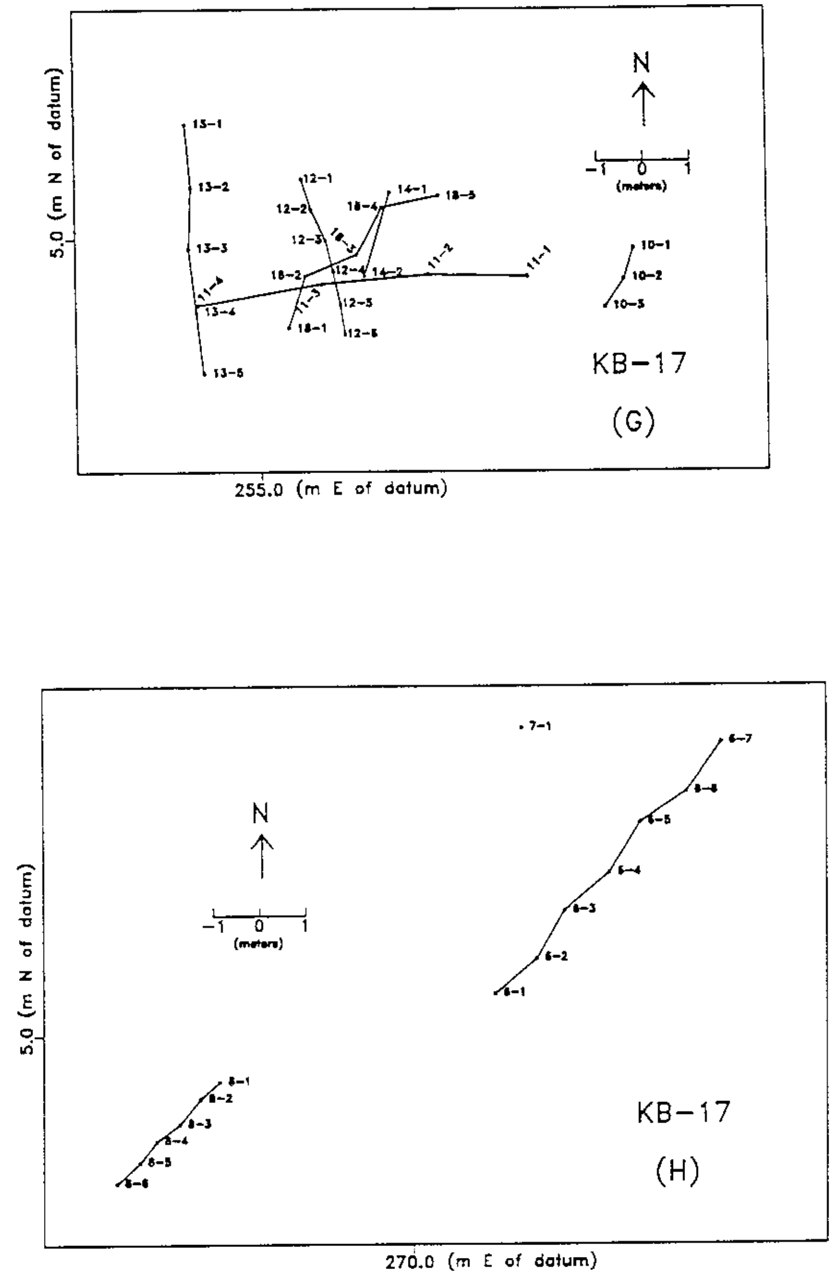


Figure 24 (continued). Detail of trackway concentrations at locality KB-17, south of Manangia, Koum basin, northern Cameroon.

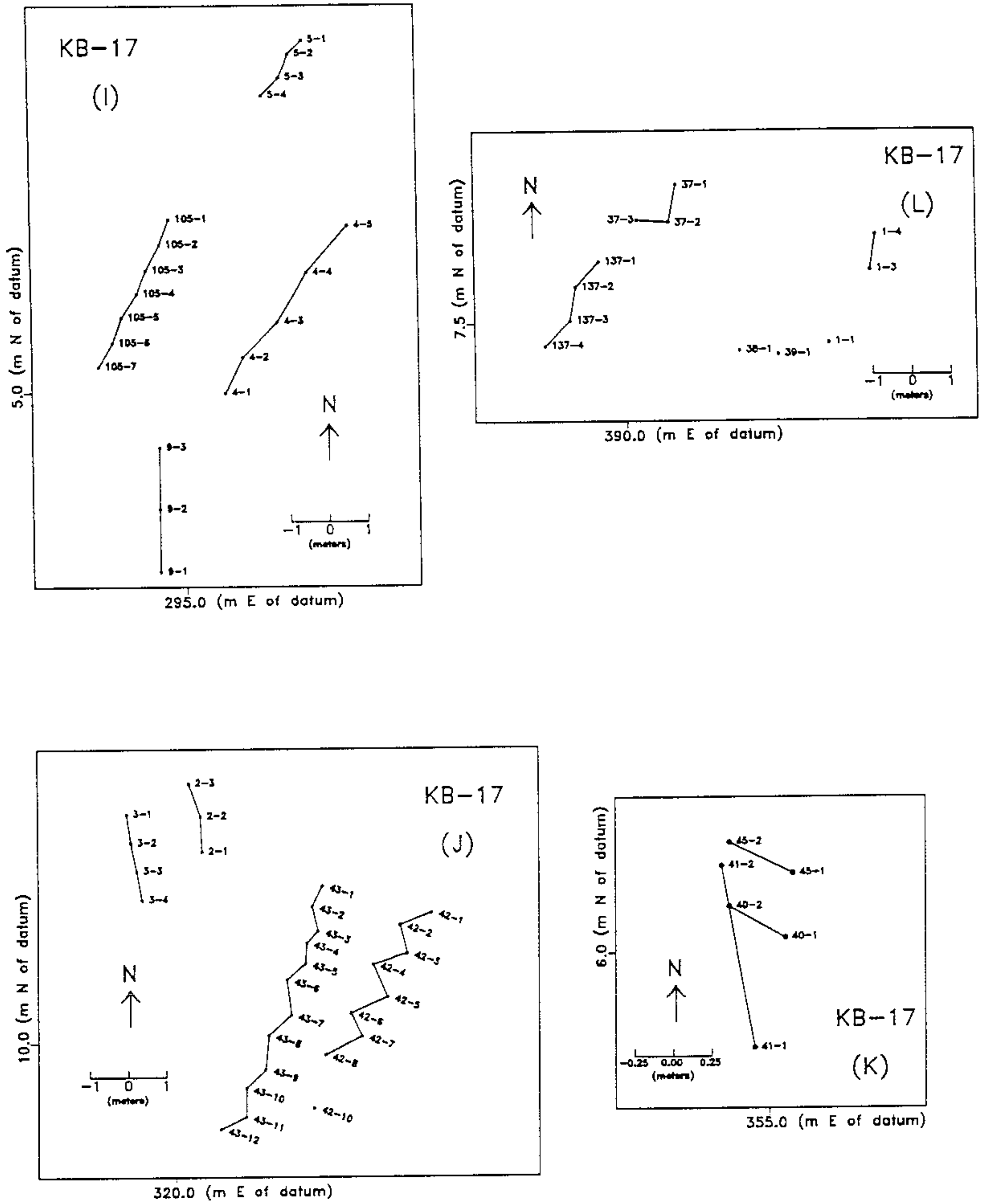


Figure 24 (continued). Detail of trackway concentrations at locality KB-17, south of Manangia, Koum basin, northern Cameroon.

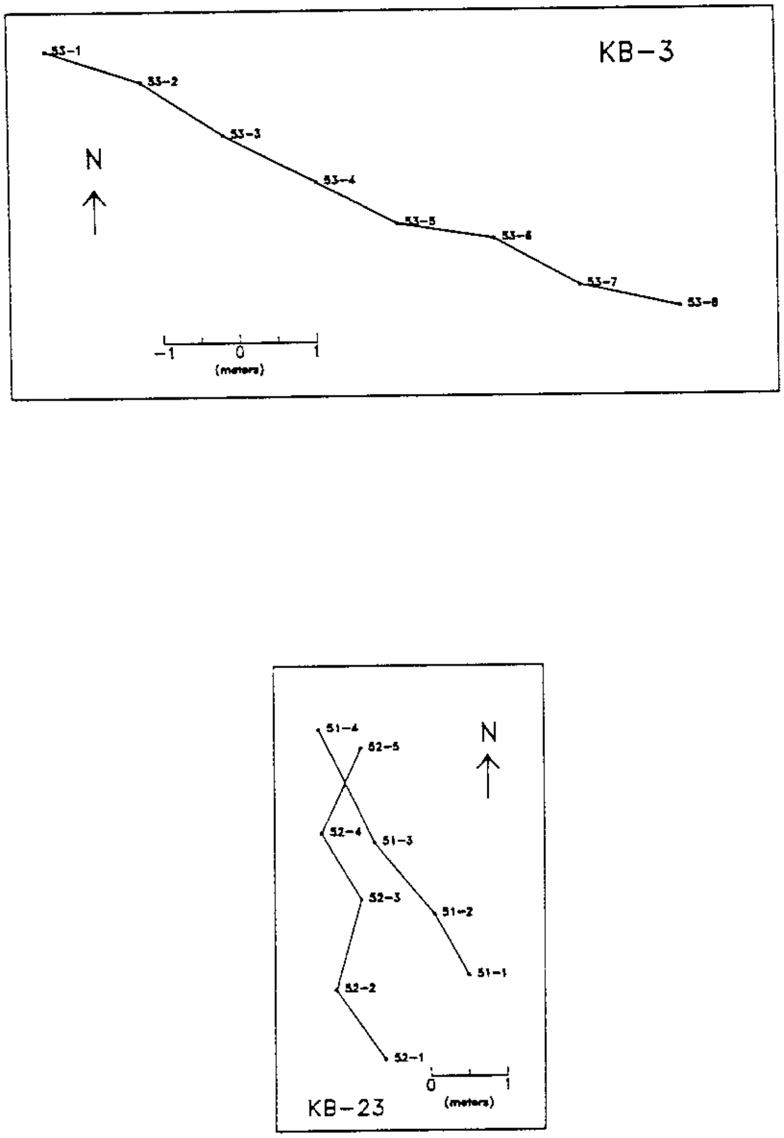


Figure 25. Detail of trackway concentrations at localities KB-3 and KB-23, Koum basin, northern Cameroon.

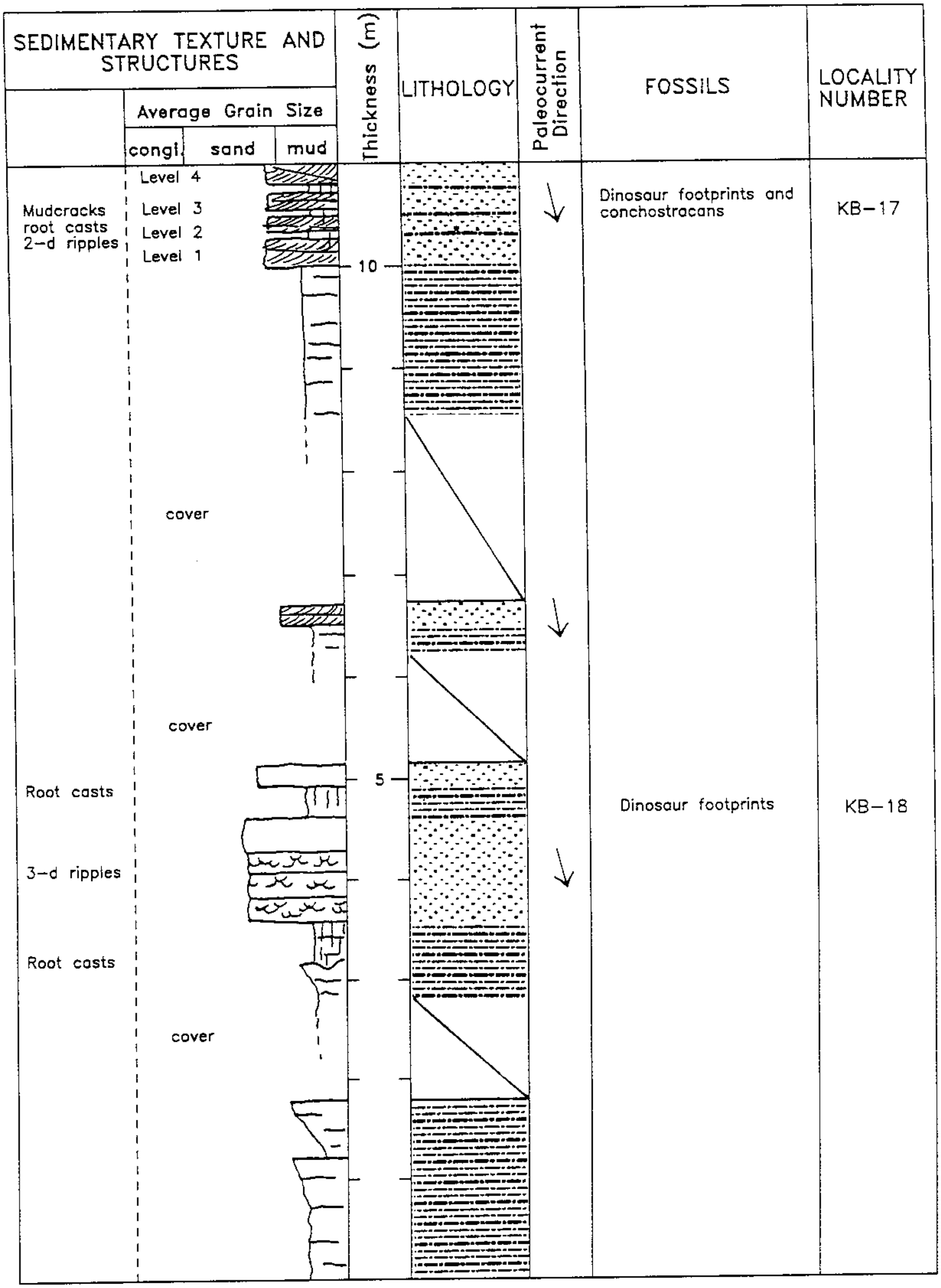


Figure 26. Stratigraphic column of footprint-bearing sediments at KB-17 and KB-18, south of Manangia, Koum basin, northern Cameroon. See figure 6 for explanation.

distinct sand sheet, possibly deposited by fluvial flood waters. These sands were later covered by muddy sediments, which served as a plane of separation between each sheet. Each is between 10 and 15 cm thick, and the fine-grained layers are from 3 to 8 cm thick. The surface upon which the trackmakers walked was in most cases probably the fine-grained layer, which when wet did not inhibit the underlying sand from taking a detailed impression of the foot.

Sedimentary structures present in the footprint-bearing levels include mudcracks and mudcrack casts from several centimeters to up to a meter in diameter. These features are not of themselves diagnostic of subaerial dessication, and may instead be the product of syneresis. However, several footprints (notably 33-5, 34-9, and 34-10) are themselves mud-cracked depressions on a non-mudcracked surface. Root casts are present in at least one level (level 3), indicating that vegetation was present on or above the track-bearing levels. Asymmetrical and symmetrical 2-d ripples are common on the surfaces of footprint levels 1 - 3 (the surface of level 4 is too weathered to preserve these features). Symmetrical ripples are sometimes attributed to wind action on calm shallow water (Tucker and Burchette 1977). No ripples occur within the footprints themselves; however, no footprints were observed to have truncated any ripples. The distinct and detailed preservation of many of the footprints argues that they were impressed when the substrate was subaerially exposed. The presence of mudcracks in only three closely associated footprints out of a total of 21 trackway 33 and 34 footprints suggests that these three were impressed in an area of water-saturated sediment or in a shallow pool of standing water. Trackway 3 demonstrates a similar phenomenon, where the trackmaker progressed from a relatively firm substrate that accepted clear pes impressions to an incohesive, muddy substrate that resulted in indistinct footprints. The digit impressions of these last footprints are infilled with collapsed mud.

Figure 27 is a plot of frequency of footprint types by stratigraphic level (footprint type is defined in the following section). Levels 2 and 3 have the greatest trackmaker diversity (5 types), level 1 has four types, and level 4 only one. These differences may be explained in two ways: there were fewer types of trackmakers present at the locality when levels 1 and 4 were freshly deposited; or, the differences reflect a preservational or collecting bias, *i.e.*, weathering of the outcrop surface has obliterated all but the largest and deepest footprints on level 4, and poor exposure of level 1 inadequately reflects the true diversity. The latter probably best explains the observed trackway-type distributions, since level 4 is badly weathered (it is the highest and therefore the longest-exposed level) and level 1 is the lowest level, and much of it is covered by the three succeeding levels.

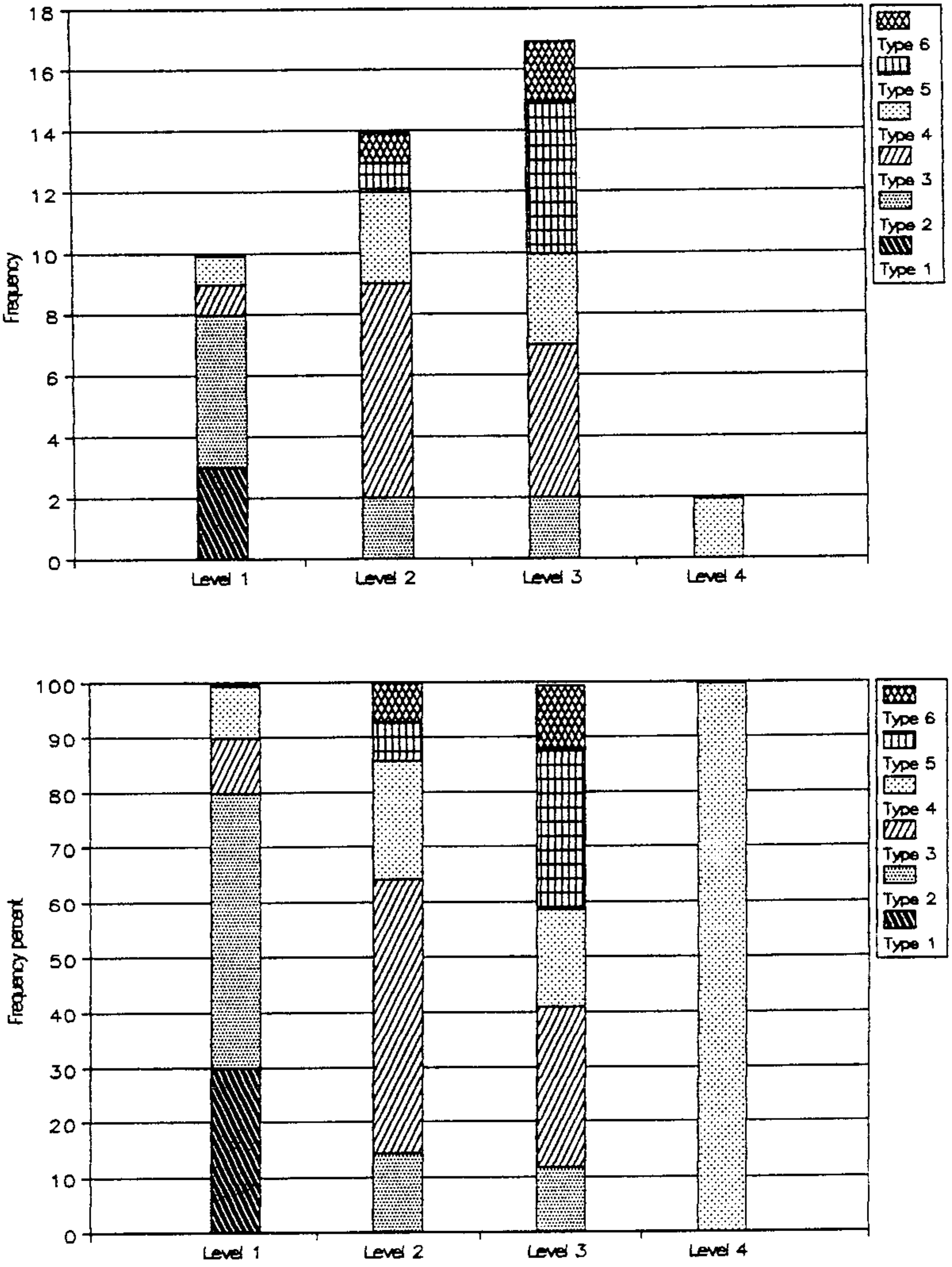


Figure 27. Frequency of trackmaker types by stratigraphic level at locality KB-17, Koum basin, northern Cameroon. a - absolute frequency of trackmaker-type by stratigraphic level. b - trackmaker-type frequency normalized to 100%.

Definition of Footprint Morphotypes

The Koum basin footprints separate into five distinct groups based on their morphology and size. The smallest (type 1) and largest (type 7) compose two distinct groups, defined by the extremity of their sizes. A third group (type 5) encompasses ichnites of only two or three distal digit impressions. A fourth group (type 6) contains relatively indistinct undertracks. The remaining trackways (73% of the total) are tridactyl pes impressions of bipedal trackmakers, and form a group of three ichnite types (types 2, 3, and 4) that intergrade in size and morphology. Since these three types are difficult to discriminate objectively, several different approaches were taken to supply a quantitative classification.

Bivariate plots used to discriminate footprint types

A number of bivariate plots of footprint data were made to test the subjective footprint classification. Out of numerous combinations of variable pairs, the following plots work best to discriminate types 2, 3, and 4 footprints: size index versus digit III skewness (figure 28a); and size index versus digit1 proportion (figure 28b).

Weems (1987) used bivariate plots of trackway variables, such as pace angle versus pace length and relative stride length versus pace angle, speed, and striding rate to discriminate six distinct trackmakers in a

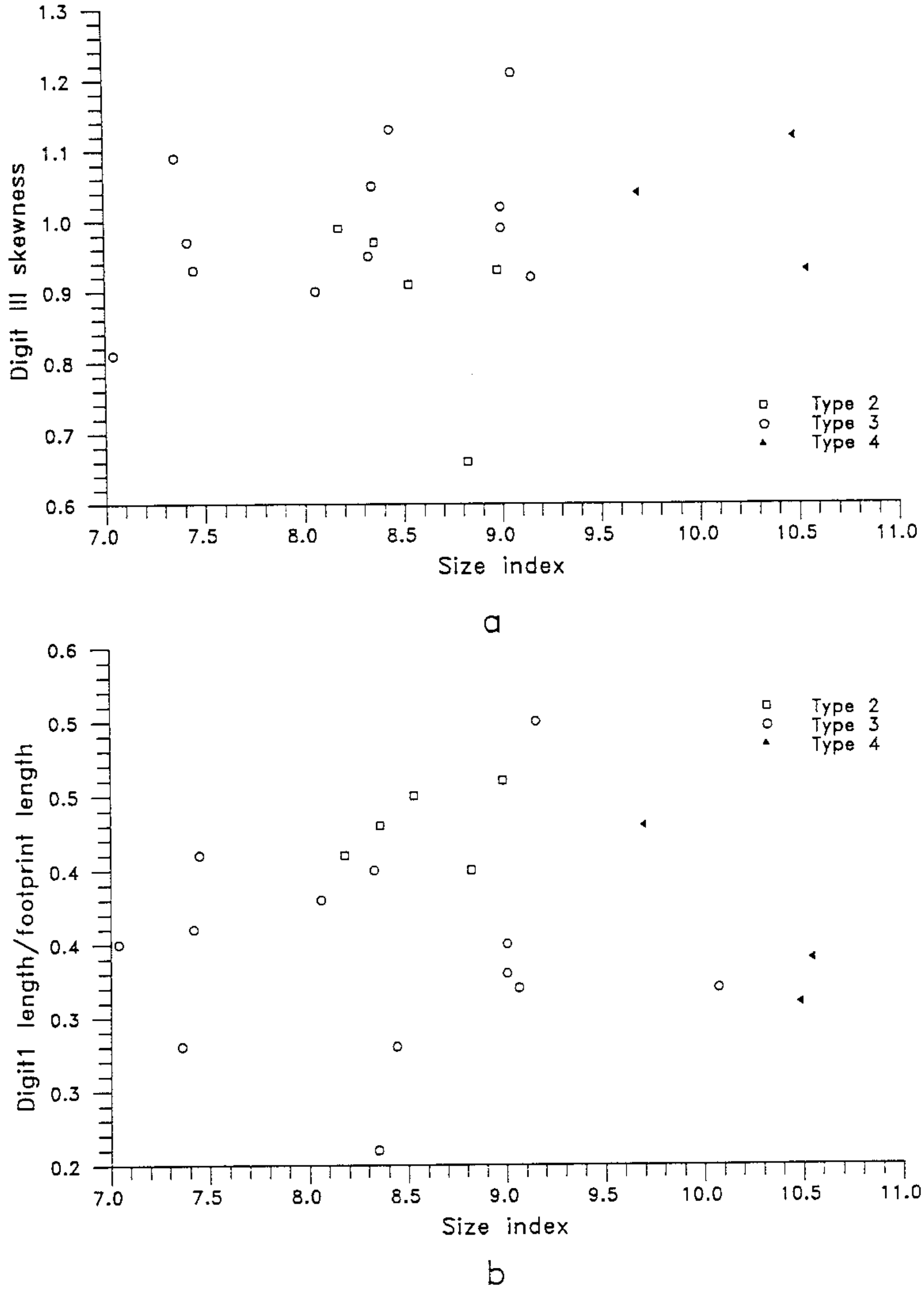


Figure 28. Scatter plots of variables useful for discriminating between tridactyl bipedal footprints from the Koum basin, northern Cameroon.

large population of dinosaur footprints. These variables have only limited discriminating ability with Koum basin footprints, probably because they are strongly influenced by behavior (see discussion on behavior below and figures 36 and 37). Nevertheless, pace angle versus footprint width (figure 29; equivalent to figure 10 in Weems [1987]) allows some discrimination of footprint types. Thulborn and Wade (1984) successfully produced clusters of different footprint types by plotting footprint length against pace/footprint length (the equivalent of relative stride length). Figure 36b is a similar plot for Koum basin footprints. Type 4 footprints are segregated, but types 2 and 3 overlap extensively. It is clear that the best variables for discriminating within this sample are related to footprint size, digit proportion, and digit morphology.

Principal Component Analysis

General remarks

Principal component analysis (PCA) is a multivariate technique used for examining relationships among several variables. It operates by rotating the axes of the original coordinate system into orthogonal axes paralleling the direction of maximum variation (principal components) of the original observations (Reyment *et al.* 1984). PCA is a valuable exploratory tool that can be used to to summarize data, detect linear relationships, or reduce the number of

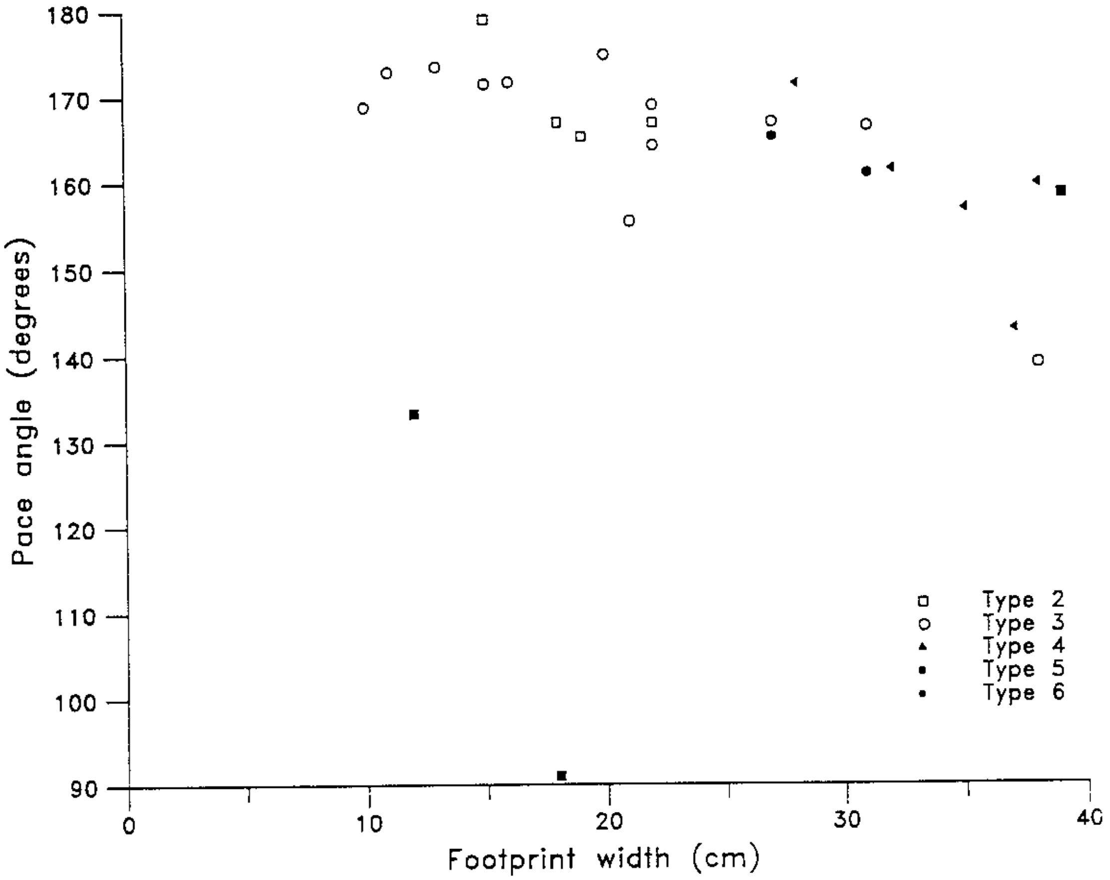


Figure 29. Pace angle versus footprint width for Koum basin footprints. Data averaged by trackway.

variables used in other multivariate analyses (SAS Institute, 1985b).

In morphometric analyses, the first few principal components usually account for most of the variability between individuals (Reyment *et al.* 1984), with the first considered a size vector. The remaining principal components summarize shape relationships.

Principal component scores (linear combinations of the original variables) can be plotted against one another to discern data clusters. Several examples using fossils and extant organisms are given by Bookstein *et al.* (1985) and Reyment *et al.* (1984). Demathieu and Wright (1988) used plots of principal component scores to successfully cluster Chirotherioid ichnotaxa.

Results of PCA

PCA was done using twenty morphological variables for the Koum basin footprint sample. The analysis works only on footprints for which complete data are available; the morphological variables alpha and beta as well as all trackway data were excluded because of their incompleteness.

The results indicate that the first five principal components account for 91.5 percent of the variability in the data set. Principal component 1, accounting for 39.5 percent of the variability, loads heavily on size-related variables, specifically footprint length, width, area and size index. Principal component 2 accounts for 23.3 percent of the variability in the data set and loads heavily on morphological variables that describe digit shape. Digit

Table 9.--Results of PCA on 20 morphological variables for the Koum basin footprint sample (n=67 observations).

Variance scores

	Eigenvalue	Difference	Proportion	Cumulative
PRIN1	8.01869	3.35851	0.400934	0.40093
PRIN2	4.66018	1.85787	0.233009	0.63394
PRIN3	2.80231	1.19923	0.140116	0.77406
PRIN4	1.60309	0.25336	0.080154	0.85421
PRIN5	1.34972	0.52444	0.067486	0.92170

Principal component loadings

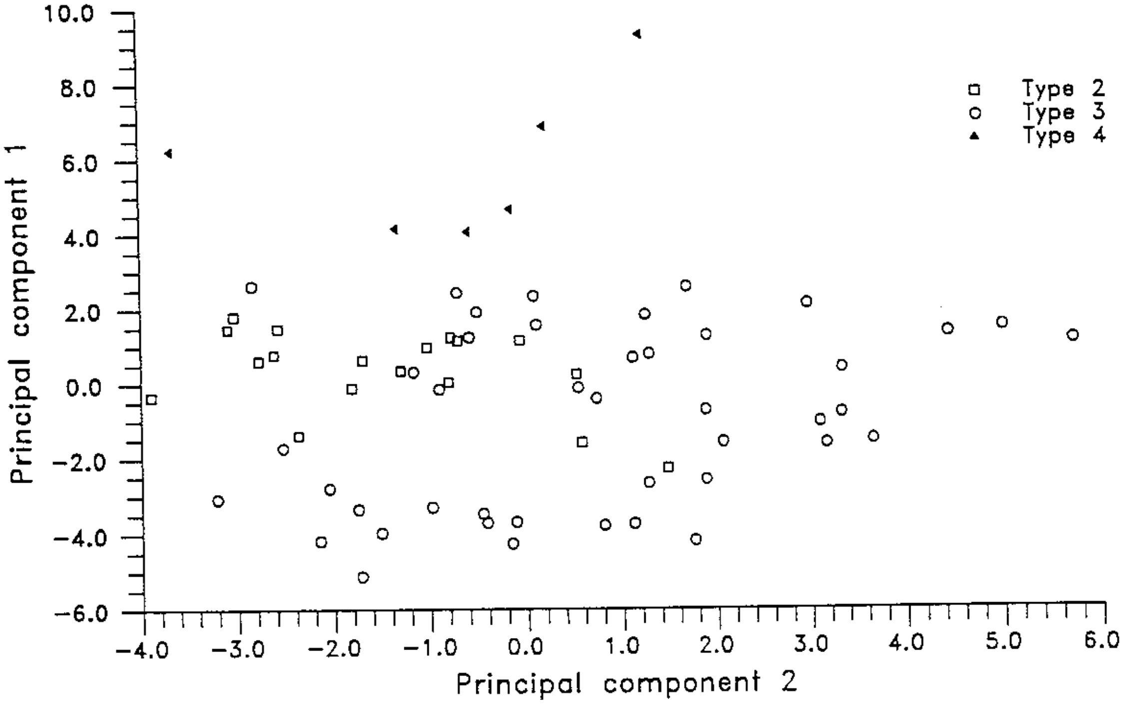
	PRIN1	PRIN2	PRIN3	PRIN4	PRIN5
FL	0.333473	0.086705	-.055471	0.138430	-.102947
FW	0.342708	-.032935	-.067539	-.089780	0.029170
ARA	0.333615	0.002595	-.092513	0.016700	-.040590
SI	0.342194	0.034241	-.031821	-.039664	-.041542
LW	-.140372	0.214678	-.016658	0.491328	-.332090
D1	0.311149	-.163252	0.104037	0.156609	-.008114
D2	0.242917	-.147175	0.279218	0.218698	-.192933
D3	0.277694	0.108926	0.259828	0.248434	0.066461
D4	0.263431	0.164793	0.280224	-.091932	-.224559
D1P	0.089341	-.353495	0.241656	0.072853	0.138190
D2P	-.156802	-.285860	0.367339	0.068575	-.006381
D3P	-.110641	0.014663	0.485737	0.156840	0.360337
D4P	-.021138	0.126290	0.491934	-.331190	-.164078
D1P2	0.193390	-.310739	-.124385	0.085008	0.102986
D2P2	-.199278	-.299640	-.054945	0.109034	-.222089
D3P2	-.064153	0.354516	0.027360	0.242687	0.424998
D4P2	0.042749	0.342478	0.125565	-.418250	-.274016
SKEW	0.092276	0.389242	0.006225	0.074675	0.368042
DA	0.094969	-.230431	-.003379	-.429088	0.385783
FD	0.273988	-.006154	-.203372	0.007824	0.083304

III skewness is the most important, followed by D3P2, D1P (digit1/footprint length), and D4P2. Principal component 3 loads most heavily on D3P and D4P; it accounts for 14 percent of the observed variability. Accounting for 14.7 percent of the variability in the data set are principal components 4 and 5, which also load heavily on morphological variables; footprint length/footprint width, angle of divarication, and several digit proportions are the most important variables.

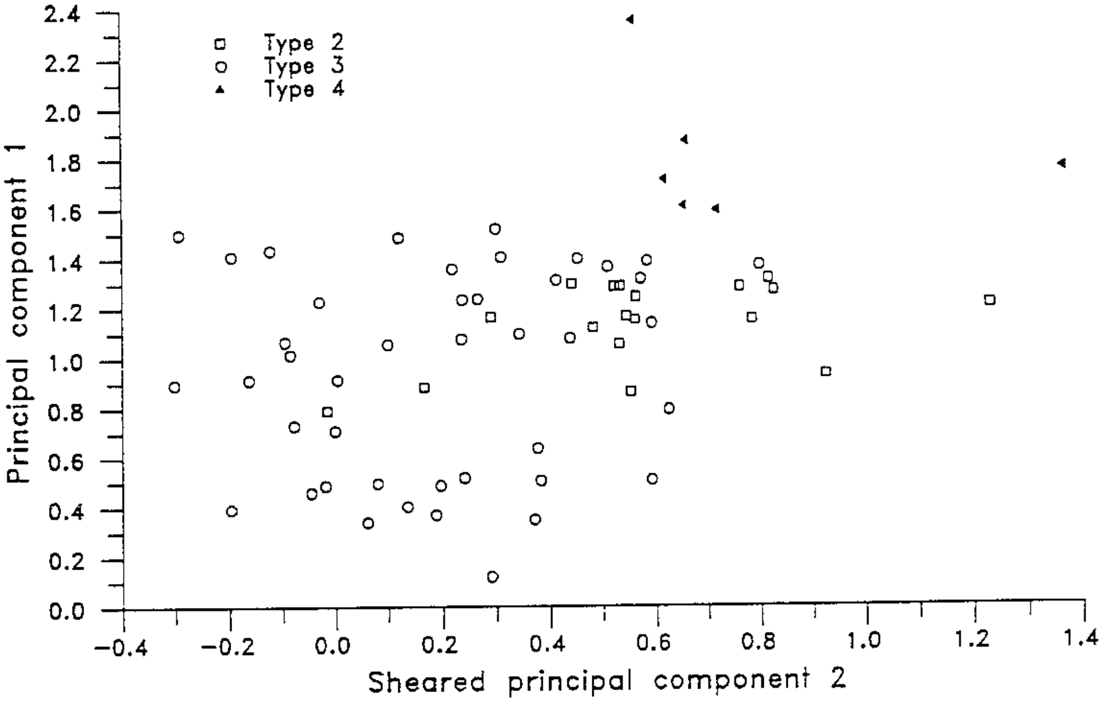
Discussion

Size-related variables account for about 40 percent of the variability in the footprint data set from the Koum basin. The remainder is accounted for by shape-related variables, mostly those that describe the relative proportions and shapes of the digits. It is therefore clear that measures of overall footprint size and digit shape are the most important variables in this data set.

Discrimination of footprint type using a bivariate plot of the first two principal components is moderately successful (figure 30a). Footprint type 4 forms a distinct cluster. There is some overlap of footprint types 2 and 3, which have considerable overlap in actual size. Demathieu and Wright (1988) produced clusters of different Chirotherioid ichnotaxa by plotting these principal components (1 and 2). Discrimination of footprint type using bivariate plots of principal components 2 and 3 was



a



b

Figure 30. Scatter plots of principal component scores for morphological variables of Koum basin footprints. See text for explanation.

unsuccessful, with all three footprint types overlapping considerably.

To remove the effects of overall size variables on principal component analyses, Bookstein et al. (1985) have proposed a method of shearing the first principal component from the others. This method of "size-free discrimination" was applied to the same data analysed above. Results are summarized in table 10. Figure 30b is a bivariate plot of principal component 1 versus sheared principal component 2. It is similar to figure 30a, except that discrimination of types 2 and 3 footprints is very slightly enhanced. Plotting sheared principal component 2 against sheared principal component 3 does not successfully discriminate footprint type; footprint type 4 data points all plot to one side of the data scatter, and fall within the general cloud; footprint types 2 and 3 overlap extensively.

The results of the sheared principal component analysis indicate that, on the basis of scores for principal components 1 and 2, footprint type 4 is distinct from types 2 and 3. Type 2 forms a relatively tight cluster embedded within the type 3 data scatter, with several outlying points. Since principal components 2 and 3 (which load on morphological variables) together fail to discriminate footprint type, size seems to be the single most important variable for this purpose.

Table 10.--Results of PCA on 20 morphological variables for the Koum basin footprint sample (n=67 observations).

Sheared principal component loadings

	PRIN1	PRIN2	PRIN3	PRIN4	PRIN5
FL	0.328789	0.075493	-.130416	0.058787	0.223201
FW	0.321493	0.165459	-.100424	-.028247	-.036358
FD	0.236475	0.119537	-.216409	0.048197	-.005343
D1	0.276888	0.239993	0.081415	0.135519	0.040656
D2	0.223826	0.200964	0.190083	0.113330	0.341076
D3	0.300710	0.007027	0.178372	0.203074	0.163743
D4	0.294028	-.015330	0.174434	-.173654	0.185121
DA	0.097938	0.229567	0.064720	-.091958	-.424742
LW	-.105653	-.227491	-.233330	0.195358	0.457483
ARA	0.278459	0.118749	-.122193	0.005878	0.039886
SI	0.371421	0.130923	-.104906	-.023199	0.070192
D1P	0.065159	0.325828	0.323922	0.159408	-.220431
D2P	-.218873	0.159564	0.460306	0.050786	0.172488
D3P	-.113814	-.158026	0.578341	0.229803	-.136499
D4P	-.013185	-.179484	0.541926	-.391421	-.048611
SKEW	0.120224	-.268861	0.020505	0.169031	-.231179
D1P2	0.147777	0.319766	-.042076	0.151124	-.211636
D2P2	-.287704	0.172290	0.115069	0.051766	0.391361
D3P2	-.043067	-.403427	0.065079	0.558112	-.148427
D4P2	0.080804	-.247685	0.100473	-.494002	0.028015

Factor analysis

Factor analysis is a multivariate technique similar to principal component analysis. A factor corresponds to an eigenvector of variance in a multidimensional data cloud, and is normally orthogonal to other variance vectors (Reyment *et al.* 1984). The results are interpreted similarly to PCA; each factor is defined by variables which "load" on it. These variables are the principal contributors of variance to the factor. Communality estimates for each variable are included. These quantify the proportion of variance in the raw data set accounted for by each variable.

Results of factor analysis

Factor analysis of the same data set used in the preceding PCA was limited to three factors, accounting for over 77 percent of the variance in the raw data (table 11). Loadings on each factor are similar to those generated by the PCA, and each can be interpreted as a discriminant for each of the three footprint types included in the analysis: factor 1 is a size component, and is diagnostic of footprint type 4; factor 2 is diagnostic of type 3 footprints, loading heavily on digit III skewness and variables which describe a relatively long digit IV and short digit II; factor 3 loads on variables which describe relatively long toes and small feet, which is diagnostic of type 2 footprints. Final communality estimates indicate that most variability for all variables except footprint length/footprint width and angle of divarication are accounted for by this analysis.

Discussion

A set of strong footprint type discriminators is generated by factor analysis when the analysis is limited to three factors. Figure 31a is a plot of factor scores of individual footprints. Three clusters, each corresponding to a footprint type, are apparent. Footprint type 4 has the best discrimination, which is attributed to factor 1 (the

Table 11.--Results of factor analysis using 20 morphological variables on Koum basin footprint types 2, 3, and 4.

Factor pattern (loadings)

	FACTOR1	FACTOR2	FACTOR3
FL	0.94430	0.18717	-0.09286
FW	0.97046	-0.07110	-0.11306
ARA	0.94471	0.00560	-0.15487
SI	0.96900	0.07392	-0.05327
LW	-0.39750	0.46343	-0.02789
D1	0.88109	-0.35242	0.17416
D2	0.68788	-0.31771	0.46741
D3	0.78636	0.23514	0.43495
D4	0.74596	0.35575	0.46910
D1P	0.25299	-0.76310	0.40454
D2P	-0.44402	-0.61710	0.61493
D3P	-0.31330	0.03165	0.81313
D4P	-0.05986	0.27263	0.82350
D1P2	0.54763	-0.67081	-0.20822
D2P2	-0.56430	-0.64685	-0.09198
D3P2	-0.18166	0.76531	0.04580
D4P2	0.12105	0.73932	0.21020
SKEW	0.26130	0.84027	0.01042
DA	0.26893	-0.49744	-0.00566
FD	0.77586	-0.01329	-0.34045

Variance accounted for by factors 1-3 - 15.48117

Proportion of total variance - 0.77405

Final communality estimates:

FL	0.935368	D2P	0.956102
FW	0.959625	D3P	0.760340
ARA	0.916485	D4P	0.756065
SI	0.947264	D1P2	0.793234
LW	0.373553	D2P2	0.745305
D1	0.930848	D3P2	0.620797
D2	0.792590	D4P2	0.605433
D3	0.862832	SKEW	0.774446
D4	0.903070	DA	0.319801
D1P	0.809981	FD	0.718039

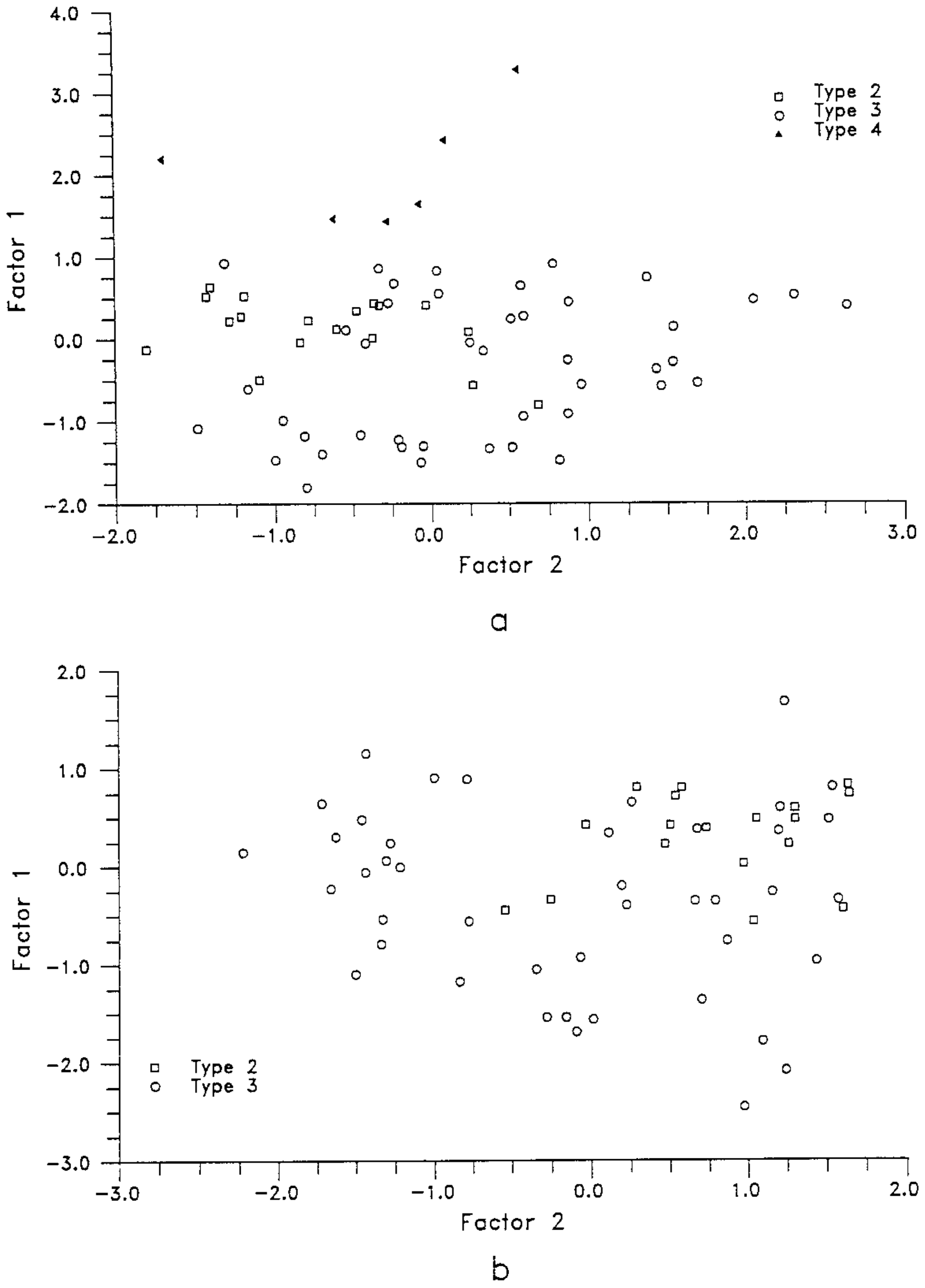


Figure 31. Plots of factor 1 versus factor 2 scores for two factor analyses. a - analysis of footprint types 2, 3, and 4. b - analysis of footprint types 2 and 3.

size factor).

A second factor analysis was executed without footprint type 4 in the data set to explore the relationship between types 2 and 3 footprints. Results are summarized in table 12. Factor 1 represents a large size component, factor 2 describes footprints with a relatively long digit II and negative digit III skewness, and factor 3 represents small footprints with a relatively long digit IV. Figure 31b plots factor 1 scores against factor 2 scores, and demonstrates a clear separation between types 2 and 3 footprints.

Discriminant analysis

General remarks

Discriminant analysis is a multivariate technique used to objectively test classifications of observations. It develops a discriminant function, or classification criterion, from a measure of generalized squared distance between groups (SAS Institute 1985b). The criterion for the analysis presented here is based on the pooled covariance matrix.

The effects of size on discriminant analyses is discussed by Bookstein *et al.* (1985), who concluded that conventional discriminant analyses largely expressed size differences between groups, instead of differences in proportion. To detect these effects, analyses were performed on both size-independent and size-dependent data.

Table 12.--Results of factor analysis using 20 morphological variables on Koum basin footprint types 2 and 3.

Factor pattern (loadings)

	FACTOR1	FACTOR2	FACTOR3
FL	0.92498	-0.17605	-0.11636
FW	0.91700	0.19802	-0.25637
ARA	0.95915	0.04849	-0.17783
SI	0.95885	0.02979	-0.20734
LW	-0.27900	-0.53815	0.21491
D1	0.73235	0.58304	0.11894
D2	0.66657	0.48474	0.39447
D3	0.83157	-0.07767	0.43294
D4	0.87878	-0.15723	0.32728
D1P	0.14551	0.87293	0.24936
D2P	-0.33588	0.69672	0.59595
D3P	-0.06969	0.09743	0.87900
D4P	0.35260	-0.07871	0.70131
D1P2	0.20316	0.77578	-0.29769
D2P2	-0.65847	0.52674	-0.03433
D3P2	-0.03303	-0.77876	0.21884
D4P2	0.44256	-0.63664	0.08827
SKEW	0.35605	-0.78576	0.09124
DA	0.12573	0.54517	-0.23022
FD	0.56265	0.01197	-0.43590

Variance accounted for by factors 1-3 - 15.23285

Proportion of total variance - 0.76164

Final communality estimates:

FL	0.900118	D2P	0.953380
FW	0.945825	D3P	0.786989
ARA	0.953941	D4P	0.622352
SI	0.963273	D1P2	0.731723
LW	0.413631	D2P2	0.712215
D1	0.890410	D3P2	0.655454
D2	0.834886	D4P2	0.608966
D3	0.884978	SKEW	0.752513
D4	0.904083	DA	0.366019
D1P	0.845360	FD	0.506730

To determine whether trackway (behavioral) data may be used to develop meaningful classification criteria, two data sets containing trackway variables were analyzed. The four data sets analyzed consist of: (1) morphological footprint measurement proportions (size-free data); (2) a mixture of proportions and distance measurements of footprints; (3) trackway proportions, angles, and distances; (4) a mixture of footprint and trackway proportions and distances.

Results of discriminant analyses

For a data set of 67 observations consisting of the 20 morphological variables FL, FW, FD, D1, D2, D3, D4, DA, LW, ARA, SI, D1P, D2P, D3P, D4P, D1P2, D2P2, D3P2, D4P2, and SKEW, a total of eight observations required reclassification. Twenty trackways are represented in this data set. Table 13 summarizes the results. All misclassifications occurred between footprint types 2 and 3; type 4 had no misclassified members.

A discriminant analysis on a data set of 70 observations for the morphologic ratios D1P, D2P, D3P, D4P, D1P2, D2P2, D3P2, D4P2, SKEW, and LW produced 21 reclassifications. A total of 21 trackways are represented in this data set. Results are summarized in table 13. Misclassified observations occurred between all three footprint types.

For a data set of 60 observations for five trackway variables (P, TW, PA, PI, and FRT). Seventeen trackways are

Table 13.--Number of observations classified into footprint types 2, 3, and 4 before and after discriminant analysis.

Twenty morphological measurements and ratios:

Footprint type	2	3	4	Original totals
2	18	3	0	21
3	5	35	0	40
4	0	0	6	6
Reclassified totals	23	38	6	67

Ten morphological ratios:

Footprint type	2	3	4	Original totals
2	13	8	1	22
3	8	31	2	41
4	1	1	5	7
Reclassified totals	22	40	8	70

represented in this data set. Twenty-three observations required reclassification. The results are summarized in table 14. All footprint types in this analysis contributed a significant number of misclassified observations.

Table 14 summarizes the results of a discriminant analysis on a data set of 28 observations with 5 morphologic

Table 14.--Number of observations classified into footprint types 2, 3, and 4 before and after discriminant analysis.

Five trackway variables:

Footprint type	2	3	4	Original totals
2	10	1	1	12
3	8	16	6	30
4	1	6	11	18
Reclassified totals	19	23	18	60

Five morphological and five trackway variables:

Footprint type	2	3	4	Original totals
2	8	0	0	8
3	3	14	0	17
4	0	0	3	3
Reclassified totals	11	14	3	28

variables (FW, DA, LW, SI, and SKEW) and 5 trackway variables (P, TW, PA, PI, and FRT). A total of 12 trackways are represented in this data set. The variables for this analysis were chosen to balance morphologic and trackway variables and to minimize the number of observations excluded as a result of incomplete data. Misclassified observations were limited to type 3 footprints, and required 3 reclassifications.

Discussion

The most successful discrimination was achieved on the data set consisting of five morphological and five trackway variables, with 10.7 percent of the observations misclassified. However, this data set was the smallest analyzed (n=28). Similar but more significant results were attained using the footprint ratio and distance measurement data set (n=67); 11.9 percent of the observations were misclassified. Misclassifications were in no cases serious in either of these analyses; they were limited to the minority of footprints out of a larger trackway group (*e.g.*, in the analysis of the ratio and distance data set, one trackway five footprint was reclassified from type 2 to type 3; the remaining eight were correctly classified).

Results were inconsistent using a data set composed of morphological ratios alone. This analysis reclassified five out of nine trackway 5 footprints from type 2 into both type 3 and type 4. Three out of seven trackway 20 footprints were reclassified from type 3 into both types 2 and 4.

Poor results were also achieved using trackway variables alone. This analysis suggested serious classification problems; for example, all trackway 22 footprints were reclassified from type 4 to type 3, and seven out of eight trackway 26 footprints were reclassified from type 3 to type 2. It is clear that the trackmakers responsible for the different footprint types were capable of behaving similarly to one another (so far as characteristics of gait were concerned). Classifications based on these variables alone are probably unreliable.

From these results it is apparent that a mixture of morphological ratios and footprint size measurements are the most effective variables for discriminating footprint type from quantitative data. Morphological ratios or trackway variables alone do not provide reliable or consistent results.

Systematic Paleoichnology

Type 1

Referred specimens: Trackways 40, 41, 45.

Locality: KB-17, south of Manangia, Koum basin, northern Cameroon.

Description: Small triangular tridactyl footprints about 7 cm in total length, width from 4 to 6 cm, made by a bipedal trackmaker (figure 32a; table 15). Digit impressions equal about one-third to one-half the overall footprint length. Angle of divarication is between 45° and 52°. No type 1 trackway contains more than two footprints, so characteristics of stride and gait are not known; pace ranges from 40 to 118 cm.

Discussion: Type 1 is represented by six footprints in three trackways. These footprints are shallow and not easily observed, suggesting that sampling bias may account for their relative scarcity. The affinity of the trackmaker is unclear, because relatively poor preservation of the prints does not allow the details of pes morphology to be observed. The trackmaker may have been a juvenile member of a species with large adults or may have been an adult of small size. Though they are small, the tracks were most likely made by a dinosaur because the trackmaker was a bipedal animal and the pes impressions are more robust than those made by birds.

Table 15.--Descriptive statistics of type 1 footprints from the Koum basin, northern Cameroon.

Variable	N	$\overline{X}$	Standard deviation	Range Min.	Range Max.
FL	4	7	0.000	7	7
FW	4	4.75	0.957	4	6
ARA	4	29.5	10.344	21	42
LW	4	1.511	0.241	1.228	1.75
D1	0	...	...	...	...
D2	0	...	...	...	...
D3	0	...	...	...	...
D4	0	...	...	...	...
D1P	0	...	...	...	...
D2P	0	...	...	...	...
D3P	0	...	...	...	...
D4P	0	...	...	...	...
D1P2	0	...	...	...	...
D2P2	0	...	...	...	...
D3P2	0	...	...	...	...
D4P2	0	...	...	...	...
SKEW	0	...	...	...	...
DA	4	47.5	3.109	45	52
A	0	...	...	...	...
B	0	...	...	...	...
FD	4	0.775	0.150	0.7	1
FRT	0	...	...	...	...
MASS	3	8	0.000	8	8
S	0	...	...	...	...
P	3	67.67	43.662	40	118
TW	0	...	...	...	...
PA	0	...	...	...	...
PI	0	...	...	...	...
RSL	0	...	...	...	...
SMS	0	...	...	...	...
STRT	0	...	...	...	...

Variable symbols explained in text.

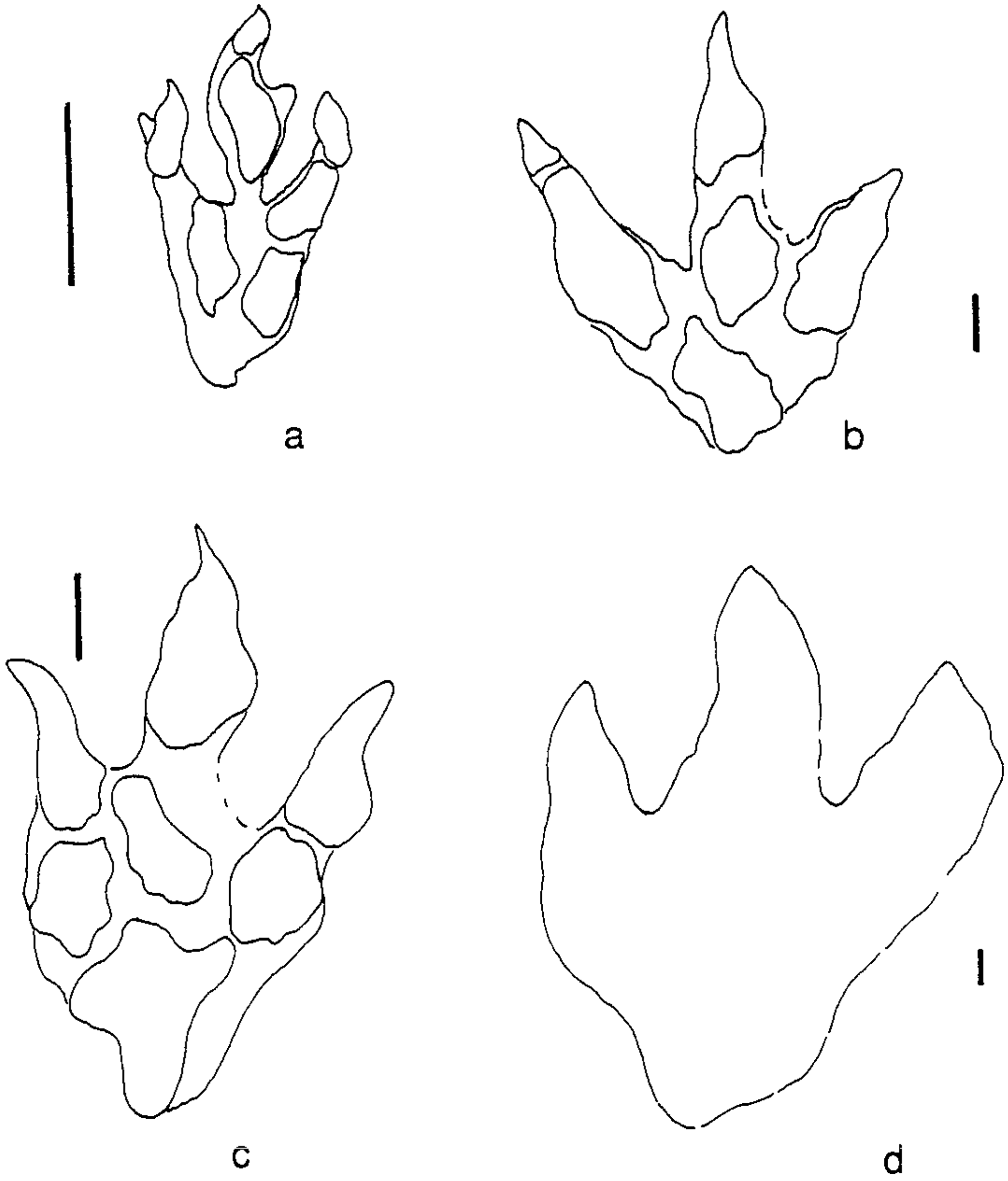


Figure 32. Footprint types from the Koum basin, northern Cameroon: a - type 1 (40-1); b - type 2 (5-10); c - type 3 (34-11); d - type 4 (32-7). Drawings are of right footprints, except a (which is questionable). Scale bars = 5 cm.

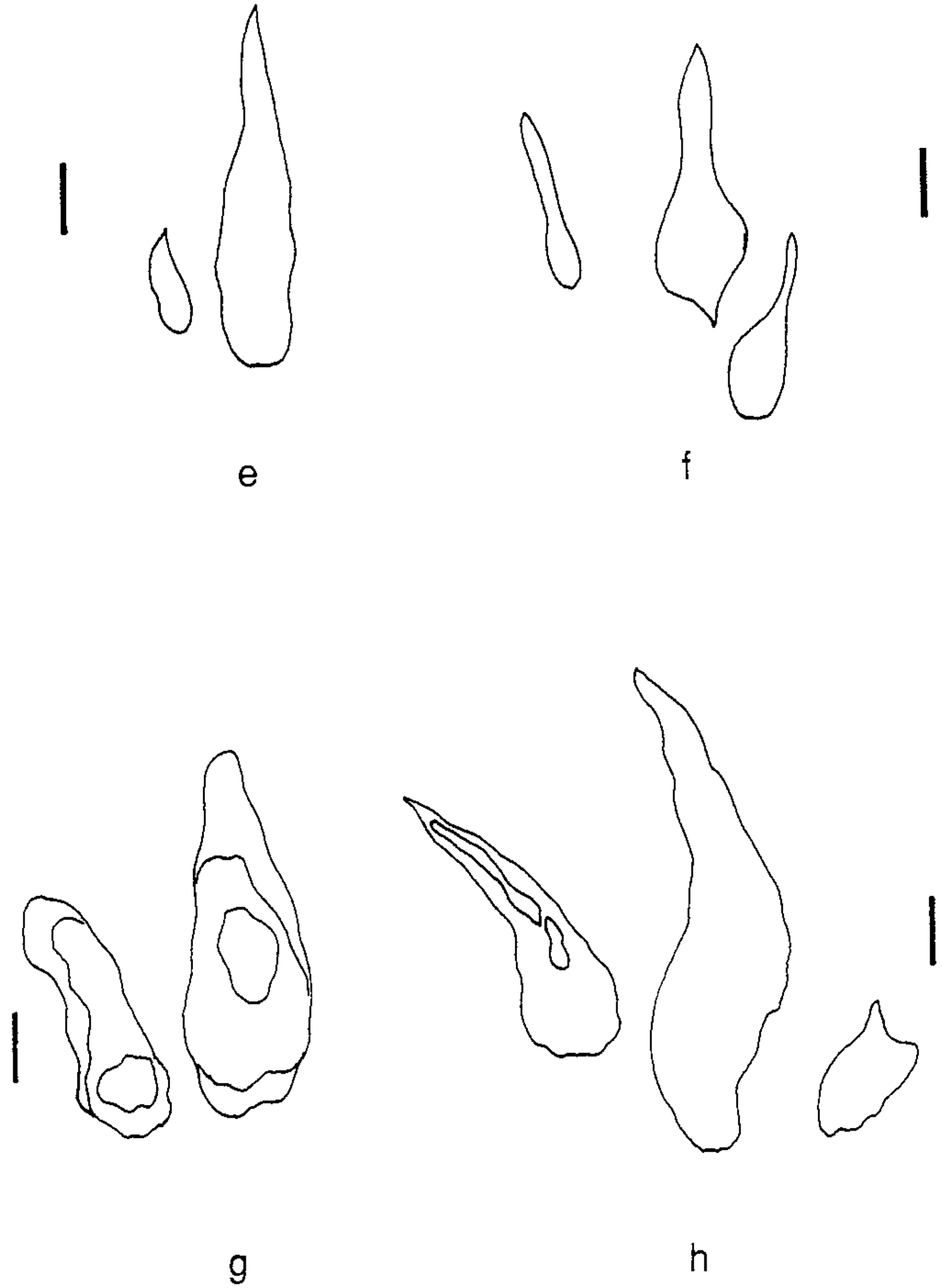


Figure 32 (continued). Footprint types from the Koum basin, northern Cameroon: e - type 5 (11-3), left; f - type 5 (14-2), right; g - type 5 (33-2) left; h - type 5 (33-1), right. Scale bar = 5 cm.

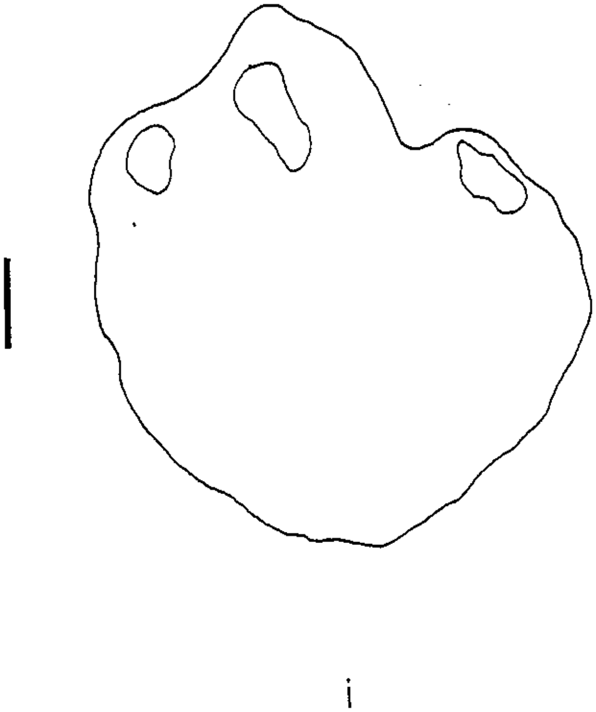


Figure 32 (continued). Footprint types from the Koum basin, northern Cameroon: i - type 6 (8-2), right footprint. Scale bar = 5 cm.

Type 2

Referred specimens: Trackways 1, 4, 5, 7, 9, 19, 38, 39.

Locality: KB-17, south of Manangia, Koum basin, northern Cameroon.

Description: Moderately small tridactyl footprints between 16-27 cm in length and 9-24 cm in width, made by a bipedal trackmaker (figure 32b; table 16). Digit impressions equal about half the overall footprint length. Angle of divarication generally large, reaching a maximum of 75°, but highly variable, ranging from 39° to 75°. In well preserved specimens, digit II impression with 2 pads; digit III with 3 pads; digit IV with 2 pads. Claw impressions seen on all three digits in one footprint in trackway 5. Pace ranges from 52 to 165 cm, with the stride length about twice the pace. Trackway width from 1 to 17 cm. Pace angle about 170°.

Discussion: Type 2 footprints show considerable variability in stride and gait. One trackway (trackway 9) was apparently made by a running dinosaur. Trackway 4 consists of five footprints, the pace length between each consecutive footprint becoming increasingly longer down the trackway, indicating the trackmaker was accelerating. Progressive change in the morphology of each succeeding footprint in trackway 4 demonstrates the changing stance and distribution of weight of the trackmaker in the process of changing gaits (figure 33). On footprints of both trackways 4 and 9, the lateral digit impressions (digits II and IV) are reduced to one pad. The central digit impression (digit III) shows three pads. The great variability of the angle of divarication in type 2 footprints can be attributed to the variable gaits of this trackmaker; slow moving animals in general splay their feet out, while the fastest of the group (9) presented the narrowest foot to the substrate, and hence the smallest angle.

Type 2 footprints are typical of ichnological remains attributed to small carnivorous dinosaurs. They closely resemble *Columbosauripus ungulatus* from the Lower Cretaceous Peace River canyon locality in British Columbia, Canada (Sternberg 1932), attributed to a small theropod dinosaur. A footprint type described from the lower Cenomanian of the Judean Hills by Avnimelech (1966), termed "type A", was considered to be coelurosaurian in affinity. A form from the Lower Cretaceous (?) Antenor Navarro Formation in the Rio do Peixe basin in northeastern Brazil (Leonardi 1979b, 1980c) also corresponds closely in both size and shape with the type 2 footprints from the Koum basin.

Table 16.--Descriptive statistics of type 2 footprints from the Koum basin, northern Cameroon.

Variable	N	$\overline{X}$	Standard deviation	Range	
				Min.	Max.
FL	22	24.182	1.763	20	27
FW	26	19.423	3.911	6	24
ARA	20	425.250	101.405	241	578
LW	22	1.233	0.145	1.02	1.54
D1	26	10.354	2.349	5	14.8
D2	26	14.773	2.951	7.8	21.4
D3	26	13.912	3.187	7.3	20.2
D4	26	8.619	1.934	4.7	11.5
D1P	20	0.446	0.076	0.32	0.67
D2P	20	0.632	0.066	0.49	0.75
D3P	21	0.594	0.100	0.41	0.8
D4P	21	0.378	0.074	0.23	0.52
D1P2	24	0.277	0.050	0.18	0.39
D2P2	24	0.453	0.039	0.38	0.54
D3P2	24	0.412	0.058	0.27	0.55
D4P2	24	0.225	0.048	0.13	0.33
SKEW	25	0.932	0.100	0.66	1.07
DA	22	59.636	8.057	42	75
A	16	29.688	5.413	21	40
B	16	29.313	4.976	20	35
FD	29	2.172	0.784	0.7	4
FRT	14	-0.071	7.237	-15	14
MASS	22	256.318	49.659	148	345
S	16	178.938	67.788	113	320
P	22	91.091	36.055	52	165
TW	15	9.200	4.709	1	17
PA	15	167.267	5.763	157	179
PI	15	0.957	0.074	0.82	1.04
RSL	10	1.576	0.833	0.95	3.31
SMS	10	1.955	1.766	0.78	5.65
STRT	10	0.983	0.367	0.69	1.77

Variable symbols explained in text.

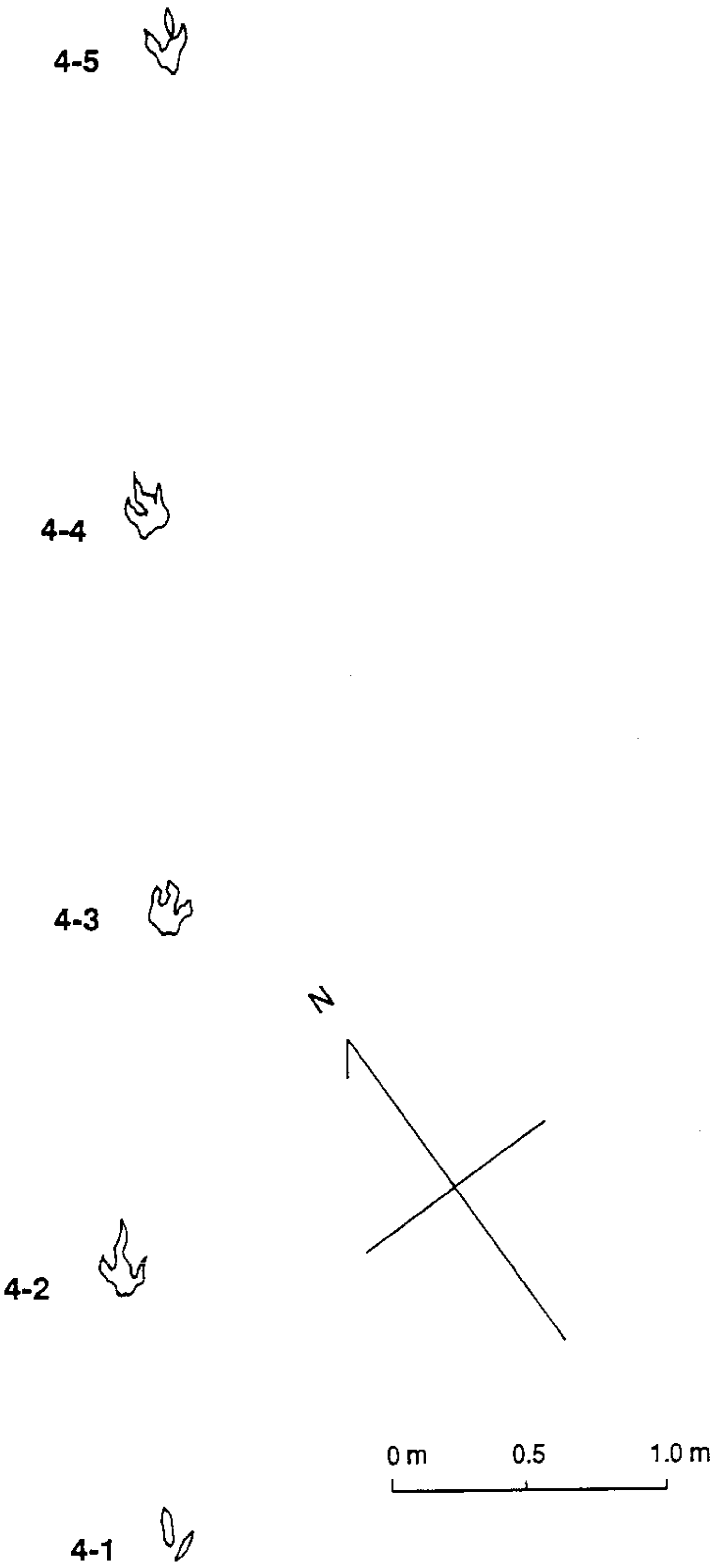


Figure 33. Trackway 4, at locality KB-17, south of Manangia, Koum basin, northern Cameroon.

Type 3

Referred specimens: Trackways 12, 13, 16, 17, 20, 22, 23, 26, 27, 30, 34, 35, 36, 44, 53.

Locality: KB-17, south of Manangia, and KB-3, east of Campement du Rhinoceros, Koum basin, northern Cameroon.

Description: Small to large bipedal tridactyl footprints with distal end of digit II and digit III impressions incurved medially (figure 32c; table 17). Generally triangular in shape, with phalangeal pads commonly well developed. In better preserved specimens, digit II impression displays 3 pads; digit III with 4 pads; digit IV with 3 pads. Distinct claw impressions rarely preserved (see footprints 26-8, 30-4, 35-2); normally, the digit impression is marked by a moderately acuminate termination. Proximal end (the "heel") of footprint commonly acute. Pace length from 63 to 140 cm; stride lengths are about twice the pace. Calculated trackway widths range from 0 to 57 cm; the larger value is anomalous and is seen in trackway 22. Pace angle high, about 170°, but as low as 129° in trackway 22.

Discussion: Type 3 footprints are the most common ichnological remains found in the Koum basin. This footprint morphotype shows a wide range of sizes, and may represent a growth series of a single trackmaker. Figure 26 is a histogram of the size distribution of type 3 trackways based on footprint lengths.

One type 3 trackway (22) shows anomalous characteristics which are interpreted as the effects of a decelerating gait. Pace lengths progressively diminish along the length of the trackway, and pace angle is

Table 17.--Descriptive statistics of type 3 footprints from the Koum basin, northern Cameroon.

Variable	N	$\bar{X}$	Standard deviation	Range	
				Min.	Max.
FL	76	27.750	9.441	13	52
FW	76	19.408	7.430	9	40
ARA	61	423.869	328.476	118	1921
LW	70	1.400	0.201	0.94	1.92
D1	58	8.403	3.270	4	19
D2	60	13.460	3.620	8.5	24
D3	53	13.245	3.519	7	20.2
D4	53	8.872	3.144	4	15.5
D1P	54	0.346	0.086	0.2	0.63
D2P	57	0.563	0.108	0.33	0.8
D3P	49	0.566	0.078	0.39	0.79
D4P	49	0.369	0.070	0.18	0.49
D1P2	47	0.226	0.041	0.13	0.34
D2P2	47	0.448	0.067	0.3	0.65
D3P2	47	0.440	0.053	0.36	0.57
D4P2	47	0.258	0.043	0.17	0.33
SKEW	52	1.015	0.172	0.7	1.57
DA	64	52.219	8.750	39	83
A	41	27.756	7.466	18	53
B	41	25.049	4.615	17	37
FD	76	2.397	1.193	0.5	5.3
FRT	48	-1.452	5.583	-16	8
MASS	76	667.500	639.018	60	3012
S	60	201.650	38.703	129	272
P	75	101.147	20.914	63	140
TW	54	12.426	12.360	0	57
PA	56	166.839	10.981	129	180
PI	56	1.010	0.055	0.78	1.14
RSL	49	1.440	0.334	0.92	2.11
SMS	49	1.680	0.458	1.09	3.08
STRT	49	0.870	0.282	0.45	1.48

Variable symbols explained in text.

unusually small (from 129° to 155°). Trackway width is unusually large, an average of 45 cm. Unfortunately, any progressive changes in footprint morphology are not clear because the substrate has been badly weathered.

Jacobs *et al.* (1989) assigned a Koum basin trackway (trackway 53, assigned to type 3 in this study) to the Theropoda because of remnant claw marks on some digits. Criteria listed by Pittman (1989) as characteristic of theropod footprints from the Gulf Coast of the U.S. are seen in many type 3 trackways from Cameroon. These include medial curvature of the distal digit II and digit III impressions; topographic separation of the digit II impression from the rest of the footprint, with an indentation along its medial edge; and the presence of claw marks. Langston (1974) notes that in Lower Cretaceous theropod footprints from Texas, digits II and III tend to curve medially, and the "heel" of the footprint forms an acute angle. These characters are seen in many type 3 footprints. Farlow (1987) presents a detailed discussion of the characteristics of theropod footprints, and lists criteria useful to distinguish them from ornithopod footprints. These criteria include longer, narrower toes on theropods as well as an overall longer and more slender shape of the entire print. However, Farlow (1987) notes that there is a continuum of shapes between ideal endmember theropod and ornithopod footprints, and unequivocal

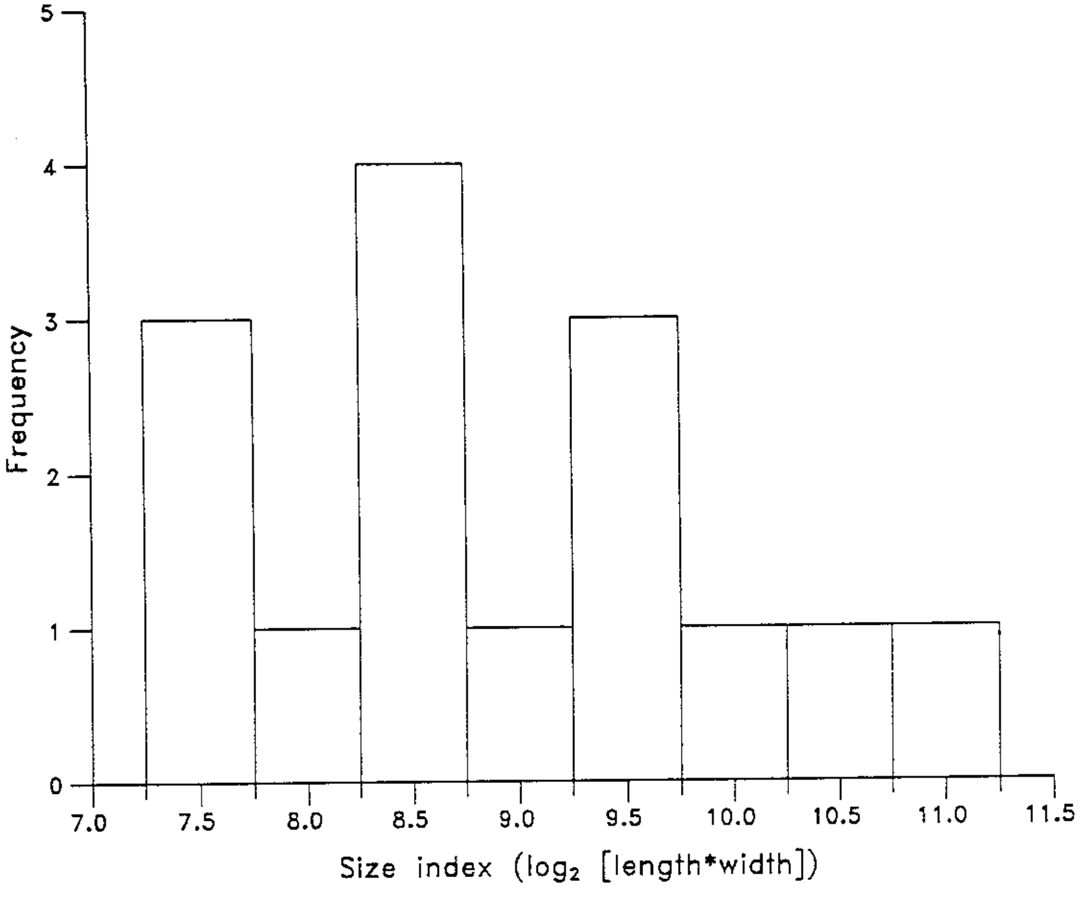


Figure 34. Histogram of footprint size index for type 3 footprints. Data averaged by trackway. From locality KB-17, south of Manangia, Koum basin, northern Cameroon.

classification is not always possible. Type 3 footprints in general match the published criteria for theropod footprints, and for that reason are assigned to this group.

Sternberg (1932) describes a large population of footprints from Lower Cretaceous rocks in the Peace River canyon of British Columbia, Canada. The most common morphology at the locality is a footprint similar in size and shape to the Koum basin type 3 morphology (named *Irenisauripus mclearni*). Leonardi (1979b, 1980b) provides figures of theropod footprints from the Lower Cretaceous Sousa Formation from the Rio do Peixe basin in northeastern Brazil that closely resemble type 3 footprints from the Koum basin. The Brazilian footprints are compared with the ichnotaxon *Eubrontes platypus* from the Triassic of North America (Leonardi 1979b, 1980b). A similar morphology of theropod footprint has been figured by Ginsburg *et al.* (1966) from Mt. Arli in Niger, from the Lower Cretaceous argiles de l'Irhazer. Dejax *et al.* (1989) report the presence of tridactyl bipedal footprints from the nearby Babouri-Figuil basin in northern Cameroon that resemble type 3 (groups A, K, and L). They are in general small (up to 25 cm long), but within the range of the Koum sample. It is clear from its wide distribution in time and space that the type 3 morphology represents a conservative pes morphology among theropod dinosaurs.

Type 4

Referred specimens: Trackways 2, 3, 6, 24, 25, 29, 31, 32, 37, 51, 52.

Locality: KB-17, south of Manangia, and KB-23, south of Mbissirri, Koum basin, northern Cameroon.

Description: Large relatively wide footprints with broad toe impressions with blunt terminations (figure 32d; table 18). Footprint length from 24 to 48 cm; footprint width ranging from 26 to 41 cm. Generally poorly preserved. Distinct claw impressions lacking; no distinct digital pads seen. Pace is variable and ranges from 79 to 170 cm, with the stride length about twice the pace. Trackway width between 7 and 52 cm (the largest value is from a poorly preserved trackway and is probably anomalous). Pace angle typically about 156°.

Discussion: Type 4 footprints are the largest of the bipedal dinosaur footprints in the Koum basin. Their large size gives them a strong potential for preservation, since they are able to resist obliteration after smaller, shallower footprints have been erased by weathering of the outcrop surface. In general, they are found on poorly preserved surfaces and are themselves in poor condition.

The type 4 morphology most closely approximates footprints which have been attributed to ornithopod dinosaurs (see Haubold 1971, 1984). *Amblydactylus gethingi*, named by Sternberg (1932) from the Lower Cretaceous Peace River canyon locality, closely approximates type 4 footprints. Sternberg (1932) referred this morphology to an *Iguanodon*-like trackmaker. Woodhams and Hines (1989)

Table 18.--Descriptive statistics of type 4 footprints from the Koum basin, northern Cameroon.

Variable	N	$\bar{X}$	Standard deviation	Range	
				Min.	Max.
FL	24	38.92	5.405	24	48
FW	26	34.62	3.753	26	41
ARA	18	1258	267.448	739	1613
LW	21	1.172	0.096	1	1.336
D1	12	14.28	2.176	10	18
D2	12	18.53	2.547	14.5	23
D3	10	18.73	3.252	13	23.5
D4	11	12.81	2.780	8	16.9
D1P	10	0.369	0.070	0.267	0.467
D2P	11	0.465	0.068	0.33	0.6
D3P	9	0.464	0.088	0.31	0.557
D4P	9	0.304	0.057	0.19	0.366
D1P2	9	0.302	0.053	0.215	0.381
D2P2	9	0.406	0.069	0.279	0.506
D3P2	9	0.411	0.058	0.317	0.489
D4P2	9	0.239	0.048	0.16	0.311
SKEW	10	1.031	0.195	0.743	1.31
DA	28	59.25	4.986	51	68
A	10	30.7	4.620	24	38
B	10	29.2	5.653	18	40
FD	33	4.652	1.609	2.6	9
FRT	23	1.391	8.887	-23	15
MASS	24	1853	673.560	453	3200
S	39	203	29.832	143	275
P	48	107.5	18.579	79	170
TW	33	21.61	11.093	7	52
PA	36	156.4	11.927	125	172
PI	35	0.993	0.114	0.737	1.234
RSL	17	0.840	0.125	0.570	1.05
SMS	17	0.885	0.191	0.490	1.20
STRT	17	0.465	0.065	0.340	0.57

Variable symbols explained in text.

describe a number of footprints from the Lower Cretaceous of East Sussex that conform well to the type 4 morphology, and are attributed to an iguanodontid trackmaker. Footprints attributed to *Iguanodon* from the European mainland and figured by Dollo (1906, reproduced in Haubold 1971, 1984, and Lehmann 1978) are similar to type 4 footprints from Koum. Among the ornithischian trackways from the Rio do Peixe basin and the Jurassic Corda Formation near Goias in northeastern Brazil (Leonardi 1979a, 1980a), none resemble any footprints from Cameroon.

Type 5

Referred specimens: Trackways 11, 14, 15, 18, 21, 33.

Locality: KB-17, south of Manangia, Koum basin, northern Cameroon.

Description: Footprints of bipedal trackmakers with two or three digit impressions and no metatarsal or proximal digit impressions (figure 32e-h). Trackway 11 was made by a trackmaker using unusually long strides and leaving at most two digit impressions; trackways 14 and 18 are clearly tridactyl, and have small pace angles; trackway 15 takes the form of two widely spaced elongate ungual impressions representing two digits; trackway 33 is comprised of asymmetrical pes impressions (left imprints differ from right) but is similar to 11 in its behavioral aspects, with long strides and only two digit impressions preserved except for one footprint which has three; trackway 21 is problematic, and is an isolated print resembling the left pes impressions of trackway 33. Footprint widths range from 11 to 39 cm; pace is highly variable, ranging from 117 to 270 cm; pace angle is low, averaging about 143° (excluding

Table 19.--Descriptive statistics of type 5 footprints from the Koum basin, northern Cameroon.

Variable	N	$\overline{X}$	Standard deviation	Range	
				Min.	Max.
FL	0	...	...	...	...
FW	11	19.36	8.286	11	39
ARA	0	...	...	...	...
LW	0	...	...	...	...
D1	8	15.05	6.729	9	25
D2	12	19.98	4.884	11.7	25.5
D3	11	21.79	5.423	14	30
D4	8	13.73	3.036	9	18
D1P	0	...	...	...	...
D2P	0	...	...	...	...
D3P	0	...	...	...	...
D4P	0	...	...	...	...
D1P2	2	0.217	0.060	0.174	0.259
D2P2	2	0.439	0.048	0.405	0.473
D3P2	2	0.536	0.058	0.495	0.577
D4P2	2	0.207	0.062	0.163	0.25
SKEW	8	1.079	0.140	0.906	1.27
DA	0	...	...	...	...
A	0	...	...	...	...
B	0	...	...	...	...
FD	19	3.389	1.060	1.4	5.5
FRT	11	6.045	13.226	-8	30
MASS	0	...	...	...	...
S	11	335.7	98.734	215	500
P	16	177.5	42.866	117	270
TW	11	40	30.083	-6	116
PA	11	149	25.263	91	183
PI	11	0.988	0.080	0.844	1.097
RSL	0	...	...	...	...
SMS	0	...	...	...	...
STRT	0	...	...	...	...

Variable symbols explained in text.

anomalous trackway 11 data); trackway widths narrow, averaging 48 cm (excluding 11) (table 19).

Discussion: The type 5 footprint category is a repository for problematic ichnites made by bipedal trackmakers, but with only the distal impressions of three or fewer digits; their pace angles are relatively low (trackway 11 excepted). Two of the trackways (11 and 33) were made by rapidly moving animals. The pes impressions show that the trackmakers were functionally didactyl over most of the preserved trackways. Reconstructions of dromaeosaurids in both walking and running position (see Norman 1985) show them as didactylous, with digit II raised above the substrate. In trackway 33, digit II on the left pes was lifted above the substrate; the right pes impressions have digit II, but digit IV was raised. In trackway 11, digit II impressions are lacking, but digit IV impressions are found on both left and right footprints. Leonardi *et al.* (1987) illustrate a footprint (*Sarmientichnus scagliai*) from the Upper Jurassic La Matilde Formation of Argentina that is very similar to trackway 11 footprints. *Sarmientichnus* has been attributed to a medium sized coelurosaur. An illustration in Haubold (1971, p.80) of an unnamed theropod footprint from the Inferior Oolite (Middle Jurassic) of Yorkshire is reminiscent of trackway 33 right footprints, trackway 18 footprints, and both trackway 14 impressions. Gillette and Thomas (1985) provide a figure of a carnosaur footprint lacking a heel impression from the Lower Cretaceous Dakota Formation of New Mexico. This footprint is intermediate in morphology between the left and right footprints of trackway 33. Gillette and Thomas (1989) illustrate problematic traces from the same Lower Cretaceous locality that resemble trackway 14 footprints almost exactly. Their morphology and unique arrangement on the substrate led Gillette and Thomas (1989) to conclude they were pterosaur manus impressions, which is unlikely because these ichnites do not resemble predicted reconstructions of pterosaur trackways (see Unwin 1989).

Type 6

Referred specimens: Trackways 8, 10, and 28.

Locality: KB-17, south of Manangia, Koum basin, northern Cameroon.

Description: Undertracks, moderate in size, nearly circular in outline, and exhibiting traces of three digits (figure 32i; table 20).

Discussion: The phenomenon of undertracks in paleoichnology has been described by Langston (1986) and Farlow (1987). Experimental work by Allen (1989) quantitatively modeled undertrack generation using engineering principles. Undertracks are created in strata immediately below the actual level where the trackmaker walked by the weight of the trackmaker deforming the underlying soft sediment; they are referred to as "stacked" footprints (Langston 1986) because of their vertical alignment or stacking. Undertracks become progressively more circular and less distinct the further below the actual footprint level one goes (Farlow 1987). Trackways 8 and 10 at KB-17 are

Table 20.--Descriptive statistics of type 6 footprints from the Koum basin, northern Cameroon.

Variable	N	$\bar{X}$	Standard deviation	Range	
				Min.	Max.
FL	11	31.82	3.219	29	39
FW	11	30.09	4.346	24	38
ARA	0	...	...	...	...
LW	11	1.07	0.092	0.906	1.213
D1	0	...	...	...	...
D2	0	...	...	...	...
D3	0	...	...	...	...
D4	0	...	...	...	...
D1P	0	...	...	...	...
D2P	0	...	...	...	...
D3P	0	...	...	...	...
D4P	0	...	...	...	...
D1P2	0	...	...	...	...
D2P2	0	...	...	...	...
D3P2	0	...	...	...	...
D4P2	0	...	...	...	...
SKEW	0	...	...	...	...
DA	0	...	...	...	...
A	0	...	...	...	...
B	0	...	...	...	...
FD	11	2.3	0.881	1	3.8
FRT	5	8.8	9.311	-3	18
MASS	11	772.3	244.163	580	1338
S	5	129.8	6.340	124	140
P	7	65.57	6.373	54	73
TW	5	9	3.162	4	12
PA	5	164.4	4.827	160	172
PI	5	0.96	0.128	0.771	1.132
RSL	5	0.831	0.073	0.752	0.937
SMS	5	0.722	0.091	0.63	0.86
STRT	5	0.553	0.044	0.504	0.613

Variable symbols explained in text.

undoubtedly undertracks, because of their nearly circular outlines, relatively indistinct margins, and lack of clear pes details. Their size suggests that they may have been produced by the same trackmaker responsible for the type 3 or type 4 footprints described above.

Type 7

Referred specimens: Trackway 54 (two footprints).

Locality: KB-18, south of Manangia, Koum basin, northern Cameroon.

Description: Very large footprints, probably made by a quadrupedal trackmaker, nearly circular in outline, forming deep steep-walled depressions resembling large potholes. Length from 61 to 67 cm; width from 63 to 67 cm (table 21). No clear toe impressions are preserved. Because only two footprints are preserved, no characteristics of stride or gait are known.

Discussion: The large size, nearly circular shape, and depth of the footprints indicates a heavy graviportal trackmaker, most likely a sauropod dinosaur. Trackway 54 is the only trackway known in the Koum basin which can be attributed to a sauropod. Two other trackway localities in Africa of Early Cretaceous age have sauropod footprints: Babouri-Figuil in northern Cameroon (Dejax *et al.* 1989) and Mt. Arli in Niger (Ginsburg *et al.* 1966). The footprints from Babouri-Figuil are all smaller and are slightly elongate or oval in shape, as are the footprints from Niger; the specimens from Niger preserve all five digit impressions, and have clear manus impressions as well. Some

Table 21.--Descriptive statistics of type 7 footprints from the Koum basin, northern Cameroon.

Variable	N	$\bar{X}$	Standard deviation	Range	
				Min.	Max.
FL	2	64	4.243	61	67
FW	2	65	2.828	63	67
ARA	0	...	...	...	...
LW	2	0.987	0.108	0.91	1.063
D1	0	...	...	...	...
D2	0	...	...	...	...
D3	0	...	...	...	...
D4	0	...	...	...	...
D1P	0	...	...	...	...
D2P	0	...	...	...	...
D3P	0	...	...	...	...
D4P	0	...	...	...	...
D1P2	0	...	...	...	...
D2P2	0	...	...	...	...
D3P2	0	...	...	...	...
D4P2	0	...	...	...	...
SKEW	0	...	...	...	...
DA	0	...	...	...	...
A	0	...	...	...	...
B	0	...	...	...	...
FD	1	29	...	29	29
FRT	0	...	...	...	...
MASS	0	...	...	...	...
S	0	...	...	...	...
P	1	198	...	198	198
TW	0	...	...	...	...
PA	0	...	...	...	...
PI	0	...	...	...	...
RSL	0	...	...	...	...
SMS	0	...	...	...	...
STRT	0	...	...	...	...

Variable symbols explained in text.

of the footprints from Babouri-Figuil also preserve manus impressions. The lack of manus impressions in the Koum footprints is probably due to overprinting and obliteration by the succeeding pes impressions. The lack of digit impressions is probably attributable to unfavorable characteristics of the substrate at the time of imprinting.

Correspondence to Osteological Groups

Most of the footprint types defined above have osteological counterparts from vertebrate localities in the eastern end of the Koum basin. Table 22 summarizes these comparisons.

Behavior and Gaits

The record of dinosaur behavior at KB-17 is reflected in preferred directions of travel and gaits. Figure 35 is a rose diagram of trackway orientations at locality KB-17. Clearly, the animals at this site favored a NNE-SSW direction of travel, and only one animal moved in an east-west direction. Travel at dinosaur trackway sites in a single directional sense has been interpreted as an indication of herding or social behavior (see Ostrom 1972, 1986). However, this may not be the case at KB-17, since several taxa are represented, the trackways are dispersed over 400 meters of outcrop, and all were not imprinted contemporaneously. Sorting by trackway type and stratigraphic level does not produce any unequivocal patterns which could be interpreted as behavioral, except

Table 22.--Footprint types and osteological counterparts from Koum basin fossil localities.

Foot-print type	Osteological counterpart	Hip height (cm)	Speed range (m/s)	Body mass (kg)
1	Type B theropod	32	....	8
2	Cf. Spinosauridae	32-124	0.78-5.65	79-345
3	Type A theropod	67-268	1.09-3.08	60-3012
4	*Ouranosaurus* sp.	137-274	0.49-1.20	453-3200
5	Type A theropod	77-189*	2.61-8.85*	90-1138*
6	Type A theropod or *Ouranosaurus* sp.	165-201	0.63-0.86	580-1338
7	Sauropodomorpha indet.	244-268	....	....

*estimated from incomplete footprint length

for all three type 1 trackways, which were travelling northeast. All other ichnotaxa are roughly bimodal in a single directional sense. The presence of only a single contrary trackway (directed east-west) among the KB-17 assemblage argues for some sort of constraining feature in the paleoenvironment. It was the presence of contrary (divergent) trackways at most of the sites studied by Ostrom (1972) that led him to conclude that social behavior was responsible for preferred directions of travel in footprint suites. The bimodal distribution of directions in a single directional sense may have been a response to a physical barrier at the site at the time the trackways were made, such as a NNE-SSW flowing river, which restricted the direction of travel of the trackmakers. Lockley (1986) states that bimodal directional trends are evidence for gregarious activity among dinosaurs *and/or* the presence of a physical barrier in the paleoenvironment, and separating the two is a difficult matter, since a physical barrier in the paleoenvironment will affect the direction of travel of an individual in the same way it affects that of a social group.

A variety of gaits are seen in the Koum basin footprint sample, including walking, trotting, sprinting, acceleration, deceleration, and asymmetrical or hobbling gaits. Gaits have been defined by Alexander (1977) and Thulborn and Wade (1984): walking - the feet move alternately and never simultaneously leave the ground; trotting - the feet move alternately, they are placed on the ground at even intervals, and they are off the ground simultaneously for part of the stride; sprinting - the feet of a pair are placed on the ground asynchronously, at uneven intervals, and they are simultaneously off the ground for part of the stride. The definition of sprinting is based on the racking-cantering transition in quadrupeds that occurs when relative stride length exceeds 2.90 (Thulborn and Wade 1984); sprinting in bipeds occurs at the same value of

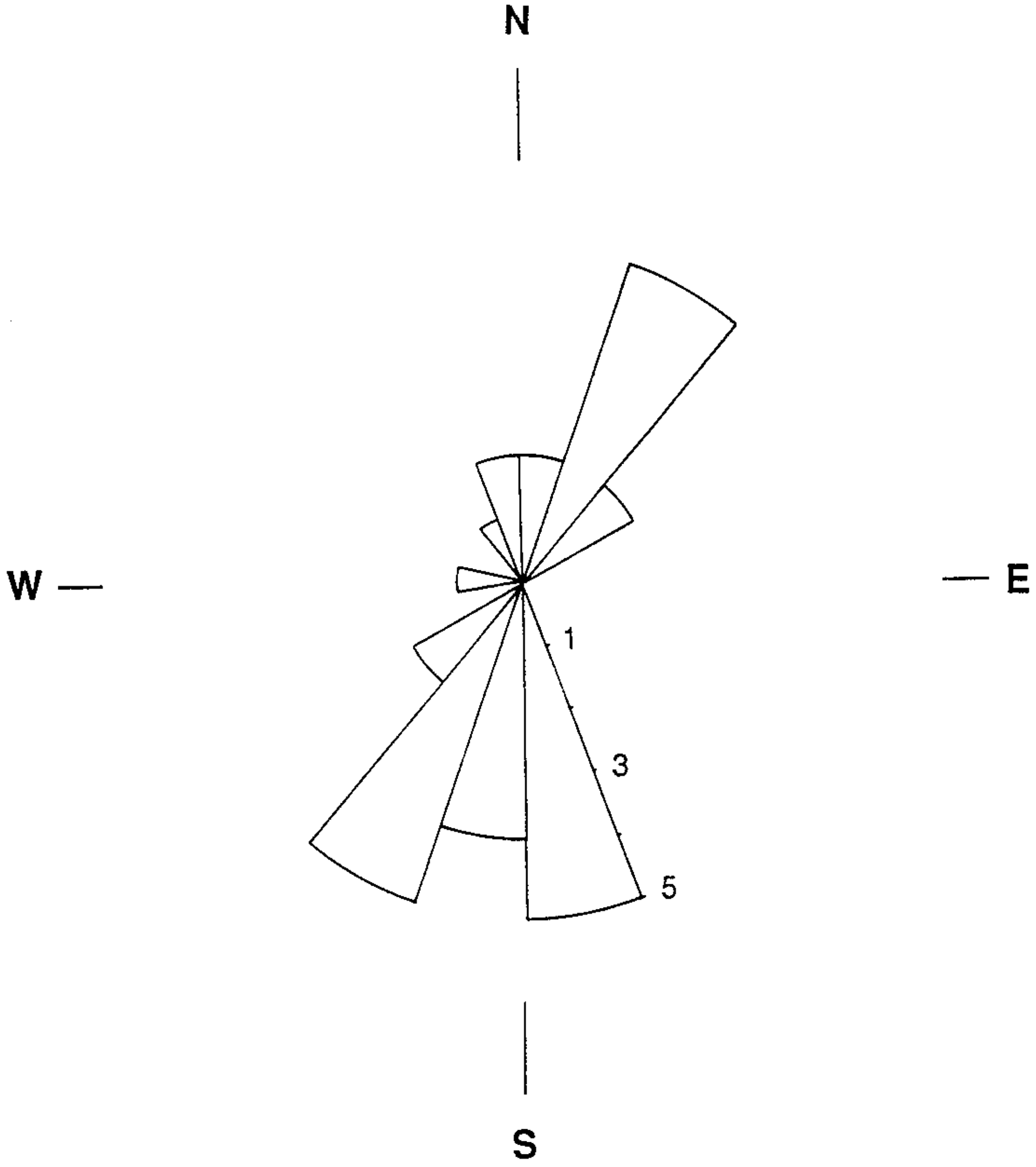


Figure 35. Rose diagram of trackway orientations at locality KB-17, Koum basin, northern Cameroon. Bars represent trackway frequency in 20° compass arcs.

relative stride length.

Figure 36a is a plot of relative stride length against pace angle. From this it is clear that the majority of trackmakers walked and did not run. One type 3 trackmaker moved at a trotting gait, and two type 2 trackmakers sprinted. At least one type 5 trackmaker probably moved at a sprinting gait as well (trackway 11); however, no type 5 footprints are plotted because none are complete enough to allow calculation of hip height (necessary for estimating relative stride length). In general, the smaller trackmakers moved at more energetic gaits (figure 36b).

When speed is plotted against footprint width, it is apparent that size and speed are related in the same manner as relative stride length and size (figure 37a). Striding rate provides the most refined means for discriminating the vitality of trackmakers by their size (figure 37b). The implication is that larger dinosaurs in the Koum basin population (types 3, 4, and 6) moved their limbs at slower rates, they tended not to move as fast, and they only walked (with the possible exception of the trackway 11 trackmaker). The smaller animals were relatively more energetic in most locomotory aspects.

Pace index, which quantifies the asymmetry of a trackmaker's gait, is a quantitative means of detecting anomalous behavior within a trackway. Among the Koum basin sample, several trackways show a consistent departure from values of 1.0; trackways 4 and 11 are substantially less

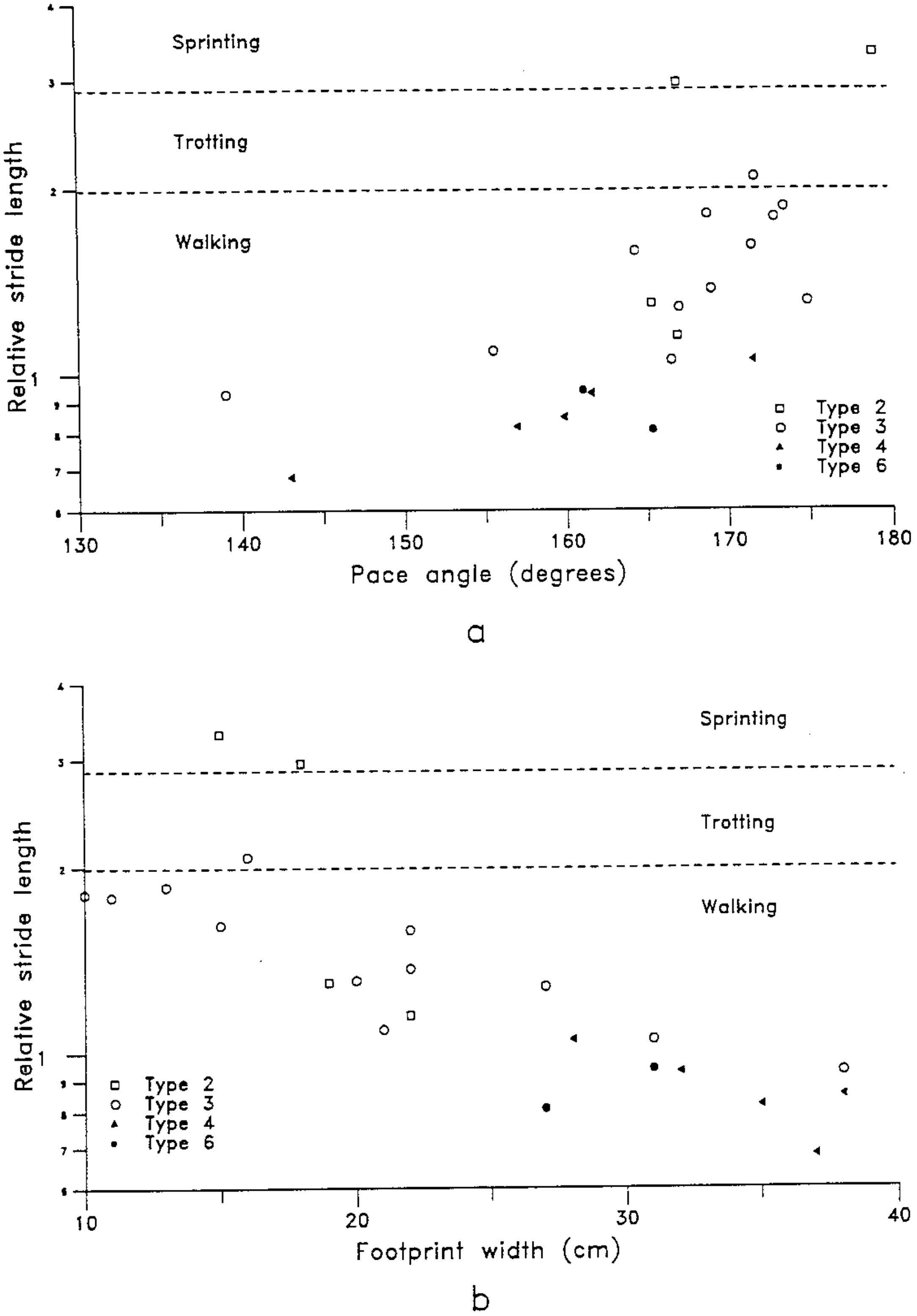


Figure 36. Scatter plots of Koum basin footprint data. Variables averaged by trackway.

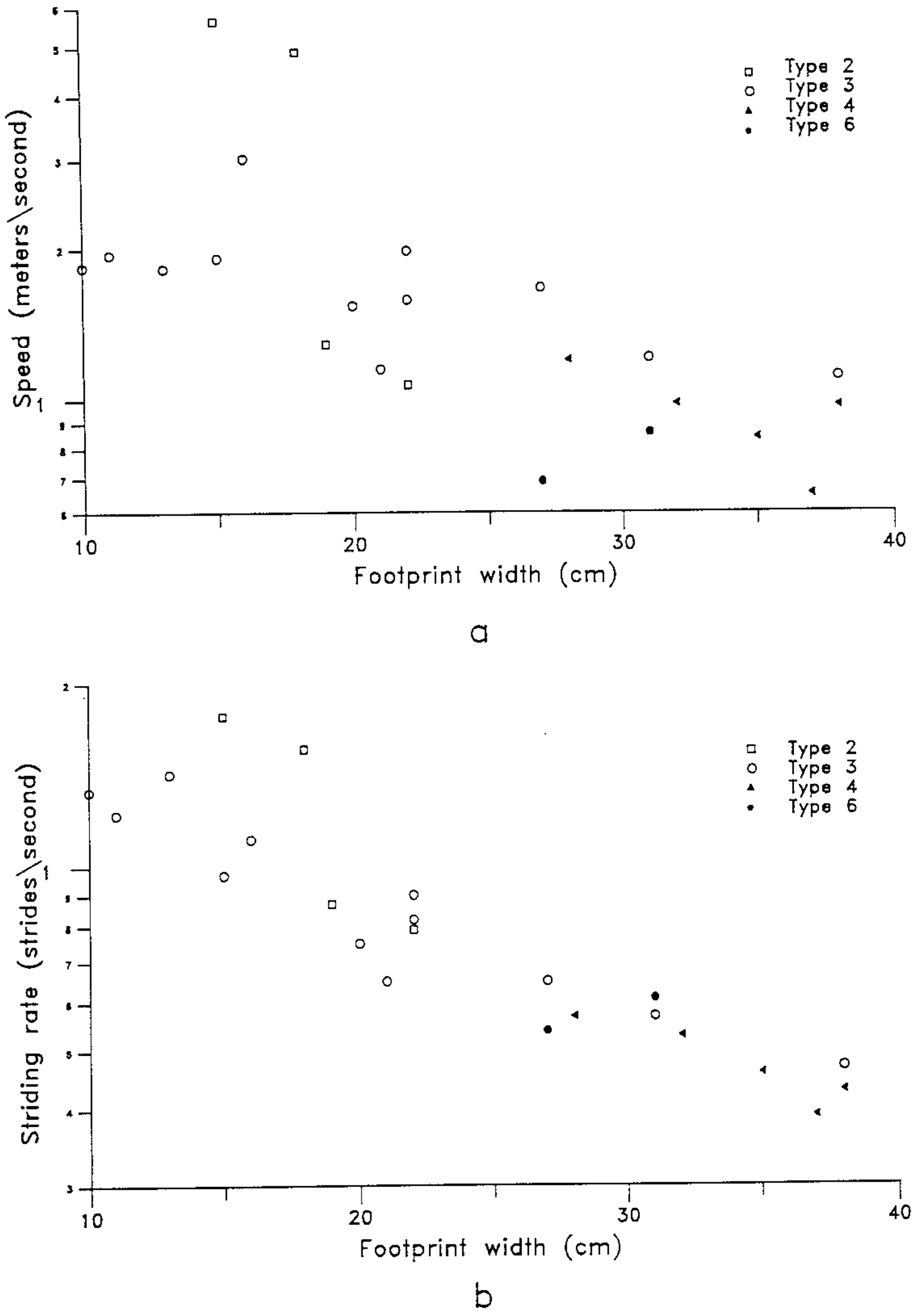


Figure 37. Scatter plots of Koum basin footprint data. Variables averaged by trackway.

than 1.0 (0.82-0.89 and 0.84-0.97), indicating an accelerating gait. Stride and pace for both trackways increase over their lengths. Trackway 33 has values of pace index that rhythmically vary between 0.95 and 1.05. This trackway is notable for the asymmetry of left and right pes impressions (figure 32g, 32h), a result of unusual behavior possibly associated with a pathological condition; the trackmaker was apparently limping or hobbling.

Footprint rotation (the orientation of the long axis of the footprint relative to the direction of stride) does not vary systematically with any other variable. It is statistically independent of footprint length, size index, relative stride length, and striding rate. It does not correlate with footprint type.

Dinosaur Footprint Localities in Africa

Footprints of archosaurian reptiles are relatively common in the Koum basin, and are known from four localities (KB-3, KB-17, KB-18, KB-23) in the central basin. A total of 232 footprints, distributed among 47 trackways, have been found in the Koum basin. The majority of trackways are concentrated at a single site about three km south of the village Manangia, at locality KB-17. One trackway of four footprints (locality KB-3) has been described (Jacobs *et al.* 1989). Dejax *et al.* (1989) describe several trackway sites in the Babouri-Figuil basin further to the north, and assign them a Neocomian-Barremian age.

Table 23 lists all African footprint localities. The majority of sites are in Lower Jurassic strata of Lesotho and Morocco. Many of the Moroccan sites are poorly constrained with regard to their age (Haubold 1986). The only reported Lower Cretaceous dinosaur footprint localities in Africa are in Cameroon and Niger (Ginsburg *et al.* 1966; Taquet 1976; Jacobs *et al.* 1989; Dejax *et al.* 1989). With the data from this study, the number of dinosaur footprints from the Lower Cretaceous of Africa is a significant proportion of the total known from Africa (about 20%). The 243 footprints described in this study comprise about 11% of reported dinosaur footprints from Africa.

Table 23.--African dinosaur footprint localities.

Age	Locality	Number of prints[1]	Type[2]	Reference
U Cret	Agadir Morocco	6	BI TD PD	Ambroggi & Lapparent (1954a&b)
U Cret	Amoura Algeria	140	BI TD	Bellair & Lapparent (1948)
L Cret	Koum Cameroon	234	BI QU TD	this study
L Cret	Koum Cameroon	4	BI TD	Jacobs *et al.* (1989)
L Cret	Babouri-Figuil Cameroon	70	BI QU TD	Dejax et al. (1989)
L Cret	Mt. Arli Niger	4	TD	Ginsburg *et al.* (1966)

Table 23 (continued).--African dinosaur footprint localities.

Age	Locality	Number of prints[1]	Type[2]	Reference
L Cret	E. Mt. Arli Niger	>119	BI TD QU PD	Ginsburg *et al.* (1966)
U Jur	Anou Aguerouf Niger	26	TD	Ginsburg *et al.* (1966)
U Jur	Azog Niger	>60	QU TD PD QD	Ginsburg *et al.* (1966)
L Jur	Aït Kelelch Morocco	*	BI TD QD	Plateau *et al.* (1937)
L Jur	Iouaridène Morocco	43	QU	Ishigaki (1989)
L Jur	Iouaridène Morocco	*	-	Jenny *et al.* (1981)
L Jur	Jbel Igoudlane Morocco	*	TD	Jenny *et al.* (1981)
L Jur	Demnat Morocco	64	QU	Dutuit & Ouazzou (1980)
L Jur	Demnat Morocco	41	BI TD	Lapparent (1942)
L Jur	Demnat Morocco	3	BI TD	Lapparent (1945)
L Jur	Demnat Morocco	6	BI	Ennouchi (1953)
L Jur	Aït Attab Morocco	-	TD	Jenny *et al.* (1981)
L Jur	Ouaouizaght Morocco	**	QU TD	Jenny *et al.* (1981)
L Jur	Taguelft Morocco	-	QU	Jenny *et al.* (1981)

Table 23 (continued).--African dinosaur footprint localities.

Age	Locality	Number of prints[1]	Type[2]	Reference
L Jur	Tizi-n-Isli Morocco	-	QU TD	Jenny *et al.* (1981)
L Jur	Imi-n-Tanout Morocco	*	QU	Jenny *et al.* (1981)
L Jur	El Mers Morocco	-	QU TD	Jenny *et al.* (1981)
L Jur	Aït Blal Morocco	*	BI TD QD	Plateau *et al.* (1937)
L Jur	Lakhdar Morocco	>43	BI QU TD QD PD	Jenny & Jossen (1982)
L Jur	Azilal Morocco	**	BI PD	Jenny & Jossen (1982)
L Jur	Aït Bou Guemez Morocco	**	BI QU PD	Jenny & Jossen (1982)
L Jur	Jbel Waougoulzat Morocco	**	BI QU TD	Jenny & Jossen (1982)
L Jur	Adrar-n-Ouglagal Morocco	153	BI TD	Monbaron *et al.* (1985)
L Jur	Morija Lesotho	-	BI	Ellenberger *et al.* (1969)
L Jur	Tsikoane Lesotho	-	BI	Ellenberger *et al.* (1969)
L Jur	Giants Castle South Africa	-	BI TD	Dijk (1978)
L Jur	Cana Lesotho	-	BI	Ellenberger *et al.* (1969)
L Jur	Ile de Moyeni Lesotho	577	TD	Ellenberger (1974)

Table 23 (continued).--African dinosaur footprint localities.

Age	Locality	Number of prints[1]	Type[2]	Reference
L Jur	Mokanametsong Lesotho	265	TD	Ellenberger (1974)
L Jur	Kubake Lesotho	-	TD	Ellenberger (1974)
L Jur	Qomoqomong Lesotho	-	TD	Ellenberger (1974)
L Jur	Mabetha Lesotho	>7	TD	Ellenberger (1974)
L Jur	Thejane Lesotho	-	BI	Ellenberger *et al.* (1969)
U Tr	Aïn Sefra Algeria	15	TD	Bassoullet (1971)
U Tr	Maphutseng Lesotho	129	BI QU	Ellenberger & Ellenberger (1960)
U Tr	Seaka Lesotho	-	BI	Ellenberger *et al.* (1969)
U Tr	Phuthiatsana Lesotho	≈100	BI TD PD	Ellenberger *et al.* (1963)
L Jur	Léribé Lesotho	42	BI QU TD PD	Ellenberger (1955)
U Tr	Qeme Lesotho	-	BI	Ellenberger et al. (1969)

Table 23 (continued).--African dinosaur footprint localities.

Age	Locality	Number of prints[1]	Type[2]	Reference
U Tr	Spring Grange Zimbabwe	3	BI TD	Raath (1972)
U Tr(?)	Maparero Namibia	*	BI TD	Gurich (1926)

Notes

1

* - "numerous" footprints
** - several trackways

2

BI - bipedal
QU - quadrupedal
TD - tridactyl
QD - quadrudactyl
PD - pentadactyl

PART V

CONCLUSIONS

Biochronological Age of the Koum Basin Sediments

In the absence of absolute dates, the sediments in the Koum basin may be most accurately dated by biochronology. The most diagnostic vertebrate taxa for age and correlation of the Koum basin sediments are found in the Mayo Djarendi area in the eastern end of the basin (at localities KB-6 and KB-13). These include the mesosuchian crocodile cf. *Araripesuchus wegeneri* and the iguanodontid dinosaur *Ouranosaurus* sp. Cf. Spinosauridae teeth from the Koum basin provide another faunal element in common with Gadoufaoua.

On the basis of these occurrences, a broad correlation of the sediments at Mayo Djarendi with those at Gadoufaoua is suggested. The age of Gadoufaoua is tentatively considered Aptian by Taquet (1976). The upper age limit there is determined by overlying marine sediments of Cenomanian age, while the lower age limit is less certain (see discussion in Taquet 1976; Reyment and Dingle 1987). An Aptian age for sediments in the Koum basin is an extension of the interpretation of the age of Gadoufaoua and includes all of the inherent uncertainties in that determination.

Data from conchostracan fossils from several central basin localities suggests a correlation of those sediments with the argiles de l'Irhazer in Niger (P. Tasch, personal communication; Defretin *et al.* 1956). On the basis of crocodile, dinosaur, and *Ceratodus* fossils similar to those found elsewhere in the Saharan 'Continental intercalaire,' as well as lamellibranch fossils (unionid and cyrenid) typical of Wealden age rocks, Defretin *et al.* (1956) considered the conchostracans from the argiles de l'Irhazer to be Early Cretaceous in age. Taquet (1976) considered the argiles de l'Irhazer to be Late Jurassic to Early Cretaceous (Neocomian) in age. In the region of Gadoufaoua, the main fossil-bearing strata lie 330 meters above the youngest argiles de l'Irhazer strata (Taquet 1976). On the basis of the conchostracan data, the localities in the central Koum basin (KB-4, KB-15, KB-19, KB-22, and KB-24) correlate with the Upper Jurassic-Lower Cretaceous argiles de l'Irhazer in Niger. The absence of *Cyzicus* (*Lioestheria*) *lamberti* in the Babouri-Figuil basin and the Mayo Oulo-Léré basin of northern Cameroon (where excellent conchostracan samples exist) suggests a less perfect correlation with Koum than is found between Koum and Niger. On the basis of both invertebrate and vertebrate fossils, it seems reasonable to conclude that the difference in age and time interval represented between the central Koum basin fossil localities and Mayo Djarendi may be similar to that found between the Argiles de l'Irhazer near In Gall and the Tégama Series rocks at the Gadoufaoua fossil beds in Niger.

Paleobiogeographical Implications of the Koum Basin Archosaurians

The osteological and footprint sample from the Koum basin provides strong evidence for archosaurian paleobiogeography in the Early Cretaceous. The notosuchian crocodile *Araripesuchus wegeneri* and/or a closely related species is known from three localities in Africa that span the breadth of the continent; the Koum basin in Cameroon, Gadoufaoua in Niger, and northern Malawi. *Araripesuchus gomesii*, a very similar form, is known from eastern Brazil. The ages of all occurrences of *Araripesuchus* are Early Cretaceous (see Congleton *et al.* in press; Buffetaut and Taquet 1979; Jacobs *et al.* 1990). The specimens from Brazil and Niger are considered Aptian in age. Since South America and Africa were probably still contiguous at this time, it is not surprising to find *Araripesuchus* on both continents.

Sebecosuchian crocodiles, previously unknown from the Mesozoic of Africa, possibly existed in the Early Cretaceous of Cameroon. If true, paleobiogeographic scenarios involving them (Langston 1956; Buffetaut 1982a-c) need to be restructured. Langston (1956) proposed a pre-Upper Jurassic origin for the Sebecosuchia within Asia, followed by migration to South America via North America prior to the end of the Cretaceous. No specific migration routes were suggested to place sebecosuchians in Europe and Africa following this event, but Langston (1956) suggests a possible later migration from South America. Buffetaut (1982a) suggested that the Sebecosuchia arose from Notosuchian stock in South America, Antarctica, or Australia in the Late Cretaceous. They then diversified in South America and migrated to Europe on a dry land route via North America, near the end of the Cretaceous or in the Early Tertiary. Buffetaut (1982a) felt that Sebecosuchians were always absent from Africa. However, he revised this scenario to include Africa, after the discovery of ziphodont crocodilian teeth in Eocene rocks of Algeria (Buffetaut 1982b, 1982c). He suggested a Late Cretaceous migration of ziphodont crocodilians from South America to Europe via a land bridge linking South America and Africa at the Walvis and Rio Grande rises (Buffetaut 1982b). This model is unnecessary if migration took place in the Early Cretaceous, when South America and Africa still adjoined. The possibility that the Sebecosuchia enjoyed an earlier, wider distribution is supported by the Koum basin data.

The sauropod dinosaur remains from the Koum basin are inadequate to formulate detailed hypotheses regarding their presence there; however, they do resemble teeth from the Late Jurassic/Early Cretaceous of South Africa (Rich *et al.* 1983), and in the presence of other faunal elements from South Africa, they suggest a rough correlation.

Theropod dinosaur teeth from Koum that resemble those of spinosaurids suggest affinities with widely scattered African localities of medial Cretaceous age, including Baharija, Egypt (Buffetaut 1989); southeastern Morocco (Buffetaut 1989); Gadoufaoua, Niger (Taquet 1984); northern Malawi (this study, but see Jacobs *et al.* [1990]) and Foum Tatahouine, Tunisia (Bouaziz *et al.* 1988). Spinosaurids are thought to be present in strata of Upper Jurassic age in Thailand (Buffetaut and Ingavat 1986), but these data are considered here to be equivocal, and no true spinosaurid is known from skeletal material outside of Africa.

The morphotype A theropod teeth from Koum resemble those of *Erectopus*, a taxon known from the Early Cretaceous of France and the Cenomanian of Egypt (Stromer 1936, cited in Molnar 1980). The implications of the occurrence of this theropod on both Gondwana and Laurasia in the Cretaceous has been noted by Molnar (1980), who stated that Early Cretaceous faunal interchange between the two landmasses was a possibility. This is in agreement with the conclusions of Sues and Taquet (1979), who argued for a trans-Tethyan migration route between Europe and Africa in the Early Cretaceous, based on similar pachycephalosaurs from the medial Cretaceous of Madagascar and the British Wealden. Galton and Taquet (1982) argued for a similar trans-Tethyan route in the Early Cretaceous. Their evidence is the occurrence of *Valdosaurus*, a hypsilophodont dinosaur, in the Wealden of Great Britain and at Gadoufaoua in Niger. Teeth of a small theropod from Koum (morphotype B) are very similar to several collected from Cape Province, South Africa (Rich *et al.* 1983), and also from Early Cretaceous rocks of eastern North America (Lull 1911). This does not necessarily mean the same animal was present on the two continents at the same time; rather, animals sharing a conservative tooth morphology were.

Ornithischian dinosaur remains at Koum are predominantly those of the iguanodont *Ouranosaurus*, known elsewhere only from Early Cretaceous deposits at Gadoufaoua, Niger (Taquet 1976). It is arguable whether the Koum basin material is conspecific with *Ouranosaurus nigeriensis*, but it is clear that the Koum basin form is at least a close relative. Other than Gadoufaoua, iguanodontid remains are known from only one other African locality, near Rémada, Tunisia (Lapparent 1951, 1960). The locality at Rémada was considered by Lapparent (1960) to be among the youngest in the "Continental intercalaire," lying between 15 and 20 meters below marine rocks of Cenomanian age. Two teeth from Rémada resemble those of *Iguanodon mantelli*, making them indistinguishable from *Ouranosaurus*. The Rémada material represents the northern extreme of the range of iguanodonts in Africa; the Koum basin material represents the southern extreme of iguanodonts (and *Ouranosaurus*) in Africa.

In overall appearance the Koum basin archosaur fauna resembles that of Gadoufaoua, Niger, especially in the presence of cf. *Araripesuchus,* cf. Spinosauridae, and *Ouranosaurus* sp. The presence of cf. *Araripesuchus* and a possible spinosaurid in Early Cretaceous deposits in Malawi provides a similar measure of resemblance; however, despite intensive collecting effort, no ornithopod dinosaur remains have been recovered from Malawi. The Malawi megafauna is dominated by saurischians, and in this respect, resembles the faunas of the "Continental intercalaire" of the central Sahara (see Lapparent 1960). The presence of iguanodonts at only three African localities (Gadoufaoua, Rémada, and Koum) uniquely unites them. If these three sites are relatively younger than the majority of sites in the central Sahara, and if the age of the Malawi deposits is older than those of Koum and Gadoufaoua, as Jacobs *et al.* (1990) allow, iguanodont dinosaurs were relatively late arrivals on the African scene. Their absence in early faunas was to the advantage of other large herbivores, specifically sauropod dinosaurs, which are well known from many sites in the Early Cretaceous of Africa but are less important in later ones. The scarcity of sauropods at Koum, and their relative unimportance at Gadoufaoua, implies that they may have been displaced ecologically by late arriving large herbivores, such as iguanodontid dinosaurs. An alternative viewpoint is given by Bonaparte (1986), suggesting that *Ouranosaurus* represents a distinct endemic iguanodontid which evolved after Laurasia split from Gondwana.

Lower Cretaceous rocks in Europe and North America are known for their abundance of ornithopod dinosaur fossils, including a diversity of primitive and derived iguanodontids. If African iguanodontids arrived from Laurasia relatively late in the Early Cretaceous, they probably did so directly via Europe and not through South America. The dinosaur faunas of South America conspicuously lack iguanodontids, with the possible exception of footprint samples from eastern Brazil (Leonardi 1979a, 1980a) and Chile (Casamiquela and Fasola 1968). No South American footprints attributed to iguanodontids resemble the classic forms from western Europe (for example, see Lehmann [1978]). It is possible that the migration event into Africa occurred after the separation from South America, precluding iguanodontids from crossing into the (departing) western portion of Gondwana. The idea that iguanodontid dinosaurs were excluded from South America for the majority of the Cretaceous is supported by the Late Cretaceous diversification of South American titanosaurid sauropods (see Bonaparte 1986). This event was attributed by Bonaparte (1986) to the coeval diversification of angiosperms, but it may be better explained by a lack of ecological competitors (specifically in the form of large ornithopods). From osteological evidence, large ornithopods did not arrive in South America until nearly the end of the Cretaceous (see Bonaparte 1986).

A large ornithopod dinosaur (*Muttaburrasaurus*) is known from fragmentary remains from the Albian of Australia. Norman (1985) notes that *Muttaburrasaurus* is primitive relative to other iguanodonts, and possesses several derived features. Bonaparte (1986) notes that the dentition of *Muttaburrasaurus* is unique among the Iguanodontidae. If *Muttaburrasaurus* is truly an iguanodontid, its presence in Australia suggests that members of that family were there prior to the breakup of the Gondwanan continents (Norman 1986; Bonaparte 1986). However, Molnar (1980) implies that *Muttaburrasaurus* is not clearly related to the Iguanodontidae, although it was assigned to that family in a later description (Bartholomai and Molnar 1981).

Summary

(1) The archosaur body fossils from the Early Cretaceous deposits of the Koum basin share similarities to other faunas across Africa and South America, and less importantly, with Europe. The Koum basin archosaurian ichnites show similarities to North and South American as well as to European trace fossils of similar age; this probably reflects conservatism in archosaur pes morphology more than actual paleobiogeographic events. South American ichnites attributed to ornithopods do not resemble those from Koum.

(2) The archosaurian ichnites from the central Koum basin show correspondence with the osteological sample from the eastern end of the basin, and were produced by theropod, sauropod, and ornithopod dinosaurs. Multivariate statistical techniques on morphological data are useful for objective discrimination between footprint types; similar

analyses using behaviorally-dependent data are not as useful.

(3) Deposition in the Koum basin occurred prior to sedimentation in the Benue trough, by virtue of the fact that the basin is structurally similar to other early basins in northern Cameroon and Nigeria, and that it contains a fauna at least as old or older than the oldest Benue trough sediments. Therefore, the Koum basin fossil localities contain samples of faunas which existed prior to the time of development of and deposition in the main body of the Benue trough. During the period when the Koum basin faunas were extant, the North and South Atlantic Oceans were still separated by land and faunal exchange with South America was still possible.

(4) The Koum basin archosaur fauna shares similarities with Early Cretaceous faunas from Gadoufaoua, Niger, northern Malawi, Rémada, southern Tunisia, and with the Kirkwood fauna from South Africa. Archosaur ichnites of Early Cretaceous age are rare in Africa, but the Koum basin ichnofauna is very similar to the ichnofaunas from the Babouri-Figuil basin in northern Cameroon and the Mount Arli fauna of the argiles de l'Irhazer in Niger. The Koum basin faunal assemblage is most similar to those closest to it in both time and space.

APPENDIX 1

Table 24.--Measurements of teeth of aff. *Araripesuchus wegeneri* from the Koum basin, northern Cameroon.

Specimen No.	Mesiodistal length (mm)	Lingual-labial width (mm)	Tooth crown height (mm)	Number of serrations	Tooth morphotype
101	....	0.98	1.64	...	3
102	1.76	0.70	1.72	...	2
103	....	0.84	....	...	2
104	1.45	0.63	1.29	20	1
105	1.78	0.98	....	>21	1
106	2.11	0.96	1.64	>20	1
107	3.54	1.82	3.91	21	1
108	....	....	2.13	>14	1
109	1.90	0.74	1.86	...	1
110	2.29	1.37	2.41	39	2
111	2.09	0.88	1.84	>17	1
112	1.58	0.67	0.90	21	1
113	2.00	0.74	1.64	24	1
114	1.21	0.74	1.62	0	3
115	1.37	0.68	1.64	> 8	1
116	1.58	0.68	1.39	18	1
117	2.48	1.86	....	37	2
118	2.47	0.96	1.94	>11	1
119	1.82	0.84	1.53	>19	1
120	2.27	1.45	....	> 5	2
121	2.50	0.94	2.23	0	*
122	2.17	0.88	2.00	>20	1
123	1.51	0.68	1.25	>10	1
124	2.82	1.35	2.19	> 5	1
125	1.64	0.74	1.78	20	1
126	1.72	0.98	2.02	21	2
127	1.39	0.80	1.33	...	3
128	1.23	0.59	1.23	19	1
129	2.23	1.15	....	>12	1
130	1.88	1.10	2.37	14	2
131	2.13	0.90	....	28	1
132	1.53	0.96	1.45	0	2
133	1.35	0.53	1.19	16	1
134	....	....	....	...	.

Table 24 (continued).--Measurements of teeth of aff. *Araripesuchus wegeneri* from the Koum basin, northern Cameroon.

Specimen No.	Mesiodistal length (mm)	Lingual-labial width (mm)	Tooth crown height (mm)	Number of serrations	Tooth morphotype
135	....	1.76	3.13	> 8	2
136	1.66	0.68	1.13	14	1
137	1.13	0.72	....	>15	2
138	....	0.84	....	> 7	3
139	1.23	0.57	1.13	>13	1
140	....	0.92	....	>11	2
141	3.68	1.86	2.88	28	1
142	....	1.13	....	>19	2
143	....	....	....	...	.
144	....	....	....	...	.
145	2.19	0.94	....	> 7	1
146	1.37	0.76	1.55	> 6	2
147	1.72	0.86	2.09	>17	1
148	2.48	1.15	....	>31	1
149	....	1.51	....	>12	1
150	1.74	1.15	....	...	2
151	2.39	1.23	1.45	21	1
152	2.97	1.64	4.46	...	2
153	2.07	0.84	1.68	...	1
154	2.82	1.39	2.15	...	1
155	2.19	0.88	1.41	>19	1
156	2.47	1.04	1.76	19	1
157	....	0.76	1.57	24	1
158	....	....	....	...	.
159	....	1.47	....	>15	2
160	1.31	0.70	....	...	2
161	3.68	2.11	2.76	29	1
162	....	1.55	....	>25	2
163	....	1.57	1.84	>11	1
164	....	0.80	1.94	>15	1
165	2.00	1.13	2.05	35	1
166	....	1.31	2.72	>18	1
167	3.89	2.02	3.07	43	1
168	1.74	0.67	1.49	> 9	1
169	1.90	0.84	....	>11	1
170	1.82	1.04	1.96	>25	1
171	2.64	2.00	....	>17	*
172	1.43	1.12	....	0	2
173	1.27	0.76	....	0	3
174	1.29	1.17	2.00	0	4
175	1.72	1.72	2.27	0	4
176	1.57	1.23	2.82	14	*

Table 24 (continued).--Measurements of teeth of aff. *Araripesuchus wegeneri* from the Koum basin, northern Cameroon.

Specimen No.	Mesiodistal length (mm)	Lingual-labial width (mm)	Tooth crown height (mm)	Number of serrations	Tooth morphotype
177	....	....	....	0	4
178	1.19	1.04	1.13	0	4
179	1.00	0.90	....	0	4
180	1.78	1.17	....	...	2
181	1.80	1.76	2.50	0	4
182	1.41	1.00	....	0	4
183	1.45	1.25	2.99	0	2
184	1.43	1.23	....	0	4
185	2.27	2.07	....	0	4
186	2.00	1.31	3.27	0	2
187	1.60	1.45	....	0	4
188	1.19	0.72	1.47	0	3
189	1.33	1.29	....	0	4
190	1.21	1.17	2.25	0	4
191	1.04	0.88	....	0	4
192	1.12	0.72	....	13	2
193	0.98	0.86	....	0	4
194	1.53	1.45	1.98	0	4
195	0.94	0.80	1.51	0	4
196	0.88	0.63	....	0	2
197	1.70	....	2.92	0	2
198	....	0.92	....	...	2
199	1.19	1.08	1.82	0	4
200	1.08	0.84	2.02	0	2
201	1.98	1.86	....	0	4
202	2.56	2.50	....	0	4
203	1.86	1.76	3.44	0	4
204	....	1.57	....	0	4
205	1.41	1.15	....	0	4
206	2.43	2.25	....	0	4
207	2.05	1.98	....	0	4
208	1.17	1.13	3.31	0	4
209	2.29	1.64	3.09	>12	*
210	1.84	1.19	2.50	0	2
211	....	....	3.80	0	4
212	1.02	0.67	....	0	2
213	1.35	1.31	....	0	2
214	....	....	....	0	4
215	....	....	....	> 9	1
216	2.62	2.23	....	0	4
217	1.53	1.41	....	0	4
218	2.50	2.66	5.52	0	4

Table 24 (continued).--Measurements of teeth of aff. *Araripesuchus wegeneri* from the Koum basin, northern Cameroon.

Specimen No.	Mesiodistal length (mm)	Lingual-labial width (mm)	Tooth crown height (mm)	Number of serrations	Tooth morphotype
219	....	....	....	0	4
220	....	1.80	2.93	0	4
221	....	....	....	...	4
222	2.48	2.35	3.89	0	4
223	1.31	1.23	....	0	4
224	2.43	1.62	3.33	> 6	2
225	2.25	....	....	0	4
226	1.02	0.61	1.25	0	3
227	....	....	....	...	.
228	1.17	0.70	1.41	0	3
229	1.23	0.74	1.37	0	3
230	1.13	0.70	1.41	0	3
231	1.00	0.53	1.04	0	3
232	1.58	0.96	1.62	0	3
233	....	1.06	1.55	>17	1
234	....	....	....	> 8	.
235	1.68	0.88	1.62	0	3
236	1.80	0.76	1.60	24	1
237	....	....	3.46	>30	1
238	....	0.65	1.37	> 4	1
239	2.03	0.92	1.88	>23	1
240	....	0.80	1.92	> 5	1
241	1.29	0.61	0.96	>11	1
242	2.05	0.76	2.31	>28	1
243	1.82	1.02	....	>15	1
244	2.02	0.86	....	>8	1
245	....	....	....	...	1
246	....	....	....	...	1
247	2.47	1.37	....	>27	*
248	3.56	1.88	....	>16	*
249	....	1.31	1.64	> 6	1
250	1.76	0.98	....	> 8	2
251	....	1.17	....	>29	1
252	....	1.19	1.53	>16	1
253	1.29	0.67	....	>13	2
254	1.82	0.88	1.80	29	1
255	....	....	....	> 8	2
256	....	1.19	1.94	>12	1
257	....	....	....	...	1
258	1.88	0.70	1.55	...	1
259	4.34	....	....	>34	1
260	3.78	1.72	....	>25	1

Table 24 (continued).--Measurements of teeth of aff. *Araripesuchus wegeneri* from the Koum basin, northern Cameroon.

Specimen No.	Mesio-distal length (mm)	Lingual-labial width (mm)	Tooth crown height (mm)	Number of serrations	Tooth morphotype
261	....	....	1.15	0	2
262	....	....	2.47	0	2
263	1.33	0.90	2.03	...	2
264	....	....	....	...	.
265	1.17	0.78	....	0	1
266	1.35	1.23	2.50	...	4
267	1.66	0.96	....	0	.
268	1.17	1.21	....	0	4
269	2.47	2.11	....	0	2
270	1.43	1.15	....	0	4
271	2.15	1.86	2.66	0	4
272	2.17	2.09	3.42	0	4
273	1.58	1.39	....	0	4
274	1.27	0.92	....	0	.
275	....	....	....	0	2
276	1.58	1.45	2.23	0	4
277	2.50	2.45	4.66	0	4
278	....	....	2.02	0	4
279	....	....	1.39	...	1
280	1.64	0.88	....	0	2
281	1.13	1.00	....	0	2
282	....	1.35	....	> 6	*
283	0.86	0.45	0.80	0	3
284	....	....	1.72	...	1
285	1.80	0.70	....	...	2
286	1.47	1.15	....	...	2
287	1.27	0.90	1.39	0	3
288	1.00	0.82	....	0	2
289	....	0.70	....	> 8	*
290	2.66	1.12	2.45	> 3	1
291	1.80	0.94	....	0	2
292	1.02	0.76	....	0	4
293	1.15	0.65	1.25	0	3
294	1.62	0.90	2.21	...	2
295	....	....	2.33	...	2
296	....	....	....	...	2
297	1.68	0.90	....	> 3	1
298	2.60	1.62	3.03	>35	*
299	2.74	1.08	....	>11	*
300	2.90	1.37	....	>24	*
301	....	1.10	1.84	> 3	1
302	1.98	1.08	1.92	28	*

Table 25.--Measurements of teeth of aff. *Araripesuchus wegeneri* from near Mwakasyunguti, Malawi:

Specimen No.	Mesio-distal length (mm)	Lingual-labial width (mm)	Tooth crown height (mm)	Number of serrations	Tooth morphotype
MAL-59	1.00	0.72	1.29	...	4
MAL-60	1.06	0.70	1.43	> 2	2
MAL-61	1.47	0.63	0.98	>12	2
MAL-63	....	0.68	....	>13	1
MAL-75	1.21	1.35	....	...	4

Table 26.--Measurements of maxillary teeth of *Araripesuchus wegeneri* from Gadoufaoua, Niger (MNHN GDF 700)

Specimen No.	Mesio-distal length (mm)	Lingual-labial width (mm)	Tooth crown height (mm)	Number of serrations	Tooth morphotype
A	3.1	....	3.3	>12	2
B	2.8	....	2.4	> 8	2
C	2.4	....	2.1	> 5	1

APPENDIX 2

This appendix contains data from trackway localities in the Koum basin in northern Cameroon. A brief explanation of identifying labels and variables not described in the preceding text follows:

Identifiers

Trackway number (T) - Trackway number is the identifying label given to each individual trackway. A trackway is defined here as the set of preserved successive footprints attributable to the passage of a single individual. The trackway numbers initially assigned at the KB-17 locality were in Roman format (*e.g.*, XV instead of 15). This format was later changed to equivalent Arabic numerals in order to facilitate the transfer of data between computer disks and applications packages.

Footprint number (F) - Footprint number is the identifying label given to each footprint within an individual trackway. A footprint is defined here as the single preserved impression of a foot or distal locomotory appendage within or upon a substrate. The footprint number within a given trackway always increases sequentially from the first footprint preserved in a trackway (assigned the number 1) to the last. Footprint numbers assigned in the field were sequential regardless of the absence of intervening footprints; for instance, in the case where a left footprint was not preserved, the numeration of the successive right footprints was continuous, as though no interruption in the sequence existed. In order to facilitate data manipulation by computer statistical packages, it was necessary to interpose a "dummy footprint" in the trackway in order to account for the missing data. The footprint number sequence in these cases was reassigned from the point of the missing footprint(s) forward. A list of footprint number reassignments is given in table 27.

Trackway length (TL) - Trackway length is the linear distance of the entire preserved trackway, measured from the distal end of the digit II impression of the first footprint in the trackway to the distal end of the digit II impression of the last footprint in the trackway. This variable quantifies the total length of preserved or accessible trackway, regardless of whether one to several intervening footprints may be missing from the trackway sequence. Values for trackway length are given in centimeters in table 28.

Number of prints (F#) - Number of prints refers to the total number of footprints potentially preservable in an individual trackway. In most cases this number corresponds to the actual number found in the trackway; in cases where

Table 27.--Footprint number (F) reassignments within trackways (T).

T	Old F	New F
1	-	2*
1	2	3
1	3	4
5	5	10
5	6	11
5	7	12
5	8	13
5	9	14
5	10	15
5	11	16
16	-	3*
16	3	4
16	4	5
16	5	6
16	6	7
19	6	9
19	7	10
19	8	11
24	-	2*
24	2	3
24	-	4*
24	3	5
24	4	6
24	5	7
25	-	16*
25	-	17*
27	-	5*
27	5	6
27	6	7
27	7	8
27	8	9
34	-	2*
34	2	3
34	3	4
34	4	5
34	5	6
34	-	7*
34	6	8
34	7	9
34	8	10
34	9	11
34	10	12
34	11	13
34	12	14
35	-	4*
35	-	5*
35	4	6
35	5	7
35	6	8
35	7	14
35	8	16

* = Dummy footprint

one or several footprints were not preserved, the number of prints refers to the number of actually preserved footprints plus the number of missing ones, assuming no anomalous excursions or unusual bounds were made by the trackmaker.

Bedding strike (BS) - Bedding strike is the structural orientation of the bedding plane which contains a particular trackway or group of trackways. This variable was recorded along with bedding dip for each trackway in order to allow the orientations of trackway and pace bearings to be rotated back to pre-tilt values for later analysis. Bedding strike is given in table 28 in degrees.

Bedding dip (BD) - Bedding dip is the structural dip of the bedding plane containing a trackway or group of associated trackways. Bedding dip is given in degrees in table 28.

Pace direction (PD) - Pace direction is the compass orientation of a line defined by the distal end of the digit III impression of two successive footprints of opposite feet, *i.e.*, the orientation of the pace length measurement. This variable was recorded in order to aid in the mapping of the trackways, and is given in table 28 in degrees between 1° and 360°.

Footprint orientation (FO) - This variable is the compass orientation of the footprint length measurement, which coincides with the footprint long axis, and is given in degrees between 1° and 360°.

Left/right print (LR) - This variable indicates whether it was the left or right foot of the trackmaker which produced the preserved footprint.

Length times width (L*W) - This variable is the product of the two linear footprint dimensions described above. It can be used as a rough approximation of footprint area. Units are given in square centimeters in table 28.

Froude number (FRNO) - Froude number is a dimensionless ratio which describes the interaction between inertia and gravity of a moving object (Alexander 1976). Alexander applied the principle of the Froude number to the locomotion of terrestrial animals using the relationship

$$\text{FRDNO} = \frac{\text{SPD}^2}{\text{g*HH}}$$

where SPD is the velocity of the animal, g is the gravitational acceleration constant, and HH is height of the acetabulum above the ground (described above).

Speed (km/h) (SKH) - This variable is trackmaker speed as calculated for speed (m/s) but is expressed in units of kilometers per hour.

Table 28.--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Variable symbols are explained at the end of this table and in the text.

T	F	TL	TO	F#	BS	BD	SL	S	P	PD	TW	PA	PI	RSL
1	1	301	23	4	97	8	1	210	...	...	...	...	...	...
1	2	301	23	4	97	8	1	...	...	...	...	...	...	...
1	3	301	23	4	97	8	1	...	96	9	...	...	...	...
1	4	301	23	4	97	8	1	...	...	...	...	...	...	...
2	1	260	349	3	90	8	2	260	132	358	19	...	1.01	...
2	2	260	349	3	90	8	2	...	131	341	...	163	...	...
2	3	260	349	3	90	8	2	...	...	...	...	...	...	...
3	1	320	177	4	90	8	2	214	108	171	7	...	1.03	1.04
3	2	320	177	4	90	8	2	210	105	179	8	172	0.98	1.05
3	3	320	177	4	90	8	2	...	107	170	...	171	...	...
3	4	320	177	4	90	8	2	...	...	...	...	...	...	...
4	1	539	36	5	90	8	1	227	103	27	17	...	0.82	...
4	2	539	36	5	90	8	1	271	125	44	15	163	0.85	...
4	3	539	36	5	90	8	1	313	147	31	12	167	0.89	2.96
4	4	539	36	5	90	8	1	...	165	40	...	171	...	...
4	5	539	36	5	90	8	1	...	...	...	...	...	...	...
5	1	1005	211	16	94	9	1	113	52	224	9	...	0.82	0.94
5	2	1005	211	16	94	9	1	123	63	205	11	161	1.00	1.07
5	3	1005	211	16	94	9	1	...	63	224	...	161	...	...
5	4	1005	211	16	94	9	1	...	...	...	...	...	...	...
5	10	1005	211	16	94	9	1	145	72	201	6	...	0.99	1.26
5	11	1005	211	16	94	9	1	144	73	210	6	171	1.04	1.25
5	12	1005	211	16	94	9	1	139	70	201	7	171	1.00	1.21
5	13	1005	211	16	94	9	1	139	70	213	8	168	1.00	...
5	14	1005	211	16	94	9	1	139	70	200	7	167	1.00	1.16
5	15	1005	211	16	94	9	1	...	70	211	...	169	...	...
5	16	1005	211	16	94	9	1	...	...	...	...	...	...	...
6	1	725	38	7	91	9	3	230	118	50	19	...	1.02	...
6	2	725	38	7	91	9	3	238	116	31	20	161	0.93	...
6	3	725	38	7	91	9	3	250	125	50	22	161	0.98	...
6	4	725	38	7	91	9	3	244	127	30	27	160	1.06	...
6	5	725	38	7	91	9	3	245	120	56	22	154	0.92	...
6	6	725	38	7	91	9	3	...	130	36	...	160	...	...
6	7	725	38	7	91	9	3	...	...	...	...	...	...	...
7	1	...	...	1	91	9	3	...	...	...	...	...	...	...
8	1	314	228	6	85	7	3	125	54	228	4	...	0.77	0.78
8	2	314	228	6	85	7	3	130	70	220	10	172	1.13	0.87
8	3	314	228	6	85	7	3	124	62	237	11	163	0.97	0.75
8	4	314	228	6	85	7	3	130	64	217	8	160	0.97	0.81
8	5	314	228	6	85	7	3	...	66	231	...	166	...	...
8	6	314	228	6	85	7	3	...	...	...	...	...	...	...
9	1	320	1	3	66	9	2	320	164	359	1	...	1.03	3.31
9	2	320	1	3	66	9	2	...	159	360	...	179	...	...
9	3	320	1	3	66	9	2	...	...	...	...	...	...	...
10	1	140	208	3	104	8	3	140	70	197	12	...	0.96	0.94
10	2	140	208	3	104	8	3	...	73	216	...	161	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	FRNO	SMS	SKH	SRT	LR	C	FL	FW	L*W	ARA	SI	LBW
1	1	...	...	...	...	r	2	...	...	...	...	...	...
1	2	...	...	...	...	l	2	...	...	...	...	...	...
1	3	...	...	...	...	r	2	...	...	...	...	...	...
1	4	...	...	...	...	l	2	...	...	...	...	...	...
2	1	...	...	...	...	l	4	...	...	...	...	...	...
2	2	...	...	...	...	r	4	...	...	...	...	...	...
2	3	...	...	...	...	l	4	...	...	...	...	...	...
3	1	0.07	1.20	4.3	0.56	r	4	36	29	1026	887	9.79	1.30
3	2	0.07	1.20	4.3	0.57	l	4	35	26	917	739	9.53	1.34
3	3	...	...	...	...	r	4	33	28	917	884	9.79	1.19
3	4	...	...	...	...	l	4	36	29	1026	798	9.64	1.26
4	1	...	...	...	...	r	2	...	20	...	...	...	...
4	2	...	...	...	...	l	2	...	18	...	...	...	...
4	3	2.31	4.90	17.6	1.56	r	2	23	16	368	284	8.15	1.44
4	4	...	...	...	...	l	2	25	19	483	357	8.48	1.30
4	5	...	...	...	...	r	2	22	17	374	347	8.44	1.29
5	1	0.05	0.78	2.8	0.69	l	2	26	22	582	525	9.04	1.16
5	2	0.08	0.94	3.4	0.76	r	2	25	23	575	547	9.10	1.09
5	3	...	...	...	...	l	2	25	24	588	578	9.17	1.06
5	4	...	...	...	...	r	2	22	22	473	546	9.09	1.02
5	10	0.14	1.23	4.4	0.85	r	2	25	24	593	552	9.11	1.05
5	11	0.13	1.22	4.4	0.85	l	2	25	21	513	413	8.69	1.22
5	12	0.12	1.15	4.1	0.83	r	2	25	22	545	498	8.96	1.15
5	13	...	...	...	...	l	2	...	21	...	...	...	...
5	14	0.10	1.10	4.0	0.79	r	2	26	22	562	476	8.89	1.20
5	15	...	...	...	...	l	2	26	22	582	466	8.86	1.16
5	16	...	...	...	...	r	2	27	22	602	462	8.85	1.21
6	1	...	...	...	...	l	4	...	...	...	...	...	...
6	2	...	...	...	...	r	4	...	...	...	...	...	...
6	3	...	...	...	...	l	4	...	...	...	...	...	...
6	4	...	...	...	...	r	4	...	...	...	...	...	...
6	5	...	...	...	...	l	4	...	...	...	...	...	...
6	6	...	...	...	...	r	4	...	...	...	...	...	...
6	7	...	...	...	...	l	4	...	...	...	...	...	...
7	1	...	...	...	...	l	2	23	23	520	451	8.82	1.02
8	1	0.03	0.66	2.4	0.53	l	6	31	28	853	...	...	1.13
8	2	0.04	0.76	2.7	0.58	r	6	29	24	693	...	...	1.21
8	3	0.02	0.63	2.3	0.50	l	6	32	27	864	...	...	1.19
8	4	0.03	0.70	2.5	0.54	r	6	31	29	899	...	...	1.07
8	5	...	...	...	...	l	6	30	28	840	...	...	1.07
8	6	...	...	...	...	r	6	30	26	780	...	...	1.15
9	1	3.37	5.65	20.3	1.77	r	2	21	15	319	252	7.98	1.38
9	2	...	...	...	...	l	2	20	13	260	241	7.91	1.54
9	3	...	...	...	...	r	2	25	17	425	404	8.66	1.47
10	1	0.05	0.86	3.1	0.61	r	6	29	32	928	...	...	0.91
10	2	...	...	...	...	l	6	31	31	946	...	...	1.02

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	D1	D2	D3	D4	D1P	D2P	D3P	D4P	D1P2	D2P2	D3P2
1	1	5.5	7.8	8.2	4.7	...	...	...	...	0.27	0.42	0.46
1	2	...	...	...	...	...	...	...	...	...	...	...
1	3	7.5	8.0	7.3	6.4	...	...	...	...	0.35	0.38	0.33
1	4	5.0	9.5	8.6	5.8	...	...	...	...	0.21	0.49	0.42
2	1	...	...	...	...	...	...	...	...	...	...	...
2	2	...	...	...	...	...	...	...	...	...	...	...
2	3	...	...	...	...	...	...	...	...	...	...	...
3	1	14.0	18.0	18.5	10.5	0.39	0.50	0.51	0.29	0.30	0.42	0.44
3	2	15.5	21.0	19.5	12.8	0.44	0.60	0.56	0.37	0.29	0.44	0.40
3	3	15.4	17.5	17.9	...	0.47	0.53	0.54	...	...	...	...
3	4	14.5	15.8	18.5	10.0	0.40	0.44	0.51	0.28	0.33	0.37	0.46
4	1	13.0	17.5	17.5	9.0	...	...	...	...	0.30	0.44	0.44
4	2	12.3	21.4	20.2	7.1	...	...	...	...	0.25	0.54	0.50
4	3	7.3	16.0	17.0	7.8	0.32	0.70	0.74	0.34	0.18	0.50	0.55
4	4	12.0	18.8	19.4	9.0	0.48	0.75	0.78	0.36	0.25	0.47	0.49
4	5	10.9	12.7	10.2	5.0	0.50	0.58	0.46	0.23	0.39	0.49	0.36
5	1	10.4	14.8	14.9	11.0	0.40	0.57	0.57	0.42	0.26	0.41	0.41
5	2	12.5	17.2	14.3	9.4	0.50	0.69	0.57	0.38	0.31	0.48	0.37
5	3	10.2	15.0	14.7	9.8	0.41	0.60	0.59	0.39	0.26	0.43	0.42
5	4	14.8	...	17.5	11.5	0.67	...	0.80	0.52	...	...	...
5	10	13.0	16.2	14.6	8.9	0.52	0.65	0.58	0.36	0.33	0.44	0.38
5	11	9.5	16.3	13.7	10.5	0.38	0.65	0.55	0.42	0.23	0.48	0.38
5	12	10.4	12.3	13.1	7.0	0.42	0.49	0.52	0.28	0.32	0.40	0.44
5	13	10.5	14.3	...	...	...	...	...	...	...	...	...
5	14	11.0	15.4	13.0	7.2	0.42	0.59	0.50	0.28	0.31	0.49	0.39
5	15	10.4	14.8	14.2	10.7	0.40	0.57	0.55	0.41	0.26	0.42	0.40
5	16	12.5	15.3	14.0	8.3	0.46	0.57	0.52	0.31	0.33	0.44	0.39
6	1	...	...	...	...	...	...	...	...	...	...	...
6	2	...	...	...	...	...	...	...	...	...	...	...
6	3	...	...	...	...	...	...	...	...	...	...	...
6	4	...	...	...	...	...	...	...	...	...	...	...
6	5	...	...	...	...	...	...	...	...	...	...	...
6	6	...	...	...	...	...	...	...	...	...	...	...
6	7	...	...	...	...	...	...	...	...	...	...	...
7	1	9.3	14.3	9.4	10.8	0.40	0.62	0.41	0.47	0.27	0.48	0.27
8	1	...	...	...	...	...	...	...	...	...	...	...
8	2	...	...	...	...	...	...	...	...	...	...	...
8	3	...	...	...	...	...	...	...	...	...	...	...
8	4	...	...	...	...	...	...	...	...	...	...	...
8	5	...	...	...	...	...	...	...	...	...	...	...
8	6	...	...	...	...	...	...	...	...	...	...	...
9	1	9.7	14.8	13.0	7.0	0.46	0.70	0.62	0.33	0.28	0.50	0.41
9	2	7.2	14.3	15.0	9.8	0.36	0.72	0.75	0.49	0.18	0.45	0.48
9	3	10.5	14.7	15.2	10.4	0.42	0.59	0.61	0.42	0.26	0.41	0.43
10	1	...	...	...	...	...	...	...	...	...	...	...
10	2	...	...	...	...	...	...	...	...	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	D4P2	SKEW	DA	A	B	FD	FO	FRT	HH	VOL	MASS
1	1	0.22	1.05	...	...	...	2.4	...	...	...	...	...
1	2	...	...	...	...	...	...	...	...	...	...	...
1	3	0.28	0.91	...	...	...	1.4	...	...	...	...	...
1	4	0.25	0.91	...	...	...	4.0	...	...	...	...	...
2	1	...	...	52	34	18	6.0	350	...	...	...	...
2	2	...	...	60	...	...	5.3	342	...	...	...	...
2	3	...	...	65	38	27	6.5	355	...	...	...	...
3	1	0.21	1.03	57	30	27	3.0	165	...	205	1422	1422
3	2	0.23	0.93	58	28	30	3.8	182	7	200	1313	1313
3	3	...	1.02	54	27	27	4.0	169	6	188	1112	1112
3	4	0.20	1.17	65	33	33	4.7	178	...	205	1422	1422
4	1	0.19	1.00	...	...	...	1.7	24	...	...	...	...
4	2	0.13	0.94	...	...	...	4.0	38	3	...	...	...
4	3	0.19	1.06	56	21	35	2.4	42	-5	106	220	220
4	4	0.18	1.03	67	...	...	2.8	21	-15	115	278	278
4	5	0.15	0.80	51	30	21	3.0	30	...	101	194	194
5	1	0.27	1.01	60	31	29	1.7	230	...	120	310	310
5	2	0.21	0.83	61	33	28	2.5	221	-7	115	278	278
5	3	0.25	0.98	60	33	27	2.2	221	7	115	278	278
5	4	...	...	52	...	...	2.2	217	...	101	194	194
5	10	0.20	0.90	65	31	34	2.5	209	...	115	278	278
5	11	0.27	0.84	65	33	32	2.3	211	6	115	278	278
5	12	0.20	1.07	60	32	28	2.6	204	2	115	278	278
5	13	...	...	...	...	...	2.1	211	4	...	...	...
5	14	0.18	0.84	62	34	28	2.1	206	1	120	310	310
5	15	0.27	0.96	70	...	...	2.1	207	2	120	310	310
5	16	0.20	0.92	70	35	35	2.5	204	...	124	345	345
6	1	...	...	...	...	...	5.2	47	...	...	...	...
6	2	...	...	62	33	29	4.1	39	2	...	...	...
6	3	...	...	60	...	...	5.1	43	3	...	...	...
6	4	...	...	...	...	...	7.6	52	-12	...	...	...
6	5	...	...	61	...	...	8.3	45	2	...	...	...
6	6	...	...	67	...	...	3.1	69	-23	...	...	...
6	7	...	...	68	35	33	9.0	46	...	...	...	...
7	1	0.33	0.66	75	40	35	2.9	207	...	106	220	220
8	1	...	...	...	...	...	1.9	249	...	160	700	700
8	2	...	...	...	...	...	3.0	227	-3	149	580	580
8	3	...	...	...	...	...	2.5	240	12	165	766	766
8	4	...	...	...	...	...	2.4	226	1	160	700	700
8	5	...	...	...	...	...	1.8	240	16	155	639	639
8	6	...	...	...	...	...	1.4	215	...	155	639	639
9	1	0.19	0.88	57	26	31	2.3	360	...	97	170	170
9	2	0.27	1.05	42	22	20	1.7	2	-3	92	148	148
9	3	0.26	1.03	43	21	22	2.4	354	...	115	278	278
10	1	...	...	...	...	...	1.0	205	...	149	580	580
10	2	...	...	...	...	...	2.2	224	18	160	700	700

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	TL	TO	F#	BS	BD	SL	S	P	PD	TW	PA	PI	RSL
10	3	140	208	3	104	8	3	...	...	...	...	...	...	...
11	1	718	274	4	104	8	3	448	220	272	16	...	0.97	...
11	2	718	274	4	104	8	3	500	228	264	-6	172	0.84	...
11	3	718	274	4	104	8	3	...	270	261	...	183	...	...
11	4	718	274	4	104	8	3	...	...	...	...	...	...	...
12	1	346	161	6	104	8	3	141	71	162	4	...	1.01	...
12	2	346	161	6	104	8	3	138	70	155	9	173	1.00	1.88
12	3	346	161	6	104	8	3	139	70	169	7	166	0.99	1.89
12	4	346	161	6	104	8	3	139	71	157	7	168	1.03	1.68
12	5	346	161	6	104	8	3	...	69	169	...	168	...	...
12	6	346	161	6	104	8	3	...	...	...	...	...	...	...
13	1	543	180	5	104	8	3	272	139	175	8	...	1.05	2.11
13	2	543	180	5	104	8	3	270	132	182	9	173	0.98	2.10
13	3	543	180	5	104	8	3	271	135	174	12	172	0.99	2.02
13	4	543	180	5	104	8	3	...	136	184	...	170	...	...
13	5	543	180	5	104	8	3	...	...	...	...	...	...	...
14	1	...	...	2	104	8	3	...	187	198	...	...	...	...
14	2	...	...	2	104	8	3	...	...	...	...	...	...	...
15	1	238	47	3	94	8	3	238	167	91	116	...	1.02	...
15	2	238	47	3	94	8	3	...	165	2	...	91	...	...
15	3	238	47	3	94	8	3	...	...	...	...	...	...	...
16	1	530	226	7	100	6	2	...	92	216	...	...	...	...
16	2	530	226	7	100	6	2	175	...	...	...	...	...	1.10
16	3	530	226	7	100	6	2	...	...	...	...	...	...	...
16	4	530	226	7	100	6	2	180	92	240	20	...	1.01	1.09
16	5	530	226	7	100	6	2	173	91	215	19	155	1.05	1.08
16	6	530	226	7	100	6	2	...	87	239	...	156	...	...
16	7	530	226	7	100	6	2	...	...	...	...	...	...	...
17	1	579	179	6	75	7	2	245	125	176	9	...	1.08	...
17	2	579	179	6	75	7	2	226	116	185	20	171	1.05	...
17	3	579	179	6	75	7	2	219	111	164	20	159	1.01	1.64
17	4	579	179	6	75	7	2	220	110	185	12	159	0.97	1.53
17	5	579	179	6	75	7	2	...	113	173	...	168	...	...
17	6	579	179	6	75	7	2	...	...	...	...	...	...	...
18	1	427	45	5	104	8	3	215	118	18	51	...	0.98	...
18	2	427	45	5	104	8	3	220	120	68	41	130	1.03	...
18	3	427	45	5	104	8	3	217	117	28	51	140	0.93	...
18	4	427	45	5	104	8	3	...	124	78	...	130	...	...
18	5	427	45	5	104	8	3	...	...	...	...	...	...	...
19	1	643	204	11	91	8	2	149	74	198	6	...	1.00	1.30
19	2	643	204	11	91	8	2	149	74	208	12	170	0.97	1.30
19	3	643	204	11	91	8	2	142	76	189	17	161	0.96	...
19	4	643	204	11	91	8	2	...	79	212	...	157	...	...
19	5	643	204	11	91	8	2	...	...	...	...	...	...	...
19	9	643	204	11	91	8	2	140	69	195	4	...	0.99	...
19	10	643	204	11	91	8	2	...	70	188	...	173	...	...
19	11	643	204	11	91	8	2	...	...	...	...	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	FRNO	SMS	SKH	SRT	LR	C	FL	FW	L*W	ARA	SI	LBW
10	3	...	...	...	...	r	6	31	31	961	...	...	1.00
11	1	...	...	...	...	l	5	...	...	...	...	...	...
11	2	...	...	...	...	r	5	...	...	...	...	...	...
11	3	...	...	...	...	l	5	...	...	...	...	...	...
11	4	...	...	...	...	r	5	...	...	...	...	...	...
12	1	...	...	...	...	l	3	...	10	...	148	7.21	...
12	2	0.51	1.91	6.9	1.39	r	3	16	10	152	...	7.11	1.68
12	3	0.52	1.94	7.0	1.39	l	3	16	10	154	124	6.95	1.67
12	4	0.35	1.69	6.1	1.21	r	3	18	9	169	118	6.88	1.91
12	5	...	...	...	...	l	3	17	12	196	...	...	1.48
12	6	...	...	...	...	r	3	...	...	...	...	...	...
13	1	0.75	3.08	11.1	1.13	r	3	25	17	425	404	8.66	1.47
13	2	0.74	3.05	11.0	1.13	l	3	25	16	388	343	8.42	1.61
13	3	0.65	2.93	10.5	1.08	r	3	26	16	403	329	8.36	1.68
13	4	...	...	...	...	l	3	24	16	372	316	8.30	1.55
13	5	...	...	...	...	r	3	25	17	413	345	8.43	1.52
14	1	...	...	...	...	l	5	...	23	...	...	...	...
14	2	...	...	...	...	r	5	...	24	...	...	...	...
15	1	...	...	...	...	l	5	...	19	...	...	...	...
15	2	...	...	...	...	r	5	...	16	...	...	...	...
15	3	...	...	...	...	l	5	...	19	...	...	...	...
16	1	...	...	...	...	r	3	...	20	...	479	8.90	...
16	2	0.08	1.15	4.1	0.66	l	3	31	23	713	670	9.39	1.35
16	3	...	...	...	...	r	3	...	...	...	...	...	...
16	4	0.08	1.16	4.2	0.65	l	3	32	22	691	591	9.21	1.48
16	5	0.08	1.13	4.1	0.65	r	3	31	22	667	555	9.12	1.44
16	6	...	...	...	...	l	3	30	...	...	...	...	...
16	7	...	...	...	...	r	3	...	...	...	...	...	...
17	1	...	...	...	...	r	3	...	...	...	...	...	...
17	2	...	...	...	...	l	3	...	...	...	...	...	...
17	3	0.32	2.05	7.4	0.94	r	3	26	21	541	436	8.77	1.25
17	4	0.26	1.90	6.8	0.86	l	3	28	22	610	561	9.13	1.28
17	5	...	...	...	...	r	3	32	23	736	547	9.10	1.39
17	6	...	...	...	...	l	3	28	21	585	507	8.99	1.34
18	1	...	...	...	...	r	5	...	...	...	...	...	...
18	2	...	...	...	...	l	5	...	12	...	...	...	...
18	3	...	...	...	...	r	5	...	14	...	...	...	...
18	4	...	...	...	...	l	5	...	11	...	...	...	...
18	5	...	...	...	...	r	5	...	11	...	...	...	...
19	1	0.15	1.29	4.6	0.87	r	2	25	19	463	369	8.53	1.35
19	2	0.15	1.29	4.6	0.87	l	2	25	20	495	...	...	1.26
19	3	...	...	...	...	r	2	...	...	...	...	...	...
19	4	...	...	...	...	l	2	...	...	...	...	...	...
19	5	...	...	...	...	r	2	...	...	...	...	...	...
19	9	...	...	...	...	l	2	...	...	...	...	...	...
19	10	...	...	...	...	r	2	24	18	432	359	8.49	1.33
19	11	...	...	...	...	l	2	23	19	437	378	8.56	1.21

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	D1	D2	D3	D4	D1P	D2P	D3P	D4P	D1P2	D2P2	D3P2
10	3	...	...	...	...	...	...	...	...	...	...	...
11	1	...	...	...	...	...	...	...	...	...	...	...
11	2	...	25.4	26.0	...	...	...	...	...	...	...	...
11	3	...	25.5	25.1	...	...	...	...	...	...	...	...
11	4	...	...	...	...	...	...	...	...	...	...	...
12	1	5.4	8.8	7.5	6.0	...	...	...	...	0.24	0.47	0.37
12	2	4.5	10.0	7.0	4.0	0.28	0.63	0.44	0.25	0.21	0.65	0.38
12	3	5.9	10.5	10.0	5.5	0.37	0.66	0.63	0.34	0.23	0.49	0.46
12	4	7.3	13.7	10.2	6.0	0.41	0.76	0.57	0.33	0.24	0.58	0.38
12	5	...	...	...	...	...	...	...	...	...	...	...
12	6	...	...	...	...	...	...	...	...	...	...	...
13	1	8.0	12.5	12.9	...	0.32	0.50	0.52	...	...	...	...
13	2	6.5	10.5	12.8	7.5	0.26	0.42	0.51	0.30	0.21	0.39	0.52
13	3	6.9	11.3	13.7	8.8	0.27	0.43	0.53	0.34	0.20	0.38	0.51
13	4	6.4	11.8	12.3	8.5	0.27	0.49	0.51	0.35	0.20	0.43	0.46
13	5	7.5	11.5	13.0	8.0	0.30	0.46	0.52	0.32	0.23	0.40	0.48
14	1	10.4	22.5	23.2	14.0	...	...	...	...	0.17	0.47	0.49
14	2	13.2	18.5	23.5	9.0	...	...	...	...	0.26	0.40	0.58
15	1	10.0	...	...	14.0	...	...	...	...	...	...	...
15	2	9.0	...	...	13.0	...	...	...	...	...	...	...
15	3	9.0	...	...	10.5	...	...	...	...	...	...	...
16	1	15.5	24.0	20.2	14.5	...	...	...	...	0.26	0.48	0.37
16	2	13.0	21.5	18.0	14.9	0.42	0.69	0.58	0.48	0.24	0.47	0.36
16	3	...	...	...	...	...	...	...	...	...	...	...
16	4	17.0	21.4	18.7	10.2	0.53	0.67	0.58	0.32	0.34	0.47	0.38
16	5	13.0	21.0	19.8	15.0	0.42	0.68	0.64	0.48	0.23	0.44	0.40
16	6	19.0	17.7	19.5	...	0.63	0.59	0.65	...	...	...	...
16	7	...	...	...	...	...	...	...	...	...	...	...
17	1	...	...	...	...	...	...	...	...	...	...	...
17	2	...	...	...	...	...	...	...	...	...	...	...
17	3	8.5	13.5	...	...	0.33	0.52	...	...	...	...	...
17	4	10.8	19.4	18.1	13.6	0.39	0.69	0.65	0.49	0.21	0.46	0.41
17	5	...	19.0	...	...	...	0.59	...	...	...	...	...
17	6	9.1	15.0	15.7	10.5	0.33	0.54	0.56	0.38	0.22	0.42	0.45
18	1	...	...	...	...	...	...	...	...	...	...	...
18	2	...	16.0	14.5	...	...	...	...	...	...	...	...
18	3	...	11.7	14.0	...	...	...	...	...	...	...	...
18	4	...	15.2	14.7	...	...	...	...	...	...	...	...
18	5	...	13.5	...	...	...	...	...	...	...	...	...
19	1	9.8	15.2	13.5	10.0	0.39	0.61	0.54	0.40	0.25	0.46	0.39
19	2	...	...	...	...	...	...	...	...	...	...	...
19	3	...	...	...	...	...	...	...	...	...	...	...
19	4	...	...	...	...	...	...	...	...	...	...	...
19	5	...	...	...	...	...	...	...	...	...	...	...
19	9	...	...	...	...	...	...	...	...	...	...	...
19	10	12.0	15.5	15.5	8.0	0.50	0.65	0.65	0.33	0.31	0.44	0.44
19	11	...	16.5	13.7	8.0	...	0.72	0.60	0.35	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	D4P2	SKEW	DA	A	B	FD	FO	FRT	HH	VOL	MASS
10	3	...	...	...	...	...	1.7	214	...	160	700	700
11	1	...	...	...	...	...	3.8	272	...	...	...	...
11	2	...	1.02	...	...	...	2.3	254	14	...	...	...
11	3	...	0.98	...	...	...	2.4	270	-8	...	...	...
11	4	...	...	...	...	...	...	267	...	...	...	...
12	1	0.28	0.85	42	...	...	1.9	157	...	...	...	...
12	2	0.19	0.70	39	18	21	1.9	168	-10	74	79	79
12	3	0.21	0.95	45	...	...	1.6	157	-5	74	79	79
12	4	0.19	0.74	45	26	19	2.0	174	-11	83	110	110
12	5	...	...	...	...	...	...	163	0.1	78	94	94
12	6	...	...	...	...	...	...	170	...	...	...	...
13	1	...	1.03	43	20	23	2.7	178	...	129	382	382
13	2	0.25	1.22	42	...	...	2.9	186	8	129	382	382
13	3	0.28	1.21	44	21	23	2.8	181	-3	134	427	427
13	4	0.28	1.04	46	25	21	1.6	183	4	124	340	340
13	5	0.25	1.13	48	27	21	2.5	180	...	129	382	382
14	1	0.25	1.03	...	...	...	4.8	164	...	...	...	...
14	2	0.16	1.27	...	...	...	3.6	148	...	...	...	...
15	1	...	...	...	...	...	4.0	56	...	...	...	...
15	2	...	...	...	...	...	3.3	33	14	...	...	...
15	3	...	...	...	...	...	4.5	50	...	...	...	...
16	1	0.24	0.84	50	21	29	2.0	228	...	...	...	...
16	2	0.28	0.84	48	20	28	1.7	221	...	160	700	700
16	3	...	...	...	...	...	...	...	...	...	...	...
16	4	0.18	0.87	48	...	...	1.8	208	...	165	766	766
16	5	0.28	0.94	51	20	31	2.1	220	8	160	700	700
16	6	...	1.10	46	...	...	1.9	211	-16	155	639	639
16	7	...	...	...	...	...	...	216	...	...	...	...
17	1	...	...	...	...	...	3.7	180	...	...	...	...
17	2	...	...	...	...	...	...	175	-6	...	...	...
17	3	...	...	63	...	...	4.0	177	-3	134	427	427
17	4	0.28	0.93	52	...	...	2.3	168	-7	144	526	526
17	5	...	...	61	...	...	...	185	-6	165	766	766
17	6	0.26	1.05	53	...	...	1.8	179	...	144	526	526
18	1	...	...	...	...	...	...	42	...	...	...	...
18	2	...	0.91	...	...	...	2.5	42	-1	...	...	...
18	3	...	1.20	...	...	...	2.1	45	3	...	...	...
18	4	...	0.97	...	...	...	1.8	45	-8	...	...	...
18	5	...	...	...	...	...	1.4	49	...	...	...	...
19	1	0.26	0.89	58	...	...	2.1	207	...	115	278	278
19	2	...	...	...	...	...	1.2	217	14	115	278	278
19	3	...	...	65	...	...	...	201	-3	...	...	...
19	4	...	...	57	27	30	...	...	...	...	...	...
19	5	...	...	...	...	...	...	...	...	...	...	...
19	9	...	...	...	...	...	...	204	...	...	...	...
19	10	0.19	1.00	56	...	...	0.7	198	-7	110	248	248
19	11	...	0.83	60	26	34	1.4	193	...	106	220	220

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	TL	TO	F#	BS	BD	SL	S	P	PD	TW	PA	PI	RSL
20	1	875	186	10	81	8	3	207	104	190	9	...	1.01	...
20	2	875	186	10	81	8	3	199	103	180	10	170	1.03	1.43
20	3	875	186	10	81	8	3	191	100	191	1	169	1.05	1.43
20	4	875	186	10	81	8	3	188	95	190	4	179	0.98	1.14
20	5	875	186	10	81	8	3	193	97	195	12	175	1.00	1.39
20	6	875	186	10	81	8	3	192	97	181	8	166	1.02	1.43
20	7	875	186	10	81	8	3	194	95	191	15	170	0.95	1.35
20	8	875	186	10	81	8	3	195	100	173	17	162	0.99	1.46
20	9	875	186	10	81	8	3	...	101	192	...	161	...	...
20	10	875	186	10	81	8	3	...	...	...	...	...	...	...
21	1	...	...	1	81	8	3	...	...	...	...	...	...	...
22	1	710	199	7	94	8	3	260	140	210	30	...	1.07	...
22	2	710	199	7	94	8	3	245	132	185	45	155	0.98	0.91
22	3	710	199	7	94	8	3	240	135	223	57	142	1.04	0.95
22	4	710	199	7	94	8	3	230	131	172	51	129	1.10	0.93
22	5	710	199	7	94	8	3	225	121	220	44	132	1.01	...
22	6	710	199	7	94	8	3	...	120	177	...	137	...	...
22	7	710	199	7	94	8	3	...	...	...	...	...	...	...
23	1	...	...	2	94	8	2	...	96	190	...	...	...	...
23	2	...	...	2	94	8	2	...	...	...	...	...	...	...
24	1	559	20	7	104	9	4	191	...	...	...	...	...	0.96
24	2	559	20	7	104	9	4	...	...	...	...	...	...	...
24	3	559	20	7	104	9	4	169	...	...	...	...	...	0.87
24	4	559	20	7	104	9	4	...	...	...	...	...	...	...
24	5	559	20	7	104	9	4	197	105	31	20	167	1.13	0.96
24	6	559	20	7	104	9	4	...	93	7	...	156	...	...
24	7	559	20	7	104	9	4	...	...	...	...	...	...	...
25	1	1805	203	20	89	8	4	181	93	201	15	...	1.01	...
25	2	1805	203	20	89	8	4	175	92	219	20	162	1.01	0.81
25	3	1805	203	20	89	8	4	175	91	194	14	155	1.08	0.85
25	4	1805	203	20	89	8	4	179	84	212	23	162	0.87	...
25	5	1805	203	20	89	8	4	179	96	181	29	149	1.09	0.83
25	6	1805	203	20	89	8	4	185	89	218	21	143	0.90	0.79
25	7	1805	203	20	89	8	4	192	98	192	16	154	1.03	0.82
25	8	1805	203	20	89	8	4	174	95	211	14	161	1.18	...
25	9	1805	203	20	89	8	4	191	81	192	12	161	0.79	...
25	10	1805	203	20	89	8	4	199	102	208	...	164	1.00	...
25	11	1805	203	20	89	8	4	191	102	183	27	155	1.01	...
25	12	1805	203	20	89	8	4	189	101	213	...	150	1.13	...
25	13	1805	203	20	89	8	4	180	90	196	19	163	0.98	...
25	14	1805	203	20	89	8	4	...	92	220	...	156	...	...
25	15	1805	203	20	89	8	4	...	...	...	...	...	...	...
25	16	1805	203	20	89	8	4	...	...	...	...	...	...	...
25	17	1805	203	20	89	8	4	...	...	...	...	...	...	...
25	18	1805	203	20	89	8	4	209	112	215	17	...	1.11	...
25	19	1805	203	20	89	8	4	...	101	197	...	162	...	...
25	20	1805	203	20	89	8	4	...	...	...	...	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	FRNO	SMS	SKH	SRT	LR	C	FL	FW	L*W	ARA	SI	LBW
20	1	...	...	...	...	l	3	...	...	...	...	...	...
20	2	0.21	1.68	6.0	0.84	r	3	27	22	586	493	8.95	1.24
20	3	0.20	1.64	5.9	0.86	l	3	26	22	572	514	9.01	1.18
20	4	0.10	1.25	4.5	0.67	r	3	32	...	...	...	...	...
20	5	0.19	1.59	5.7	0.83	l	3	27	23	610	550	9.10	1.19
20	6	0.21	1.65	5.9	0.86	r	3	26	22	564	457	8.84	1.20
20	7	0.17	1.54	5.5	0.79	l	3	28	23	641	515	9.01	1.22
20	8	0.22	1.69	6.1	0.87	r	3	26	22	580	514	9.01	1.17
20	9	...	...	...	...	l	3	28	22	616	537	9.07	1.27
20	10	...	...	...	...	r	3	...	...	...	...	...	...
21	1	...	...	...	...	r	5	...	25	...	...	...	...
22	1	...	...	...	...	l	3	...	...	...	...	...	...
22	2	0.05	1.10	4.0	0.45	r	3	52	...	...	...	...	...
22	3	0.05	1.14	4.1	0.48	l	3	49	40	1960	...	...	1.23
22	4	0.05	1.09	3.9	0.47	r	3	48	36	1728	...	...	1.33
22	5	...	...	...	...	l	3	...	...	...	...	...	...
22	6	...	...	...	...	r	3	43	40	1720	1921	10.91	1.08
22	7	...	...	...	...	l	3	49	36	1764	1641	10.68	1.36
23	1	...	...	...	...	r	3	24	18	420	345	8.43	1.37
23	2	...	...	...	...	l	3	25	16	400	302	8.24	1.56
24	1	0.05	1.03	3.7	0.54	l	4	35	32	1134	...	...	1.08
24	2	...	...	...	...	r	4	...	...	...	...	...	...
24	3	0.04	0.87	3.1	0.51	l	4	34	33	1129	1260	10.30	1.02
24	4	...	...	...	...	r	4	...	...	...	...	...	...
24	5	0.05	1.05	3.8	0.53	l	4	36	...	...	...	...	...
24	6	...	...	...	...	r	4	...	...	...	...	...	...
24	7	...	...	...	...	l	4	36	31	1116	...	...	1.00
25	1	...	...	...	...	r	4	...	35	...	...	...	...
25	2	0.03	0.81	2.9	0.46	l	4	38	35	1330	1218	10.25	1.09
25	3	0.04	0.86	3.1	0.49	r	4	36	33	1170	1154	10.17	1.11
25	4	...	...	...	...	l	4	...	...	...	...	...	...
25	5	0.03	0.84	3.0	0.47	r	4	38	35	1330	1283	10.33	1.09
25	6	0.03	0.81	2.9	0.44	l	4	41	36	1476	1530	10.58	1.14
25	7	0.03	0.86	3.1	0.45	r	4	41	35	1435	1446	10.50	1.17
25	8	...	...	...	...	l	4	...	...	...	...	...	...
25	9	...	...	...	...	r	4	...	...	...	...	...	...
25	10	...	...	...	...	l	4	...	...	...	...	...	...
25	11	...	...	...	...	r	4	...	...	...	...	...	...
25	12	...	...	...	...	l	4	...	...	...	...	...	...
25	13	...	...	...	...	r	4	...	36	...	...	...	...
25	14	...	...	...	...	l	4	...	...	...	...	...	...
25	15	...	...	...	...	r	4	...	...	...	...	...	...
25	16	...	...	...	...	l	4	...	...	...	...	...	...
25	17	...	...	...	...	r	4	...	...	...	...	...	...
25	18	...	...	...	...	l	4	...	...	...	...	...	...
25	19	...	...	...	...	r	4	...	34	...	1322	10.37	...
25	20	...	...	...	...	l	4	...	...	...	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	D1	D2	D3	D4	D1P	D2P	D3P	D4P	D1P2	D2P2	D3P2
20	1	...	...	...	...	...	...	...	...	...	...	...
20	2	10.5	13.0	12.0	10.0	0.39	0.48	0.44	0.37	0.30	0.40	0.36
20	3	12.5	16.0	15.0	10.0	0.48	0.62	0.58	0.38	0.30	0.43	0.39
20	4	7.7	16.5	...	...	0.24	0.52	...	...	...	...	...
20	5	11.5	17.6	17.2	12.0	0.43	0.65	0.64	0.44	0.25	0.43	0.42
20	6	8.0	12.2	11.0	6.5	0.31	0.47	0.42	0.25	0.27	0.48	0.41
20	7	7.2	11.0	16.1	11.2	0.26	0.39	0.58	0.40	0.19	0.32	0.55
20	8	5.7	12.2	10.0	9.0	0.22	0.47	0.38	0.35	0.18	0.49	0.37
20	9	8.5	12.0	13.7	10.0	0.30	0.43	0.49	0.36	0.24	0.37	0.45
20	10	...	...	...	...	...	...	...	...	...	...	...
21	1	...	...	...	...	...	...	...	...	...	...	...
22	1	...	...	...	...	...	...	...	...	...	...	...
22	2	...	...	...	...	...	...	...	...	...	...	...
22	3	...	...	...	...	...	...	...	...	...	...	...
22	4	...	...	...	...	...	...	...	...	...	...	...
22	5	...	...	...	...	...	...	...	...	...	...	...
22	6	...	...	...	...	...	...	...	...	...	...	...
22	7	...	...	...	...	...	...	...	...	...	...	...
23	1	8.5	14.7	15.0	10.2	0.35	0.61	0.63	0.43	0.21	0.44	0.45
23	2	11.3	18.0	16.0	11.5	0.45	0.72	0.64	0.46	0.25	0.46	0.39
24	1	...	...	...	...	...	...	...	...	...	...	...
24	2	...	...	...	...	...	...	...	...	...	...	...
24	3	...	...	...	...	...	...	...	...	...	...	...
24	4	...	...	...	...	...	...	...	...	...	...	...
24	5	...	...	...	...	...	...	...	...	...	...	...
24	6	...	...	...	...	...	...	...	...	...	...	...
24	7	...	...	...	...	...	...	...	...	...	...	...
25	1	...	...	...	...	...	...	...	...	...	...	...
25	2	...	...	...	...	...	...	...	...	...	...	...
25	3	...	...	...	...	...	...	...	...	...	...	...
25	4	...	...	...	...	...	...	...	...	...	...	...
25	5	...	...	...	...	...	...	...	...	...	...	...
25	6	...	...	...	...	...	...	...	...	...	...	...
25	7	...	...	...	...	...	...	...	...	...	...	...
25	8	...	...	...	...	...	...	...	...	...	...	...
25	9	...	...	...	...	...	...	...	...	...	...	...
25	10	...	...	...	...	...	...	...	...	...	...	...
25	11	...	...	...	...	...	...	...	...	...	...	...
25	12	...	...	...	...	...	...	...	...	...	...	...
25	13	...	...	...	...	...	...	...	...	...	...	...
25	14	...	...	...	...	...	...	...	...	...	...	...
25	15	...	...	...	...	...	...	...	...	...	...	...
25	16	...	...	...	...	...	...	...	...	...	...	...
25	17	...	...	...	...	...	...	...	...	...	...	...
25	18	...	...	...	...	...	...	...	...	...	...	...
25	19	...	...	...	...	...	...	...	...	...	...	...
25	20	...	...	...	...	...	...	...	...	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	D4P2	SKEW	DA	A	B	FD	FO	FRT	HH	VOL	MASS
20	1	...	...	...	...	...	...	...	...	...	...	...
20	2	0.28	0.92	60	35	25	2.2	188	-3	139	474	474
20	3	0.23	0.94	59	...	...	...	189	4	134	427	427
20	4	...	...	...	...	...	1.7	188	3	165	766	766
20	5	0.26	0.98	58	31	27	3.2	189	-4	139	474	474
20	6	0.21	0.90	66	36	30	3.5	183	5	134	427	427
20	7	0.33	1.46	65	31	34	2.6	185	-1	144	526	526
20	8	0.32	0.82	61	33	28	2.9	189	-7	134	427	427
20	9	0.29	1.14	56	28	28	3.2	187	5	144	526	526
20	10	...	...	...	...	...	...	...	...	...	...	...
21	1	...	...	...	...	...	...	210	...	...	...	...
22	1	...	...	...	...	...	...	211	...	...	...	...
22	2	...	...	...	...	...	2.8	201	-4	268	3012	3012
22	3	...	...	...	...	...	4.5	202	-2	252	2547	2547
22	4	...	...	...	...	...	4.9	207	-10	247	2404	2404
22	5	...	...	...	...	...	...	...	...	...	...	...
22	6	...	...	51	...	...	3.5	199	-1	221	1763	1763
22	7	...	...	48	19	29	4.5	193	...	252	2547	2547
23	1	0.27	1.02	55	...	...	2.2	187	...	124	340	340
23	2	0.25	0.89	52	...	...	2.0	194	...	129	382	382
24	1	...	...	...	...	...	3.5	...	...	200	1313	1313
24	2	...	...	...	...	...	...	...	...	...	...	...
24	3	...	...	54	...	...	2.7	...	...	194	1210	1210
24	4	...	...	...	...	...	...	...	...	...	...	...
24	5	...	...	...	...	...	...	...	...	205	1422	1422
24	6	...	...	...	...	...	...	...	...	...	...	...
24	7	...	...	...	...	...	2.7	...	...	205	1422	1422
25	1	...	...	...	...	...	...	...	...	...	...	...
25	2	...	...	64	...	...	...	216	6	217	1656	1656
25	3	...	...	57	...	...	...	216	-10	205	1422	1422
25	4	...	...	...	...	...	...	...	...	...	...	...
25	5	...	...	60	...	...	3.5	206	-10	217	1656	1656
25	6	...	...	52	...	...	5.0	209	10	234	2052	2052
25	7	...	...	52	24	28	4.0	198	7	234	2052	2052
25	8	...	...	...	...	...	...	212	11	...	...	...
25	9	...	...	...	...	...	...	193	9	...	...	...
25	10	...	...	...	...	...	...	...	...	...	...	...
25	11	...	...	...	...	...	...	...	...	...	...	...
25	12	...	...	...	...	...	...	...	...	...	...	...
25	13	...	...	...	...	...	...	190	15	...	...	...
25	14	...	...	...	...	...	...	...	...	...	...	...
25	15	...	...	...	...	...	...	...	...	...	...	...
25	16	...	...	...	...	...	...	...	...	...	...	...
25	17	...	...	...	...	...	...	...	...	...	...	...
25	18	...	...	...	...	...	...	...	...	...	...	...
25	19	...	...	54	...	...	...	197	9	...	...	...
25	20	...	...	...	...	...	...	...	...	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	TL	TO	F#	BS	BD	SL	S	P	PD	TW	PA	PI	RSL
26	1	802	32	11	103	7	2	161	81	33	5	...	0.98	1.74
26	2	802	32	11	103	7	2	163	83	26	5	173	1.00	1.86
26	3	802	32	11	103	7	2	163	83	33	5	173	1.02	1.76
26	4	802	32	11	103	7	2	161	81	40	4	173	1.01	1.74
26	5	802	32	11	103	7	2	159	80	35	6	175	1.00	...
26	6	802	32	11	103	7	2	160	80	27	6	172	1.01	...
26	7	802	32	11	103	7	2	158	79	35	6	172	1.00	1.80
26	8	802	32	11	103	7	2	158	79	26	4	171	1.03	1.80
26	9	802	32	11	103	7	2	160	77	32	5	174	0.94	1.83
26	10	802	32	11	103	7	2	...	82	25	...	173	...	...
26	11	802	32	11	103	7	2	...	...	...	...	...	...	...
27	1	837	355	9	101	7	3	205	93	12	17	...	0.78	1.08
27	2	837	355	9	101	7	3	222	119	354	14	162	1.14	1.11
27	3	837	355	9	101	7	3	...	105	8	...	166	...	...
27	4	837	355	9	101	7	3	212	...	...	...	...	...	1.06
27	5	837	355	9	101	7	3	...	...	...	...	...	...	...
27	6	837	355	9	101	7	3	211	109	338	12	...	1.08	0.98
27	7	837	355	9	101	7	3	210	101	351	...	167	0.96	1.05
27	8	837	355	9	101	7	3	...	105	342	...	171	...	...
27	9	837	355	9	101	7	3	...	...	...	...	...	...	...
28	1	...	...	2	83	6	2	...	...	...	...	...	...	...
28	2	...	...	2	83	6	2	...	...	...	...	...	...	...
29	1	...	...	1	100	7	1	...	...	...	...	...	...	...
30	1	301	334	4	84	7	1	199	101	344	15	...	1.03	1.61
30	2	301	334	4	84	7	1	195	98	327	0	163	0.98	...
30	3	301	334	4	84	7	1	...	100	327	...	180	...	...
30	4	301	334	4	84	7	1	...	...	...	...	...	...	...
31	1	...	...	2	80	6	3	...	170	18	...	...	...	...
31	2	...	...	2	80	6	3	...	...	...	...	...	...	...
32	1	666	360	7	95	8	3	238	120	356	9	...	1.01	...
32	2	666	360	7	95	8	3	237	119	5	8	171	1.04	0.87
32	3	666	360	7	95	8	3	235	114	357	11	172	0.97	0.92
32	4	666	360	7	95	8	3	215	117	8	30	169	1.10	...
32	5	666	360	7	95	8	3	199	107	337	38	149	1.02	0.78
32	6	666	360	7	95	8	3	...	105	19	...	138	...	...
32	7	666	360	7	95	8	3	...	...	...	...	...	...	...
33	1	1110	192	7	93	8	2	373	197	179	34	...	1.10	...
33	2	1110	192	7	93	8	2	372	180	200	27	159	0.94	...
33	3	1110	192	7	93	8	2	365	192	183	43	163	1.08	...
33	4	1110	192	7	93	8	2	370	178	210	38	153	0.91	...
33	5	1110	192	7	93	8	2	375	195	186	29	156	1.07	...
33	6	1110	192	7	93	8	2	...	182	204	...	162	...	...
33	7	1110	192	7	93	8	2	...	...	...	...	...	...	...
34	1	1319	164	14	93	8	2	209	...	...	...	...	...	1.40
34	2	1319	164	14	93	8	2	...	...	...	...	...	...	...
34	3	1319	164	14	93	8	2	208	101	167	3	...	0.97	1.39
34	4	1319	164	14	93	8	2	201	104	170	5	177	1.04	1.26

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	FRNO	SMS	SKH	SRT	LR	C	FL	FW	L*W	ARA	SI	LBW
26	1	0.39	1.89	6.8	1.17	l	3	18	10	185	127	6.99	1.75
26	2	0.50	2.06	7.4	1.26	r	3	17	...	...	...	...	...
26	3	0.41	1.93	6.9	1.18	l	3	18	11	189	148	7.21	1.71
26	4	0.39	1.89	6.8	1.17	r	3	18	13	230	200	7.64	1.41
26	5	...	...	...	...	l	3	...	11	...	...	...	...
26	6	...	...	...	...	r	3	...	12	...	...	...	...
26	7	0.45	1.96	7.0	1.24	l	3	17	11	194	185	7.53	1.49
26	8	0.45	1.96	7.0	1.24	r	3	17	13	216	216	7.75	1.34
26	9	0.47	2.00	7.2	1.25	l	3	17	11	189	162	7.34	1.53
26	10	...	...	...	...	r	3	18	12	216	179	7.48	1.50
26	11	...	...	...	...	l	3	...	11	...	...	...	...
27	1	0.08	1.22	4.4	0.60	l	3	37	30	1114	1088	10.09	1.23
27	2	0.09	1.31	4.7	0.59	r	3	39	30	1182	1066	10.06	1.29
27	3	...	...	...	...	l	3	...	...	...	...	...	...
27	4	0.07	1.21	4.4	0.57	r	3	39	32	1248	...	...	1.22
27	5	...	...	...	...	...	3	...	...	...	...	...	...
27	6	0.06	1.10	4.0	0.52	r	3	42	32	1344	...	...	1.31
27	7	0.07	1.19	4.3	0.57	l	3	39	...	...	...	...	...
27	8	...	...	...	...	r	3	...	...	...	...	...	...
27	9	...	...	...	...	l	3	...	...	...	...	...	...
28	1	...	...	...	...	...	6	39	38	1482	...	...	1.03
28	2	...	...	...	...	...	6	37	37	1369	...	...	1.00
29	1	...	...	...	...	...	4	24	...	...	...	...	...
30	1	0.31	1.92	6.9	0.97	l	3	24	15	350	298	8.22	1.64
30	2	...	...	...	...	r	3	...	...	...	...	...	...
30	3	...	...	...	...	l	3	27	15	408	340	8.41	1.79
30	4	...	...	...	...	r	3	25	16	400	343	8.42	1.56
31	1	...	...	...	...	...	4	...	...	...	...	...	...
31	2	...	...	...	...	...	4	46	36	1656	1357	10.41	1.28
32	1	...	...	...	...	r	4	...	...	...	...	...	...
32	2	0.04	1.02	3.7	0.43	l	4	48	38	1800	1382	10.43	1.28
32	3	0.05	1.08	3.9	0.46	r	4	45	35	1593	1312	10.36	1.27
32	4	...	...	...	...	l	4	...	40	...	...	...	...
32	5	0.03	0.82	3.0	0.41	r	4	45	36	1607	...	...	1.26
32	6	...	...	...	...	l	4	...	41	...	1613	10.66	...
32	7	...	...	...	...	r	4	...	...	...	...	...	...
33	1	...	...	...	...	r	5	...	...	...	...	...	...
33	2	...	...	...	...	l	5	...	...	...	...	...	...
33	3	...	...	...	...	r	5	...	...	...	...	...	...
33	4	...	...	...	...	l	5	...	...	...	...	...	...
33	5	...	...	...	...	r	5	...	...	...	...	...	...
33	6	...	...	...	...	l	5	...	...	...	...	...	...
33	7	...	...	...	...	r	5	...	39	...	...	...	...
34	1	0.19	1.67	6.0	0.80	r	3	29	22	641	541	9.08	1.31
34	2	...	...	...	...	l	3	...	...	...	...	...	...
34	3	0.19	1.66	6.0	0.80	r	3	29	19	545	474	8.89	1.54
34	4	0.13	1.45	5.2	0.72	l	3	31	...	...	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	D1	D2	D3	D4	D1P	D2P	D3P	D4P	D1P2	D2P2	D3P2
26	1	7.5	11.4	9.9	7.8	0.42	0.63	0.55	0.43	0.26	0.45	0.37
26	2	...	...	...	...	...	...	...	...	...	...	...
26	3	6.3	11.6	11.6	7.0	0.35	0.64	0.64	0.39	0.21	0.47	0.47
26	4	7.0	11.2	12.7	8.0	0.39	0.62	0.71	0.44	0.22	0.40	0.48
26	5	4.8	10.0	9.5	7.3	...	...	...	...	0.18	0.46	0.43
26	6	...	...	...	...	...	...	...	...	...	...	...
26	7	4.9	9.4	8.6	6.7	0.29	0.55	0.51	0.39	0.20	0.47	0.41
26	8	6.6	10.5	...	6.0	0.39	0.62	...	0.35	...	...	...
26	9	4.5	9.7	10.2	6.0	0.26	0.57	0.60	0.35	0.17	0.47	0.50
26	10	7.2	11.4	9.9	5.1	0.40	0.63	0.55	0.28	0.27	0.51	0.42
26	11	4.0	...	9.1	5.0	...	...	...	...	...	...	...
27	1	12.4	20.7	...	15.5	0.34	0.56	...	0.42	...	...	...
27	2	12.8	16.0	...	10.5	0.33	0.41	...	0.27	...	...	...
27	3	...	...	...	...	...	...	...	...	...	...	...
27	4	...	...	...	...	...	...	...	...	...	...	...
27	5	...	...	...	...	...	...	...	...	...	...	...
27	6	12.0	...	...	...	0.29	...	...	...	...	...	...
27	7	...	...	...	...	...	...	...	...	...	...	...
27	8	...	...	...	...	...	...	...	...	...	...	...
27	9	...	...	...	...	...	...	...	...	...	...	...
28	1	...	...	...	...	...	...	...	...	...	...	...
28	2	...	...	...	...	...	...	...	...	...	...	...
29	1	...	...	...	...	...	...	...	...	...	...	...
30	1	5.0	11.5	11.0	7.0	0.21	0.48	0.46	0.29	0.17	0.50	0.47
30	2	...	...	...	...	...	...	...	...	...	...	...
30	3	6.3	12.9	14.2	9.0	0.23	0.48	0.53	0.33	0.17	0.44	0.50
30	4	5.0	13.0	14.3	10.2	0.20	0.52	0.57	0.41	0.13	0.44	0.51
31	1	...	...	...	...	...	...	...	...	...	...	...
31	2	...	...	...	...	...	...	...	...	...	...	...
32	1	...	...	...	...	...	...	...	...	...	...	...
32	2	...	23.0	...	16.9	...	0.48	...	0.35	...	...	...
32	3	16.3	21.6	23.5	13.3	0.36	0.48	0.52	0.30	0.28	0.41	0.46
32	4	14.2	18.0	23.1	15.0	...	...	...	...	0.25	0.34	0.49
32	5	12.0	20.0	19.8	16.1	0.27	0.44	0.44	0.36	0.21	0.42	0.41
32	6	13.0	...	...	12.3	...	...	...	...	...	...	...
32	7	...	...	...	...	...	...	...	...	...	...	...
33	1	...	...	21.0	...	...	...	...	...	...	...	...
33	2	...	20.0	...	14.0	...	...	...	...	...	...	...
33	3	22.3	...	20.7	...	...	...	...	...	...	...	...
33	4	...	24.0	...	17.3	...	...	...	...	...	...	...
33	5	21.5	...	27.0	...	...	...	...	...	...	...	...
33	6	...	23.5	...	18.0	...	...	...	...	...	...	...
33	7	25.0	24.0	30.0	...	...	...	...	...	...	...	...
34	1	...	13.3	...	...	...	0.46	...	...	...	...	...
34	2	...	...	...	...	...	...	...	...	...	...	...
34	3	10.0	12.4	14.2	...	0.34	0.43	0.49	...	...	...	...
34	4	...	...	...	...	...	...	...	...	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	D4P2	SKEW	DA	A	B	FD	FO	FRT	HH	VOL	MASS
26	1	0.27	0.87	51	...	...	0.5	35	...	93	151	151
26	2	...	...	...	...	...	...	33	-4	88	129	129
26	3	0.24	1.00	45	...	...	0.8	34	5	93	151	151
26	4	0.26	1.13	50	...	...	0.8	32	-5	93	151	151
26	5	0.30	0.95	...	...	...	0.8	35	3	...	...	...
26	6	...	...	...	...	...	0.7	39	-8	...	...	...
26	7	0.29	0.91	42	...	...	1.2	38	7	88	129	129
26	8	...	...	45	...	...	1.3	39	-9	88	129	129
26	9	0.25	1.05	46	29	17	0.9	30	1	88	129	129
26	10	0.18	0.87	49	30	19	1.1	33	-5	93	151	151
26	11	...	...	...	...	...	0.8	22	...	...	...	...
27	1	...	...	51	...	...	2.9	5	...	191	1154	1154
27	2	...	...	53	22	31	3.4	4	-1	201	1338	1338
27	3	...	...	...	...	...	...	358	-3	...	...	...
27	4	...	...	...	...	...	1.8	3	...	201	1338	1338
27	5	...	...	...	...	...	...	...	...	...	...	...
27	6	...	...	...	...	...	3.8	...	...	216	1649	1649
27	7	...	...	50	26	24	...	346	2	201	1338	1338
27	8	...	...	...	...	...	...	349	-3	...	...	...
27	9	...	...	...	...	...	...	353	...	...	...	...
28	1	...	...	...	...	...	3.6	183	...	201	1338	1338
28	2	...	...	...	...	...	3.8	135	...	191	1154	1154
29	1	...	...	...	...	...	3.2	171	...	137	453	453
30	1	0.25	0.96	43	...	...	1.4	316	...	124	340	340
30	2	...	...	...	...	...	...	...	...	...	...	...
30	3	0.27	1.10	40	21	19	1.1	324	3	139	474	474
30	4	0.32	1.10	45	19	26	2.0	330	...	129	382	382
31	1	...	...	61	...	...	...	342	...	...	...	...
31	2	...	...	60	...	...	4.3	17	...	262	2838	2838
32	1	...	...	...	...	...	...	...	...	...	...	...
32	2	...	...	65	25	40	2.6	360	1	274	3200	3200
32	3	0.22	1.09	60	...	...	3.5	359	2	257	2667	2667
32	4	0.27	1.28	...	...	...	4.3	1	-2	...	...	...
32	5	0.31	0.99	...	...	...	3.8	360	-8	257	2667	2667
32	6	...	...	67	...	...	4.9	357	-1	...	...	...
32	7	...	...	...	...	...	...	...	...	...	...	...
33	1	...	...	...	...	...	3.8	163	...	...	...	...
33	2	...	...	...	...	...	4.0	189	-1	...	...	...
33	3	...	...	...	...	...	3.8	165	27	...	...	...
33	4	...	...	...	...	...	3.6	195	-2	...	...	...
33	5	...	...	...	...	...	3.5	168	30	...	...	...
33	6	...	...	...	...	...	5.5	194	-1	...	...	...
33	7	...	1.25	...	...	...	3.7	177	...	...	...	...
34	1	...	...	56	30	26	3.5	171	...	149	580	580
34	2	...	...	...	...	...	...	...	...	...	...	...
34	3	...	1.15	45	26	19	3.0	170	...	149	580	580
34	4	...	...	47	25	22	4.6	175	7	160	700	700

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	TL	TO	F#	BS	BD	SL	S	P	PD	TW	PA	PI	RSL
34	5	1319	164	14	93	8	2	...	100	165	...	175	...	...
34	6	1319	164	14	93	8	2	208	...	...	...	...	...	1.35
34	7	1319	164	14	93	8	2	...	...	...	...	...	...	...
34	8	1319	164	14	93	8	2	205	105	162	5	...	1.04	1.33
34	9	1319	164	14	93	8	2	208	101	157	2	175	0.95	...
34	10	1319	164	14	93	8	2	206	106	155	4	178	0.99	1.38
34	11	1319	164	14	93	8	2	199	107	151	4	176	1.05	1.17
34	12	1319	164	14	93	8	2	201	102	155	12	176	1.01	1.22
34	13	1319	164	14	93	8	2	...	101	142	...	167	...	...
34	14	1319	164	14	93	8	2	...	...	...	...	...	...	...
35	1	824	160	15	93	8	2	129	66	...	1	...	1.05	1.93
35	2	824	160	15	93	8	2	...	63	161	...	178	...	...
35	3	824	160	15	93	8	2	...	...	163	...	...	...	...
35	4	824	160	15	93	8	2	...	...	...	...	...	...	...
35	5	824	160	15	93	8	2	...	...	...	...	...	...	...
35	6	824	160	15	93	8	2	129	70	...	7	...	1.08	1.79
35	7	824	160	15	93	8	2	...	65	170	...	169	...	...
35	8	824	160	15	93	8	2	...	...	159	...	...	...	...
35	14	824	160	15	93	8	2	...	...	...	...	...	...	...
35	16	824	160	15	97	8	2	...	...	...	...	...	...	...
36	1	...	...	2	99	8	3	...	75	356	...	...	...	...
36	2	...	...	2	99	8	3	...	...	...	...	...	...	...
37	1	542	212	8	97	8	2	143	96	192	...	...	...	0.57
37	2	542	212	8	97	8	2	175	79	272	...	...	...	0.67
37	3	542	212	8	97	8	2	...	...	...	...	...	...	...
37	5	542	212	8	97	8	2	162	89	224	28	...	1.01	0.77
37	6	542	212	8	97	8	2	175	88	188	30	144	0.91	0.73
37	7	542	212	8	97	8	2	...	96	226	...	142	...	...
37	8	542	212	8	97	8	2	...	...	...	...	...	...	...
38	1	...	...	1	97	8	1	...	...	...	...	...	...	...
39	1	...	...	1	97	8	1	...	...	...	...	...	...	...
40	1	...	...	2	97	8	1	...	40	122	...	...	...	...
40	2	...	...	2	97	8	1	...	...	...	...	...	...	...
41	1	...	...	2	97	8	1	...	118	...	...	...	...	...
41	2	...	...	2	97	8	1	...	...	...	...	...	...	...
44	1	...	...	2	94	8	2	...	91	161	...	...	...	...
44	2	...	...	2	94	8	2	...	...	...	...	...	...	...
45	1	...	...	2	97	8	1	...	45	120	...	...	...	...
45	2	...	...	2	97	8	1	...	...	...	...	...	...	...
51	1	375	326	4	85	10	.	212	91	330	9	...	0.76	...
51	2	375	326	4	85	10	.	275	120	320	18	170	0.74	...
51	3	375	326	4	85	10	.	...	162	335	...	165	...	...
51	4	375	326	4	85	10	.	...	...	...	...	...	...	...
52	1	410	355	5	85	10	.	205	110	145	49	...	0.90	...
52	2	410	355	5	85	10	.	210	120	195	40	130	1.23	...
52	3	410	355	5	85	10	.	190	100	150	52	135	0.79	...
52	4	410	355	5	85	10	.	...	120	205	...	125	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	FRNO	SMS	SKH	SRT	LR	C	FL	FW	L*W	ARA	SI	LBW
34	5	...	...	...	...	r	3	29	23	664	619	9.27	1.27
34	6	0.17	1.60	5.7	0.77	l	3	30	21	630	558	9.12	1.43
34	7	...	...	...	...	r	3	...	...	...	...	...	...
34	8	0.16	1.56	5.6	0.76	l	3	30	20	588	486	8.92	1.53
34	9	...	...	...	...	r	3	...	...	...	...	...	...
34	10	0.18	1.63	5.9	0.79	l	3	29	19	563	495	8.95	1.49
34	11	0.11	1.33	4.8	0.67	r	3	33	21	693	616	9.27	1.57
34	12	0.12	1.40	5.0	0.70	l	3	32	19	598	469	8.87	1.71
34	13	...	...	...	...	r	3	30	21	618	569	9.15	1.46
34	14	...	...	...	...	l	3	...	...	...	...	...	...
35	1	0.55	1.91	6.9	1.48	r	3	13	14	181	185	7.53	0.94
35	2	...	...	...	...	l	3	15	14	212	198	7.63	1.06
35	3	...	...	...	...	r	3	14	13	175	166	7.38	1.12
35	4	...	...	...	...	l	3	...	...	...	...	...	...
35	5	...	...	...	...	r	3	...	...	...	...	...	...
35	6	0.43	1.75	6.3	1.36	l	3	14	13	178	179	7.48	1.10
35	7	...	...	...	...	r	3	16	13	211	185	7.53	1.21
35	8	...	...	...	...	l	3	...	12	...	163	7.35	...
35	14	...	...	...	...	l	3	16	14	222	205	7.68	1.15
35	16	...	...	...	...	r	3	18	12	207	128	7.00	1.57
36	1	...	...	...	...	r	3	16	13	208	139	7.12	1.23
36	2	...	...	...	...	l	3	17	15	255	195	7.61	1.13
37	1	0.01	0.49	1.8	0.34	r	4	44	39	1716	1593	10.64	1.13
37	2	0.02	0.65	2.3	0.37	l	4	46	37	1702	...	...	1.24
37	3	...	...	...	...	r	4	40	40	1600	...	...	1.00
37	5	0.03	0.73	2.6	0.45	l	4	37	35	1295	1471	10.52	1.06
37	6	0.02	0.72	2.6	0.41	r	4	42	36	1491	1397	10.45	1.18
37	7	...	...	...	...	l	4	...	...	...	...	...	...
37	8	...	...	...	...	r	4	42	...	...	...	...	...
38	1	...	...	...	...	l	2	24	20	480	...	...	1.20
39	1	...	...	...	...	...	2	...	6	...	...	...	...
40	1	...	...	...	...	...	1	7	6	39.9	42	5.39	1.23
40	2	...	...	...	...	...	1	7	5	35	34	5.09	1.40
41	1	...	...	...	...	...	1	...	...	...	...	...	...
41	2	...	...	...	...	...	1	...	...	...	...	...	...
44	1	...	...	...	...	r	3	25	15	375	246	7.94	1.67
44	2	...	...	...	...	l	3	21	16	336	288	8.17	1.31
45	1	...	...	...	...	...	1	7	4	28	21	4.39	1.75
45	2	...	...	...	...	...	1	7	4	29.4	21	4.39	1.67
51	1	...	...	...	...	r	4	...	...	...	...	...	...
51	2	...	...	...	...	l	4	...	...	...	...	...	...
51	3	...	...	...	...	r	4	...	...	...	...	...	...
51	4	...	...	...	...	l	4	...	...	...	...	...	...
52	1	...	...	...	...	l	4	...	...	...	...	...	...
52	2	...	...	...	...	r	4	...	...	...	...	...	...
52	3	...	...	...	...	l	4	...	...	...	...	...	...
52	4	...	...	...	...	r	4	...	...	...	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	D1	D2	D3	D4	D1P	D2P	D3P	D4P	D1P2	D2P2	D3P2
34	5	11.5	14.6	17.0	13.2	0.40	0.50	0.59	0.46	0.26	0.35	0.43
34	6	11.6	15.2	16.8	11.9	0.39	0.51	0.56	0.40	0.26	0.38	0.43
34	7	...	...	...	...	...	...	...	...	...	...	...
34	8	9.8	17.5	17.6	12.1	0.33	0.58	0.59	0.40	0.21	0.44	0.45
34	9	...	...	...	...	...	...	...	...	...	...	...
34	10	7.5	13.5	15.2	12.0	0.26	0.47	0.52	0.41	0.18	0.39	0.46
34	11	7.5	13.0	17.6	11.9	0.23	0.39	0.53	0.36	0.18	0.35	0.54
34	12	8.0	10.5	16.5	10.7	0.25	0.33	0.52	0.33	0.21	0.30	0.57
34	13	10.7	14.0	17.2	13.5	0.36	0.47	0.57	0.45	0.24	0.34	0.45
34	14	...	...	...	...	...	...	...	...	...	...	...
35	1	5.5	9.2	...	...	0.42	0.71	...	...	...	...	...
35	2	5.6	9.7	9.2	5.8	0.37	0.65	0.61	0.39	0.23	0.47	0.44
35	3	5.0	8.5	8.0	5.7	0.36	0.61	0.57	0.41	0.23	0.45	0.42
35	4	...	...	...	...	...	...	...	...	...	...	...
35	5	...	...	...	...	...	...	...	...	...	...	...
35	6	5.5	10.6	11.0	6.5	0.39	0.76	0.79	0.46	0.20	0.46	0.49
35	7	7.7	12.8	11.6	7.0	0.48	0.80	0.73	0.44	0.25	0.49	0.42
35	8	...	...	...	...	...	...	...	...	...	...	...
35	14	7.0	10.7	8.5	4.8	0.44	0.67	0.53	0.30	0.29	0.53	0.38
35	16	...	...	...	...	...	...	...	...	...	...	...
36	1	4.5	11.2	10.0	5.0	0.28	0.70	0.63	0.31	0.17	0.57	0.48
36	2	...	9.0	11.5	5.7	...	0.53	0.68	0.34	...	...	...
37	1	18.0	14.5	19.0	15.0	0.41	0.33	0.43	0.34	0.37	0.28	0.40
37	2	...	...	...	...	...	...	...	...	...	...	...
37	3	...	...	...	...	...	...	...	...	...	...	...
37	5	10.0	16.0	...	...	0.27	0.43	...	...	...	...	...
37	6	16.0	19.5	14.5	8.0	0.38	0.46	0.35	0.19	0.38	0.51	0.33
37	7	...	...	...	...	...	...	...	...	...	...	...
37	8	12.5	17.5	13.0	11.0	0.30	0.42	0.31	0.26	0.30	0.48	0.32
38	1	12.0	15.5	14.0	11.0	0.50	0.65	0.58	0.46	0.30	0.42	0.36
39	1	...	...	...	...	...	...	...	...	...	...	...
40	1	...	...	...	...	...	...	...	...	...	...	...
40	2	...	...	...	...	...	...	...	...	...	...	...
41	1	...	...	...	...	...	...	...	...	...	...	...
41	2	...	...	...	...	...	...	...	...	...	...	...
44	1	...	12.8	12.7	4.4	...	0.51	0.51	0.18	...	...	...
44	2	8.0	13.5	11.0	5.5	0.38	0.64	0.52	0.26	0.27	0.55	0.41
45	1	...	...	...	...	...	...	...	...	...	...	...
45	2	...	...	...	...	...	...	...	...	...	...	...
51	1	...	...	...	...	...	...	...	...	...	...	...
51	2	...	...	...	...	...	...	...	...	...	...	...
51	3	...	...	...	...	...	...	...	...	...	...	...
51	4	...	...	...	...	...	...	...	...	...	...	...
52	1	...	...	...	...	...	...	...	...	...	...	...
52	2	...	...	...	...	...	...	...	...	...	...	...
52	3	...	...	...	...	...	...	...	...	...	...	...
52	4	...	...	...	...	...	...	...	...	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	D4P2	SKEW	DA	A	B	FD	FO	FRT	HH	VOL	MASS
34	5	0.31	1.16	52	25	27	3.1	166	2	149	580	580
34	6	0.27	1.11	48	27	21	2.2	173	...	155	639	639
34	7	...	...	...	...	...	...	...	...	...	...	...
34	8	0.27	1.01	48	30	18	1.6	168	...	155	639	639
34	9	...	...	...	...	...	...	158	2	...	...	...
34	10	0.33	1.13	46	22	24	1.8	165	-9	149	580	580
34	11	0.31	1.35	43	22	21	2.9	153	0.1	170	836	836
34	12	0.31	1.57	45	24	21	3.0	157	4	165	766	766
34	13	0.32	1.23	45	22	23	2.9	150	-2	155	639	639
34	14	...	...	...	...	...	...	147	...	...	...	...
35	1	...	...	67	...	...	1.1	161	...	67	60	60
35	2	0.24	0.95	64	35	29	0.8	162	0.1	77	90	90
35	3	0.27	0.94	59	36	23	0.8	158	...	72	74	74
35	4	...	...	...	...	...	...	...	...	...	...	...
35	5	...	...	...	...	...	...	...	...	...	...	...
35	6	0.24	1.04	56	...	...	1.2	161	...	72	74	74
35	7	0.22	0.91	59	34	25	1.8	160	5	82	108	108
35	8	...	...	58	33	25	0.9	168	...	...	...	...
35	14	0.18	0.79	59	...	...	1.0	140	...	82	108	108
35	16	...	...	66	39	27	...	144	...	93	151	151
36	1	0.19	0.89	83	46	37	2.2	3	...	82	108	108
36	2	...	1.28	77	53	25	2.4	358	...	88	129	129
37	1	0.29	1.31	60	...	...	7.2	214	...	251	2504	2504
37	2	...	...	...	...	...	4.7	210	...	262	2838	2838
37	3	...	...	...	...	...	5.0	214	...	228	1914	1914
37	5	...	...	51	...	...	3.1	220	...	211	1536	1536
37	6	0.16	0.74	56	...	...	5.4	204	2	239	2196	2196
37	7	...	...	...	...	...	...	213	6	...	...	...
37	8	0.26	0.74	57	...	...	4.4	218	...	239	2196	2196
38	1	0.27	0.90	...	...	...	0.9	...	...	110	248	248
39	1	...	...	...	...	...	0.9	26	...	...	...	...
40	1	...	...	47	...	...	1.0	301	...	32	8	8
40	2	...	...	45	...	...	0.7	294	...	32	8	8
41	1	...	...	...	...	...	...	3	...	...	...	...
41	2	...	...	...	...	...	...	354	...	...	...	...
44	1	...	0.99	57	27	30	1.9	179	...	129	382	382
44	2	0.17	0.81	55	24	31	2.9	165	...	108	234	234
45	1	...	...	46	...	...	0.7	307	...	32	8	8
45	2	...	...	52	...	...	0.7	303	...	32	8	8
51	1	...	...	...	...	...	...	...	...	...	...	...
51	2	...	...	...	...	...	...	...	...	...	...	...
51	3	...	...	...	...	...	...	...	...	...	...	...
51	4	...	...	...	...	...	...	...	...	...	...	...
52	1	...	...	...	...	...	...	...	...	...	...	...
52	2	...	...	...	...	...	...	...	...	...	...	...
52	3	...	...	...	...	...	...	...	...	...	...	...
52	4	...	...	...	...	...	...	...	...	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	TL	TO	F#	BS	BD	SL	S	P	PD	TW	PA	PI	RSL
52	5	410	355	5	85	10	.	...	...	...	...	...	...	...
53	1	900	111	8	91	13	.	260	130	108	16	...	1.03	...
53	2	900	111	8	91	13	.	263	127	123	7	165	0.95	1.50
53	3	900	111	8	91	13	.	253	133	117	1	174	1.14	1.29
53	4	900	111	8	91	13	.	240	117	118	...	179	0.92	1.14
53	5	900	111	8	91	13	.	255	128	99	22	161	1.01	1.27
53	6	900	111	8	91	13	.	261	127	119	19	160	0.95	1.21
53	7	900	111	8	91	13	.	...	134	102	...	163	...	...
53	8	900	111	8	91	13	.	...	...	...	...	...	...	...
54	1	...	...	2	112	9	.	...	198	35	...	...	...	...
54	2	...	...	2	112	9	.	...	...	...	...	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	FRNO	SMS	SKH	SRT	LR	C	FL	FW	L*W	ARA	SI	LBW
52	5	...	...	...	...	l	4	...	...	...	...	...	...
53	1	...	...	...	...	r	3	...	...	...	...	...	...
53	2	0.24	2.04	7.3	0.78	l	3	34	30	1020	...	...	1.13
53	3	0.15	1.68	6.0	0.66	r	3	38	30	1140	...	...	1.27
53	4	0.10	1.41	5.1	0.59	l	3	41	27	1107	...	...	1.52
53	5	0.14	1.65	5.9	0.65	r	3	39	25	975	...	...	1.56
53	6	0.12	1.57	5.7	0.60	l	3	42	28	1176	...	...	1.50
53	7	...	...	...	...	r	3	37	25	925	...	...	1.48
53	8	...	...	...	...	l	3	39	27	1053	...	...	1.44
54	1	...	...	...	...	r	7	67	63	4221	...	...	1.06
54	2	...	...	...	...	l	7	61	67	4087	...	...	0.91

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	D1	D2	D3	D4	D1P	D2P	D3P	D4P	D1P2	D2P2	D3P2
52	5	...	...	...	...	...	...	...	...	...	...	...
53	1	...	...	...	...	...	...	...	...	...	...	...
53	2	...	...	...	...	...	...	...	...	...	...	...
53	3	...	...	...	...	...	...	...	...	...	...	...
53	4	...	...	...	...	...	...	...	...	...	...	...
53	5	...	...	...	...	...	...	...	...	...	...	...
53	6	...	...	...	...	...	...	...	...	...	...	...
53	7	...	...	...	...	...	...	...	...	...	...	...
53	8	...	...	...	...	...	...	...	...	...	...	...
54	1	...	...	...	...	...	...	...	...	...	...	...
54	2	...	...	...	...	...	...	...	...	...	...	...

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

T	F	D4P2	SKEW	DA	A	B	FD	FO	FRT	HH	VOL	MASS
52	5	...	...	...	...	...	...	...	...	...	...	...
53	1	...	...	...	...	...	3.8	...	...	...	...	...
53	2	...	...	...	...	...	...	...	...	175	909	909
53	3	...	...	...	...	...	5.2	...	...	196	1244	1244
53	4	...	...	...	...	...	...	...	...	211	1541	1541
53	5	...	...	...	...	...	5.3	...	...	201	1338	1338
53	6	...	...	...	...	...	4.4	...	...	216	1649	1649
53	7	...	...	...	...	...	3.8	...	...	191	1154	1154
53	8	...	...	...	...	...	3.9	...	...	201	1338	1338
54	1	...	...	...	...	...	29	...	...	268	3019	3019
54	2	...	...	...	...	...	...	...	...	244	2317	2317

Variable symbols used:

T - Trackway number
F - Footprint number
TL - Trackway length (cm)
TO - Trackway orientation (degrees)
F# - Number of footprints in the trackway
BS - Bedding strike (degrees)
BD - Bedding dip (degrees)
SL - Stratigraphic level
S - Stride length (cm)
P - Pace length (cm)
PD - Pace direction (degrees)
TW - Trackway width (cm)
PA - Pace angle (degrees)
PI - Pace index
RSL - Relative stride length
FRNO - Froude number
SMS - Speed (meters/second)
SKH - Speed (kilometers/hour)
SRT - Striding rate (strides/sec)
LR - Left or right footprint
C - Footprint class
FL - Footprint length (cm)
FW - Footprint width (cm)
L*W - Footprint length times width (cm^2)
ARA - Footprint area (cm^2)
SI - Footprint size index
LBW - Footprint length/width
D1 - Digit1 length (cm)
D2 - Digit2 length (cm)
D3 - Digit3 length (cm)

Table 28 (continued).--Trackway and footprint variables for localities in the Koum basin, northern Cameroon. Symbols explained at end of table and in text.

Variable symbols used (continued):

D4 - Digit4 length (cm)
D1P - D1/FL
D2P - D2/FL
D3P - D3/FL
D4P - D4/FL
D1P2 - D1/(D2+D3+D4)
D2P2 - D2/(D1+D3+D4)
D3P2 - D3/(D1+D2+D4)
D4P2 - D4/(D1+D2+D3)
SKEW - D3/D2
DA - Angle of divarication (degrees)
A - Alpha (degrees)
B - Beta (degrees)
FD - Footprint depth (cm)
FO - Footprint long axis orientation (degrees)
FRT - Footprint rotation (degrees)
HH - Height of acetabulum above ground (cm)
VOL - Trackmaker body volume (liters)
MASS - Trackmaker mass (kg)

Table 29.--Trackway and footprint variables averaged by trackway for localities in the Koum basin, northern Cameroon. Variable symbols are the same as for table 26.

T	SL	S	P	TW	PA	PI	RSL	FRNO	SMS	SKH	SRT	C
1	1	210	96	...	...	...	...	...	...	...	...	2
2	2	260	132	19.4	163	1.01	...	...	...	...	...	4
3	2	212	107	7.9	172	1.00	1.05	0.07	1.20	4.33	0.57	4
4	1	270	135	14.7	167	0.85	2.96	2.31	4.90	17.63	1.56	2
5	1	135	67	7.6	167	0.98	1.15	0.10	1.07	3.85	0.79	2
6	3	241	123	22.0	159	0.98	...	...	...	...	...	4
7	3	...	...	...	...	...	...	...	...	...	...	2
8	3	127	63	8.2	165	0.96	0.81	0.03	0.69	2.47	0.54	6
9	2	320	162	1.4	179	1.03	3.31	3.37	5.65	20.34	1.77	2
10	3	140	72	11.9	161	0.96	0.94	0.05	0.86	3.09	0.61	6
11	3	474	239	4.6	178	0.90	...	...	...	...	...	5
12	3	139	70	6.9	169	1.01	1.81	0.46	1.84	6.64	1.33	2
13	3	271	136	9.7	172	1.01	2.08	0.71	3.02	10.87	1.11	3
14	3	...	187	...	...	...	...	...	...	...	...	5
15	3	238	166	116	91	1.02	...	...	...	...	...	5
16	2	176	91	19.2	156	1.03	1.09	0.08	1.15	4.13	0.65	3
17	2	228	115	15.4	164	1.03	1.58	0.29	1.98	7.11	0.90	3
18	3	217	120	47.6	133	0.98	...	...	...	...	...	5
19	2	145	74	9.9	165	0.98	1.30	0.15	1.29	4.65	0.87	2
20	3	195	99	9.5	169	1.00	1.37	0.18	1.58	5.68	0.82	3
21	3	...	...	...	...	...	...	...	...	...	...	5
22	3	240	130	45.5	139	1.04	0.93	0.05	1.11	4.01	0.47	3
23	2	...	96	...	...	...	...	...	...	...	...	3
24	4	186	99	20.0	162	1.13	0.93	0.05	0.98	3.53	0.53	4
25	4	184	95	18.8	157	1.01	0.82	0.03	0.84	3.01	0.46	4
26	2	160	81	5.0	173	1.00	1.79	0.44	1.95	7.03	1.22	3
27	3	212	105	14.0	167	0.99	1.05	0.07	1.21	4.35	0.57	3
28	2	...	...	...	...	...	...	...	...	...	...	6
29	1	...	...	...	...	...	...	...	...	...	...	4
30	1	197	100	7.3	172	1.01	1.61	0.31	1.92	6.92	0.97	3
31	3	...	170	...	...	...	...	...	...	...	...	4
32	3	225	114	19.2	160	1.03	0.85	0.04	0.97	3.51	0.43	4
33	2	371	187	34.2	159	1.02	...	...	...	...	...	5
34	2	205	103	4.6	175	1.01	1.31	0.16	1.54	5.53	0.75	3
35	2	129	66	3.9	174	1.06	1.86	0.49	1.83	6.59	1.42	3
36	3	...	75	...	...	...	...	...	...	...	...	3
37	2	164	90	29.1	143	0.96	0.68	0.02	0.65	2.33	0.39	4
38	1	...	...	...	...	...	...	...	...	...	...	2
39	1	...	...	...	...	...	...	...	...	...	...	2
40	1	...	40	...	...	...	...	...	...	...	...	1
41	1	...	118	...	...	...	...	...	...	...	...	1
44	2	...	91	...	...	...	...	...	...	...	...	3
45	1	...	45	...	...	...	...	...	...	...	...	1
51	...	244	124	13.6	168	0.75	...	...	...	...	...	4
52	...	202	113	47.1	130	0.97	...	...	...	...	...	4
53	...	255	128	13.0	167	1.00	1.28	0.15	1.67	6.01	0.65	3
54	...	...	198	...	...	...	...	...	...	...	...	7

Table 29 (continued). Trackway and footprint variables averaged by trackway for localities in the Koum basin, northern Cameroon. Symbols are the same as for table 26.

T	FL	FW	L*W	ARA	SI	LBW	D1	D2	D3	D4	D1P
1	...	...	...	...	...	...	6.0	8.4	8.0	5.6	...
2	...	...	...	...	...	...	...	...	...	...	...
3	35	28	972	827	9.69	1.27	14.9	18.1	18.6	11.1	0.43
4	23	18	408	329	8.36	1.34	11.1	17.3	16.9	7.6	0.43
5	25	22	562	506	8.98	1.13	11.4	15.2	14.4	9.4	0.46
6	...	...	...	...	...	...	...	...	...	...	...
7	23	23	520	451	8.82	1.02	9.3	14.3	9.4	10.8	0.40
8	31	27	822	...	...	1.14	...	...	...	...	...
9	22	15	335	299	8.18	1.46	9.1	14.6	14.4	9.1	0.41
10	30	31	945	...	...	0.98	...	...	...	...	...
11	...	...	...	...	...	...	...	25.5	25.6	...	...
12	17	10	168	130	7.04	1.69	5.8	10.8	8.7	5.4	0.35
13	25	16	400	347	8.44	1.57	7.1	11.5	12.9	8.2	0.28
14	...	24	...	...	...	...	11.8	20.5	23.4	11.5	...
15	...	18	...	...	...	...	9.0	...	...	13.0	...
16	31	21	690	574	9.15	1.42	15.5	21.1	19.2	13.7	0.50
17	29	22	618	513	9.00	1.32	9.5	16.7	16.9	12.1	0.35
18	...	12	...	...	...	...	...	14.1	14.4	...	...
19	24	19	457	369	8.53	1.29	10.9	15.7	14.2	8.7	0.45
20	28	22	596	511	9.00	1.21	9.0	13.8	13.6	9.8	0.33
21	...	25	...	...	...	...	...	...	...	...	...
22	48	38	1793	1781	10.79	1.25	...	...	...	...	...
23	25	17	410	324	8.33	1.47	9.9	16.4	15.5	10.9	0.40
24	34	32	1075	1260	10.30	1.03	...	...	...	...	...
25	39	35	1348	1326	10.37	1.12	...	...	...	...	...
26	18	11	203	174	7.42	1.53	5.9	10.7	10.2	6.5	0.36
27	39	31	1222	1077	10.07	1.26	12.4	18.4	...	13.0	0.32
28	38	38	1426	...	...	1.02	...	...	...	...	...
29	24	...	...	...	...	...	...	...	...	...	...
30	25	15	386	327	8.35	1.66	5.4	12.5	13.2	8.7	0.21
31	46	36	1656	1357	10.41	1.28	...	...	...	...	...
32	46	38	1667	1436	10.48	1.27	13.9	20.7	22.1	14.7	0.31
33	...	39	...	...	...	...	22.9	22.9	24.7	16.4	...
34	30	20	616	536	9.06	1.48	9.6	13.8	16.5	12.2	0.32
35	15	13	198	176	7.45	1.16	6.1	10.3	9.7	6.0	0.41
36	17	14	232	167	7.36	1.18	4.5	10.1	10.8	5.4	0.28
37	42	37	1561	1487	10.54	1.12	14.1	16.9	15.5	11.3	0.34
38	24	20	480	...	...	1.20	12.0	15.5	14.0	11.0	0.50
39	7	6	40	...	...	1.23	...	...	...	...	...
40	7	5	38	38	5.24	1.32	...	...	...	...	...
41	...	...	...	...	...	...	...	...	...	...	...
44	23	16	356	267	8.06	1.49	8.0	13.2	11.9	5.0	0.38
45	7	4	29	21	4.39	1.71	...	...	...	...	...
51	...	...	...	...	...	...	...	...	...	...	...
52	...	...	...	...	...	...	...	...	...	...	...
53	39	27	1057	...	...	1.41	...	...	...	...	...
54	64	65	4154	...	...	...	...	...	...	...	...

Table 29 (continued). Trackway and footprint variables averaged by trackway for localities in the Koum basin, northern Cameroon. Symbols are the same as for table 26.

T	D2P	D3P	D4P	D1P2	D2P2	D3P2	D4P2	SKEW	DA	A	B
1	...	...	...	0.27	0.43	0.40	0.25	0.96	...	...	...
2	...	...	...	...	...	...	...	...	59	36	23
3	0.52	0.53	0.31	0.31	0.41	0.43	0.21	1.04	59	30	29
4	0.67	0.66	0.31	0.27	0.49	0.47	0.17	0.97	58	26	28
5	0.60	0.57	0.38	0.29	0.44	0.40	0.23	0.93	63	33	30
6	...	...	...	...	...	...	...	...	64	34	31
7	0.62	0.41	0.47	0.27	0.48	0.27	0.33	0.66	75	40	35
8	...	...	...	...	...	...	...	...	...	...	...
9	0.67	0.66	0.41	0.24	0.45	0.44	0.24	0.99	47	23	24
10	...	...	...	...	...	...	...	...	...	...	...
11	...	...	...	...	...	...	...	1.00	...	...	...
12	0.68	0.54	0.31	0.23	0.55	0.40	0.22	0.81	43	22	20
13	0.46	0.52	0.33	0.21	0.40	0.49	0.26	1.13	45	23	22
14	...	...	...	0.22	0.44	0.54	0.21	1.15	...	...	...
15	...	...	...	...	...	...	...	...	...	...	...
16	0.66	0.61	0.43	0.27	0.46	0.38	0.25	0.92	49	20	29
17	0.59	0.60	0.43	0.22	0.44	0.43	0.27	0.99	57	...	...
18	...	...	...	...	...	...	...	1.02	...	...	...
19	0.66	0.59	0.36	0.28	0.45	0.41	0.22	0.91	59	27	32
20	0.50	0.50	0.36	0.25	0.42	0.42	0.27	1.02	61	32	29
21	...	...	...	...	...	...	...	...	...	...	...
22	...	...	...	...	...	...	...	...	50	19	29
23	0.67	0.63	0.44	0.23	0.45	0.42	0.26	0.95	54	...	...
24	...	...	...	...	...	...	...	...	54	...	...
25	...	...	...	...	...	...	...	...	57	24	28
26	0.61	0.59	0.38	0.22	0.46	0.44	0.25	0.97	47	30	18
27	0.48	...	0.34	...	...	...	...	...	51	24	28
28	...	...	...	...	...	...	...	...	...	...	...
29	...	...	...	...	...	...	...	...	...	...	...
30	0.49	0.52	0.34	0.16	0.46	0.49	0.28	1.05	43	20	22
31	...	...	...	...	...	...	...	...	61	...	...
32	0.47	0.48	0.34	0.25	0.39	0.45	0.27	1.12	64	25	40
33	...	...	...	...	...	...	...	1.25	...	...	...
34	0.46	0.55	0.40	0.22	0.36	0.48	0.30	1.21	48	25	22
35	0.70	0.65	0.40	0.24	0.48	0.43	0.23	0.93	61	35	26
36	0.61	0.65	0.32	0.17	0.57	0.48	0.19	1.09	80	50	31
37	0.41	0.36	0.26	0.35	0.42	0.35	0.24	0.93	56	...	...
38	0.65	0.58	0.46	0.30	0.42	0.36	0.27	0.90	...	...	...
39	...	...	...	...	...	...	...	...	...	...	...
40	...	...	...	...	...	...	...	...	46	...	...
41	...	...	...	...	...	...	...	...	...	...	...
44	0.58	0.52	0.22	0.27	0.55	0.41	0.17	0.90	56	26	30
45	...	...	...	...	...	...	...	...	49	...	...
51	...	...	...	...	...	...	...	...	...	...	...
52	...	...	...	...	...	...	...	...	...	...	...
53	...	...	...	...	...	...	...	...	...	...	...
54	...	...	...	...	...	...	...	...	...	...	...

Table 29 (continued). Trackway and footprint variables averaged by trackway for localities in the Koum basin, northern Cameroon. Symbols are the same as for table 26.

T	FD	FRT	HH	VOL	MASS
1	2.6	...	...	...	...
2	5.9	...	...	...	...
3	3.9	6.25	200	1317	1317
4	2.8	-5.50	107	230	230
5	2.3	1.86	116	286	286
6	6.1	-5.80	...	...	...
7	2.9	...	106	220	220
8	2.2	6.50	157	671	671
9	2.1	-2.50	101	199	199
10	1.6	18.00	156	660	660
11	2.8	3.25	...	...	...
12	1.9	-6.35	77	90	90
13	2.5	2.83	129	383	383
14	4.2	...	...	...	...
15	3.9	13.50	...	...	...
16	1.9	-4.25	160	701	701
17	3.0	-5.13	147	561	561
18	2.0	-2.00	...	...	...
19	1.4	1.67	112	256	256
20	2.8	0.13	142	506	506
21	...	...	...	...	...
22	4.0	-3.88	248	2455	2455
23	2.1	...	126	361	361
24	3.0	...	201	1342	1342
25	4.2	5.17	221	1767	1767
26	0.9	-1.56	90	140	140
27	3.0	-1.25	202	1364	1364
28	3.7	...	196	1246	1246
29	3.2	...	137	453	453
30	1.5	3.00	130	399	399
31	4.3	...	262	2838	2838
32	3.8	-1.50	262	2845	2845
33	4.0	10.70	...	...	...
34	2.9	0.44	156	654	654
35	1.1	2.30	78	95	95
36	2.3	...	85	119	119
37	5.0	4.00	238	2197	2197
38	0.9	...	110	248	248
39	0.9	...	32	8	8
40	0.9	...	32	8	8
41	...	...	...	...	...
44	2.4	...	118	308	308
45	0.7	...	32	8	8
51	...	...	...	...	...
52	...	...	...	...	...
53	4.4	...	199	1310	1310
54	29	...	256	2668	2668

APPENDIX 3

Correlation of variables

All primary and derived footprint and trackway variables were analyzed for correlation using the Pearson product-moment correlation statistic. This statistic, denoted p_{xy}, is defined as

$$p_{xy} = \frac{\text{cov}(x,y)}{[\text{var}(x) \cdot \text{var}(y)]^{0.5}} \tag{10}$$

where cov(x,y) is the covariance matrix of the variables (SAS Institute 1985a).

The correlation statistic is a measure of the closeness of the linear relationship between two variables. If a variable x varies directly (linearly) with another variable y, then the correlation between the two is 1 or -1, the latter being the result of a perfect inverse relationship between the two. A correlation of zero signifies that the two variables are independent of one another, and one has no predictive ability for the other. The underlying assumption for this statistic is that the sample populations are normally distributed. Because of this assumption, and the fact that some variables may not be linearly related but logarithmically or exponentially, all data were normalized to gaussian distributions by each variable. The correlation matrix presented in table 28 was calculated with missing data for some of the cases; this means that some of the correlations were computed using more observations than others.

Table 30.--Correlation matrix of selected footprint and trackway variables, all cases.

	FL	FW	ARA	SI	LW	D1	D2	D3
FL	1.000	0.937	0.914	0.933	-0.298	0.697	0.721	0.760
FW		1.000	0.964	0.942	-0.567	0.775	0.652	0.724
ARA			1.000	0.865	-0.444	0.714	0.610	0.675
SI				1.000	-0.467	0.773	0.678	0.761
LW					1.000	-0.362	-0.178	-0.101
D1						1.000	0.815	0.808
D2							1.000	0.861
D3								1.000
D4								

	D4	D1P	D2P	D3P	D4P	D1P2	D2P2	D3P2
FL	0.763	-0.129	-0.594	-0.458	-0.174	0.338	-0.497	-0.091
FW	0.695	0.065	-0.477	-0.375	-0.086	0.451	-0.483	-0.107
ARA	0.672	0.048	-0.494	-0.369	-0.115	0.504	-0.464	-0.159
SI	0.765	0.082	-0.526	-0.336	-0.025	0.446	-0.551	-0.120
LW	-0.162	-0.421	-0.093	-0.043	-0.138	-0.458	0.076	0.411
D1	0.634	0.605	-0.116	-0.053	-0.025	0.683	-0.283	-0.273
D2	0.759	0.375	0.097	0.032	0.130	0.265	0.009	-0.132
D3	0.790	0.244	-0.186	0.192	0.226	0.082	-0.423	0.328
D4	1.000	0.032	-0.289	-0.030	0.482	-0.006	-0.550	-0.001
D1P		1.000	0.555	0.408	0.224	0.743	0.111	-0.537
D2P			1.000	0.660	0.363	-0.003	0.637	-0.261
D3P				1.000	0.565	-0.308	0.012	0.430
D4P					1.000	-0.383	-0.279	0.027
D1P2						1.000	-0.080	-0.577
D2P2							1.000	-0.339
D3P2								1.000

Table 30 (continued).--Correlation matrix of selected footprint and trackway variables, all cases.

	D4P2	SKEW	DA	A	B	FD	FRT	MASS
FL	0.211	0.240	0.062	-0.395	0.217	0.624	0.065	0.938
FW	0.084	0.252	0.293	-0.116	0.474	0.642	0.175	0.869
ARA	0.067	0.198	0.139	-0.277	0.324	0.767	0.228	0.931
SI	0.167	0.240	0.191	-0.297	0.316	0.745	0.259	0.753
LW	0.090	0.191	-0.655	-0.569	-0.593	-0.191	-0.226	-0.213
D1	-0.232	0.101	0.203	-0.023	0.319	0.516	0.351	0.623
D2	-0.194	-0.094	0.122	-0.286	0.411	0.415	-0.002	0.637
D3	0.005	0.407	-0.010	-0.382	0.127	0.480	0.268	0.647
D4	0.517	0.294	0.011	-0.369	0.178	0.490	0.096	0.682
D1P	-0.507	-0.343	0.266	0.294	0.276	-0.063	-0.216	-0.153
D2P	-0.438	-0.590	0.154	0.133	0.165	-0.544	-0.282	-0.533
D3P	-0.113	0.193	-0.001	-0.018	0.054	-0.460	-0.214	-0.444
D4P	0.629	0.117	-0.085	-0.108	-0.051	-0.314	0.031	-0.191
D1P2	-0.480	-0.283	0.366	0.341	0.245	0.328	0.071	0.314
D2P2	-0.548	-0.810	0.067	0.152	0.090	-0.264	-0.251	-0.391
D3P2	0.047	0.801	-0.293	-0.331	-0.232	0.009	0.049	-0.112
D4P2	1.000	0.364	-0.212	-0.227	-0.137	-0.062	0.114	0.159
SKEW		1.000	-0.173	-0.137	-0.241	0.234	0.124	0.193
DA			1.000	0.839	0.724	0.299	-0.040	0.037
A				1.000	0.233	0.132	0.146	-0.315
B					1.000	0.182	0.220	0.223
FD						1.000	0.032	0.697
FRT							1.000	-0.007
MASS								1.000

	S	P	TW	PA	PI	RSL	SMS	STRT
FL	0.365	0.518	0.664	-0.563	0.032	-0.720	-0.518	-0.852
FW	0.113	0.267	0.274	-0.292	0.064	-0.771	-0.594	-0.855
ARA	0.074	0.216	0.665	-0.733	-0.060	-0.720	-0.548	-0.793
SI	0.177	0.355	0.615	-0.627	-0.059	-0.755	-0.540	-0.904
LW	0.276	0.174	-0.159	0.398	0.036	0.455	0.412	0.393
D1	0.388	0.315	0.329	-0.287	0.044	-0.625	-0.463	-0.710
D2	0.466	0.549	0.288	-0.202	-0.306	-0.577	-0.400	-0.681
D3	0.597	0.640	0.343	-0.085	-0.038	-0.501	-0.295	-0.682
D4	0.349	0.482	0.423	-0.307	-0.049	-0.635	-0.459	-0.760
D1P	-0.288	-0.225	-0.209	-0.231	0.036	-0.045	-0.083	0.034
D2P	-0.265	-0.210	-0.306	0.020	0.018	0.343	0.218	0.473
D3P	0.034	0.090	-0.358	0.274	0.056	0.367	0.305	0.416
D4P	-0.148	-0.034	-0.198	0.182	-0.058	-0.015	-0.069	0.037
D1P2	-0.156	-0.220	0.139	-0.389	-0.114	-0.390	-0.324	-0.388
D2P2	-0.118	-0.145	-0.094	-0.182	-0.127	0.276	0.173	0.392
D3P2	0.447	0.423	-0.033	0.444	-0.087	0.350	0.371	0.260
D4P2	-0.107	0.033	0.013	0.156	0.291	-0.189	-0.175	-0.224

Table 30 (continued).--Correlation matrix of selected footprint and trackway variables, all cases.

	S	P	TW	PA	PI	RSL	SMS	STRT
SKEW	0.214	0.204	0.077	0.209	-0.000	0.020	0.084	-0.088
DA	-0.073	-0.028	0.219	-0.306	-0.061	-0.288	-0.250	-0.270
A	-0.292	-0.444	0.075	-0.146	-0.211	-0.263	-0.300	-0.187
B	0.077	-0.092	0.193	-0.435	-0.065	-0.050	0.042	-0.134
FD	0.347	0.387	0.392	-0.349	0.106	-0.418	-0.240	-0.564
FRT	0.304	0.053	-0.013	-0.055	-0.102	-0.160	-0.138	-0.168
MASS	0.337	0.364	0.723	-0.589	0.069	-0.631	-0.468	-0.730
S	1.000	0.972	0.231	-0.093	-0.063	0.258	0.496	-0.042
P		1.000	0.381	-0.134	0.085	0.216	0.453	-0.073
TW			1.000	-0.828	0.044	-0.412	-0.307	-0.472
PA				1.000	-0.066	0.424	0.345	0.438
PI					1.000	0.020	0.003	0.020
RSL						1.000	0.953	0.949
SMS							1.000	0.812
STRT								1.000

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