PERMIAN CAPTORHINID REPTILES FROM THE ARGANA FORMATION, MOROCCO
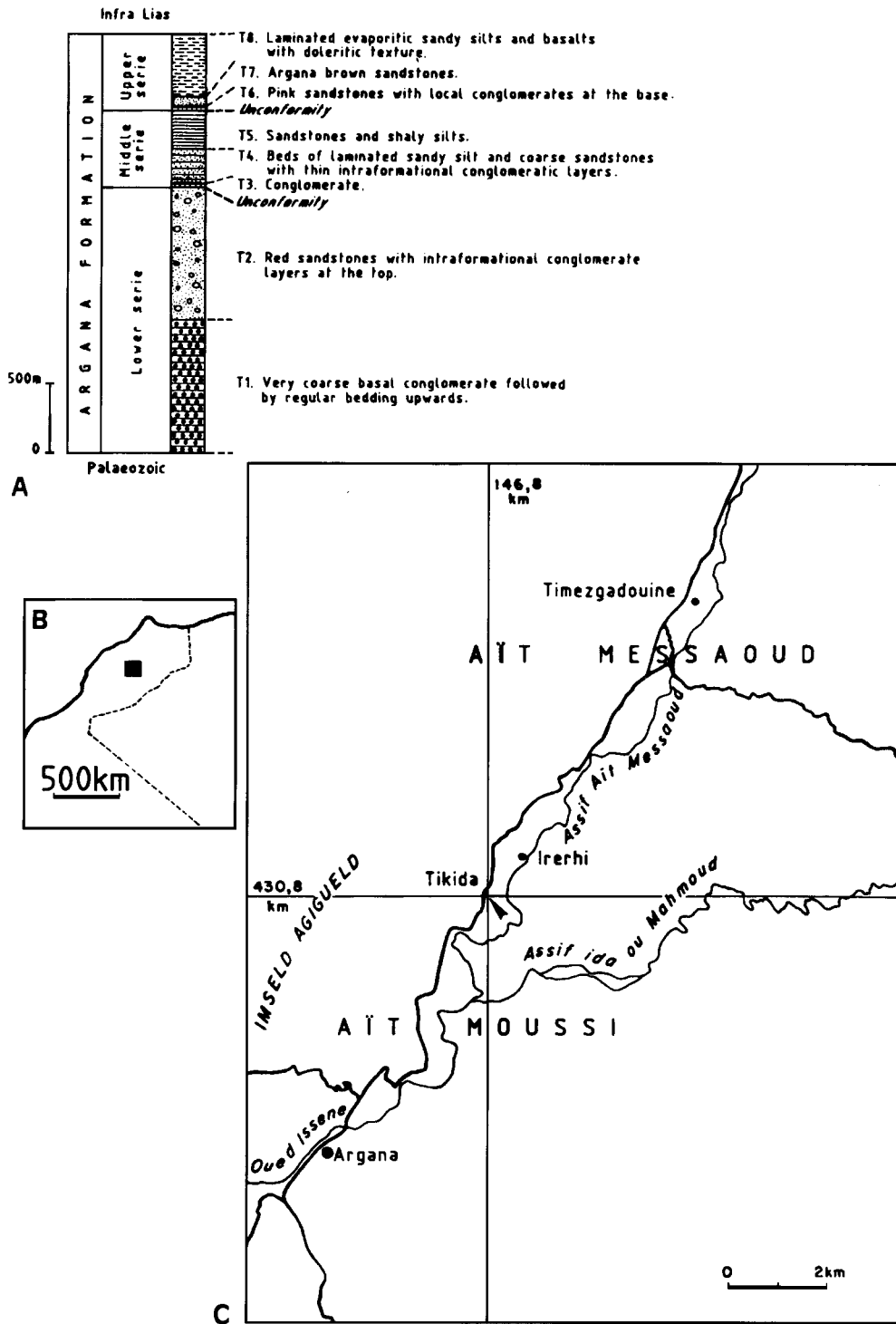
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ABSTRACT. New and previously reported captorhinid material from the upper part of the Permian level T2 of the Argana Formation of Morocco is described. A maxilla bearing three tooth-rows forms the holotype of *Acrodonta irerhi*. *Acrodonta* is a medium-sized captorhinid with three rows of long and sharply pointed maxillary teeth, which differs from all other captorhinids in its acrodont tooth implantation. Dental plates and postcranial material are attributed to an unnamed member of the captorhinid subfamily Moradisaurinae. The moradisaurine remains are too poorly preserved to be attributed to either an existing or a new taxon. Nevertheless, together with *Acrodonta*, they indicate that the Captorhinidae were diverse in the Permian of North Africa. Comparison of the fauna of the upper part of Argana level T2 (diplocaulid nectrideans, the captorhinid *Acrodonta* and the moradisaurine) with other faunas of Euramerica and Gondwana supports an Upper Permian age (Kazanian) for this part of the Argana Formation.

THE Argana Formation crops out in the western Upper Atlas mountains of Morocco, between Marrakech in the north and Agadir in the south (Text-fig. 1). These outcrops, known as 'Couloir d'Argana' are 70 km long and have a maximum width of 20 km. They overlie the Palaeozoic massif of Ida-ou-Mahmoud in the east and are overlain by the Jurassic tablelands of Ida-ou-Tanan and Ida-ou-Bouzia in the west. Eight lithostratigraphical units were established by Tixeront (*in* Dutuit 1976a; Brown 1980) in the Argana Formation, namely T1–T8 (Text-fig. 1). For the lithostratigraphical data, see Brown (1980).

Following the first description of vertebrate remains from the Argana Formation (Arambourg and Duffaud 1960), the formation was carefully explored by Dutuit in the 1960s and 1970s. An extensive collection was made from at least 23 localities (Dutuit 1976a) and brought for study to the Laboratoire de Paléontologie of the Muséum National d'Histoire Naturelle, Paris. Most of this vertebrate material proved to be Upper Triassic and is from the levels T4 and T5 (Text-fig. 1). The pre-Triassic tetrapods are from the upper part of level T2, which is Permian. The fauna includes abundant, mostly unprepared, cranial and postcranial material of diplocaulid nectrideans, (*Diplocaulus minimus*; Dutuit 1976c, 1988), and further unprepared material of large reptiles that may include synapsids (A. de Ricqlès, pers. comm.).

Dutuit (1976b) recorded three tooth-bearing bones (one maxilla and two maxillary dental plates) from the upper part of the T2 level. Working on the contemporary assumption that this level was Triassic and giving weight to the acrodont dental implantation in these specimens, he referred this material to a 'rhynchocephalian' for which he coined the name *Acrodonta irerhi*. Later, in describing the nectridean diplocaulids from the upper part of T2, he suggested instead that this material could be referred to a captorhinomorph reptile (Dutuit 1988). Further preparation of this material and its restudy in the light of recent data show that it actually belongs to two distinct captorhinid taxa including one member of the subfamily Moradisaurinae. The present study reappraises the cranial material described by Dutuit (1976b) as well as new postcranial remains from the same stratigraphical level and collected at the same time.

First known from the terrestrial deposits of Lower Permian and the lower part of the Upper Permian of USA (New Mexico, Oklahoma and Texas), the Captorhinidae have been described from the Upper Permian of Russia (Vyushkov and Chudinov 1957; Ivachnenko 1990), Niger (Taquet 1969; de Ricqlès and Taquet 1982), Zimbabwe (Gaffney and McKenna 1979), and India (Kutty 1972). Whereas the most primitive Lower Permian captorhinids were small and probably

Infra Lias

T8. Laminated evaporitic sandy silts and basalts
    with doleritic texture.
T7. Argana brown sandstones.
T6. Pink sandstones with local conglomerates at the base.
--- *Unconformity*

T5. Sandstones and shaly silts.
T4. Beds of laminated sandy silt and coarse sandstones
    with thin intraformational conglomeratic layers.
T3. Conglomerate.
Unconformity

T2. Red sandstones with intraformational conglomerate
    layers at the top.

500m

0

T1. Very coarse basal conglomerate followed
    by regular bedding upwards.

Palaeozoic

A

B

500km

146,8
km

Timezgadouine

AÏT   MESSAOUD

Assif Aït Messaoud

430,8
km

IMSELD AGIGUELD

Tikida   Irerhi

Assif ida ou Mahmoud

AÏT   MOUSSI

Oued Issene

Argana

0   2km

C

TEXT-FIG. 1. A, stratigraphical section of the Argana Formation near Argana village. B, map of Morocco
showing area of study. C, map showing the *Acrodonta irerhi* locality.
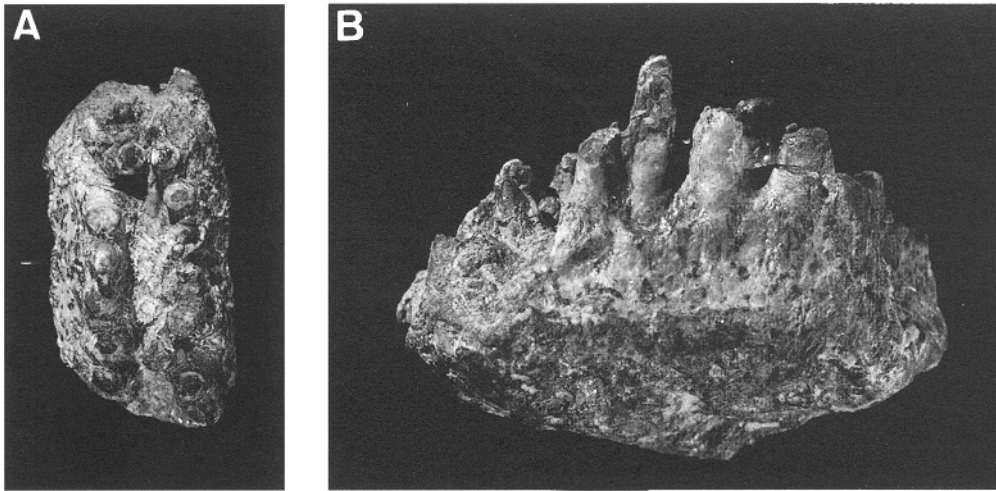
TEXT-FIG. 2. *Acrodonta irerhi* Dutuit, 1976*b*; holotype, ARG 506; Lower Argana Formation, Permian of Morocco; right maxilla in (A) occlusal and (B) lingual views. A, ×2; B, ×3.

insectivorous, the most advanced Upper Permian forms, the subfamily Moradisaurinae, show trends towards increased body size. This pattern, associated with the acquisition of multiple rows of marginal teeth, is thought to be a strong indication of herbivory and the Moradisaurinae are regarded as one of the earlier clades of tetrapod herbivores. This first record of a moradisaurine in North Africa is thus important in biogeographical studies of captorhinids and in our understanding of the development of terrestrial ecosystems.

The relationships of captorhinids within the early Amniota remain controversial (Clark and Carroll 1973; Gaffney and McKenna 1979; Gaffney 1980, 1990; Heaton and Reisz 1986; Gaffney and Meylan 1988; Gauthier *et al.* 1988; Reisz and Laurin 1991; Benton 1993; Lee 1993; Laurin and Reisz 1995). They are beyond the scope of this study, which is to consider the identity of the Moroccan captorhinids. For the purposes of this study, we follow the hypothesis of amniote phylogeny of Laurin and Reisz (1995) in which the Captorhinidae are closely related to the clade *Paleothyris* + Diapsida.

SYSTEMATIC PALAEONTOLOGY

COTYLOSAURIA Cope, 1880
SAUROPSIDA Huxley, 1864
REPTILIA Laurenti, 1768
Family CAPTORHINIDAE Case, 1911

Genus ACRODONTA Dutuit 1976*b*

Type species. Acrodonta irerhi Dutuit 1976*b*

Diagnosis. As for the type and only species.

Acrodonta irerhi Dutuit 1976*b*

Text-figure 2

Holotype. ARG 506 (69.Ir.JMD of Dutuit 1976*b*): fragment of a right maxilla (Text-fig. 2); from scree, 200 m from Irerhi village, between Timesgadouine and Argana (Dutuit 1976*a*; Text-fig. 1).

Diagnosis. Medium-sized captorhinid with three rows of sharply pointed marginal teeth. It differs from all other captorhinids by its acrodont tooth implantation.

Description. ARG 506 is a fragment of a maxilla bearing three rows of marginal teeth. A pattern of scattered shallow pits is faintly visible and these may be the remains of dermal ornamentation. The absence of a well-marked ornamentation is certainly due to erosion. The specimen is badly crushed but its lateral and medial walls seem to be in their original form. A longitudinal crest runs along its lingual side (Text-fig. 2B), half-way up the preserved height, whereas its labial side is slightly convex laterally. This convexity is surmounted by a shallow depression which may correspond to the sutural area for the jugal or the lacrimal. Three parallel tooth-rows are seen in occlusal view. Only the bases of the teeth of the median row are now visible (Text-fig. 2A). The teeth are conical, long, straight and sharp. They are circular in cross section, with a pulp cavity which is large at its base but narrows towards the apex of the tooth. The tooth implantation is acrodont. The teeth are fused indistinguishably with the underlying bone (Text-fig. 2B). This character state is interpreted as an autapomorphy of *Acrodonta irerhi*. The tooth implantation in all other captorhinids is subthecodont.

Family CAPTORHINIDAE Case, 1911
Subfamily MORADISAURINAE de Ricqlès and Taquet, 1982

Gen. et sp. indet.

Plate 1; Text-figures 3–6

Material. ARG 507 (74 XXII.1.JMD of Dutuit 1976*b*), dental plate of right maxilla (Text-fig. 3A); ARG 508 (74.XXII.2.JMD of Dutuit 1976*b*), dental plate of left maxilla (Text-fig. 3B–C); ARG 504, left humerus (Text-fig. 5D); ARG 505, proximal end of a femur (Text-fig. 5E); ARG 509, two articulated caudal vertebrae (Text-fig. 5A–C); ARG 510, three articulated presacral vertebrae; ARG 511, four articulated presacral neural arches (Pl. 1); ARG 512, three articulated caudal centra; ARG 513, badly preserved pelvis (Text-fig. 6).

Locality. ARG 507 and ARG 508 are from the same stratigraphical level. They were recovered in a small basin (100 m across), from a 0·5–1 m thick sandstone bed. The post-cranial material (ARG 504–505, ARG 509–513) is from the same basin as ARG 507–508 but was found separated by a few metres from the latter. This locality, called Tikida, is situated between Argana in the south and Timezgadouine in the north (Lambert coordinates: 146·8 km East and 430·8 km North) (Text-fig. 1).

Description. Labidosaurus and the smaller captorhinids may be characterized by a rather large and massive head in comparison to the size of the postcranial skeleton. However, this does not necessarily apply to the larger captorhinids of the subfamily Moradisaurinae. If a large head is assumed, then the dental plates (ARG 507–508) and the post-cranial material (ARG 504–505, ARG 509–513) could be attributed to the same individual, as suggested by the taphonomic circumstances. Indeed, the dental plates and the postcranial material were collected from the same locality separated by only few metres, no other large tetrapods bones were found in this area and none of the described elements were duplicated. Moreover, the characteristics of the studied postcranial material do not contradict the systematic position suggested by the dental plates. Consequently, the dental plates and the postcranial material are attributed to the same individual here, with the reservation that the discovery of further material is needed to reinforce or falsify this association.

The similarity in size, proportions and shape of the right and left maxillary dental plates (respectively ARG 507 and 508), suggests that they belong to the same species if not the same individual, as they were found in close association (Dutuit 1976*b*). ARG 507 and 508 (Text-fig. 3) are larger and significantly different from ARG 506 (Text-fig. 2). The best preserved specimen (ARG 508) is 44 mm long, with a maximal width of 21 mm. The dental plate is enlarged laterally, dorsoventrally flattened and seems separated from the underlying bone (Text-fig. 3C). Its medial border is convex and overhangs the underlying bones. In *Moradisaurus* (de Ricqlès and Taquet 1982), the transition from the dental plate to the ornamented external surface of the maxilla is gradual. This seems also to be the case in ARG 508. The posteriormost part of the lateral side of ARG 508 is convex laterally, as in *Moradisaurus*, and indicates that the jugal region of the skull of this specimen was certainly rounded in shape. A lateral crest arises from the underlying bone and delimits the posterior border of the dentary plate. This well-developed crest ends abruptly, both laterally and medially. The anterior part of

EXPLANATION OF PLATE 1

Figs 1–2. Moradisaurinae gen. et sp. indet.; ARG 511; Lower Argana Formation, Permian of Morocco; four presacral neural arches in 1, dorsal and 2, lateral views. Both × 1.
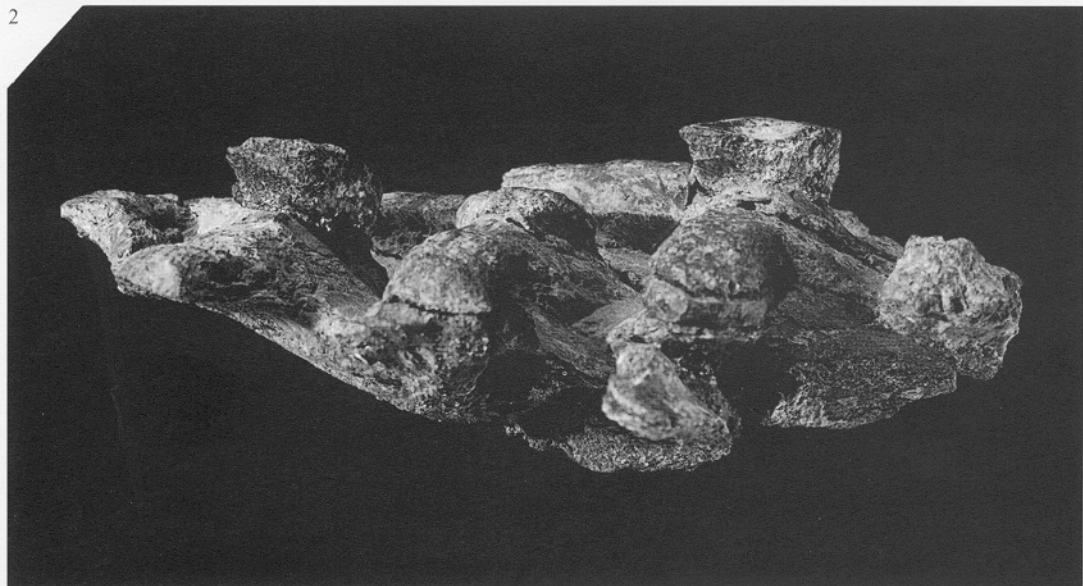
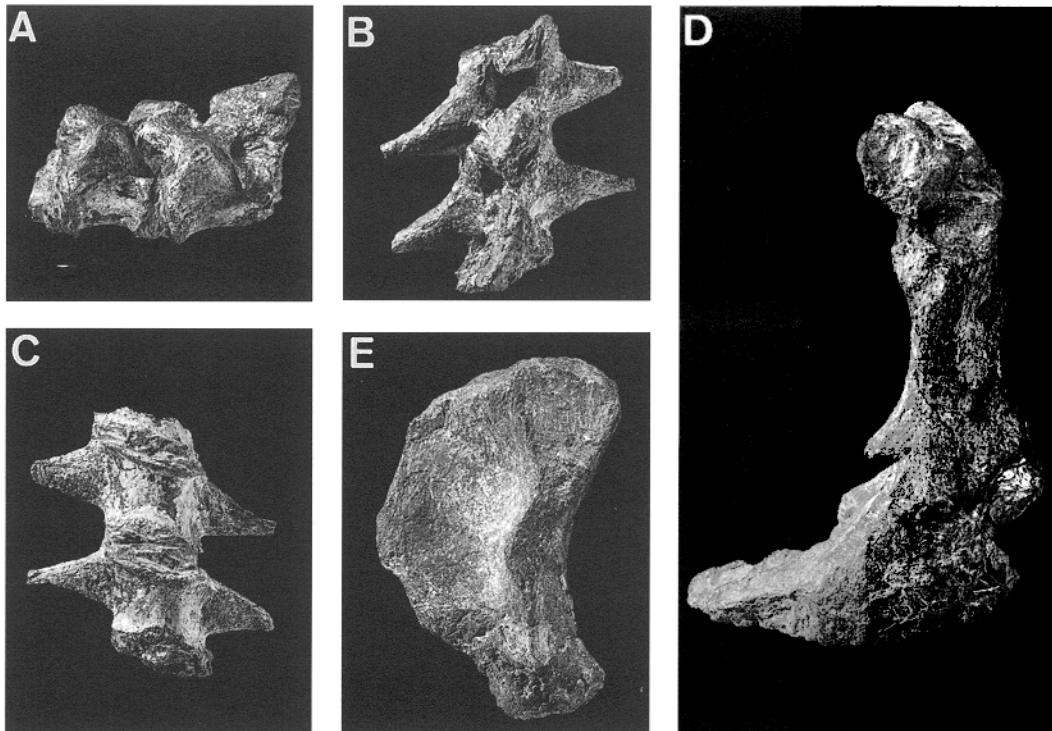PLATE 1

JALIL and DUTUIT, Moradisaurinae gen. et sp. indet.
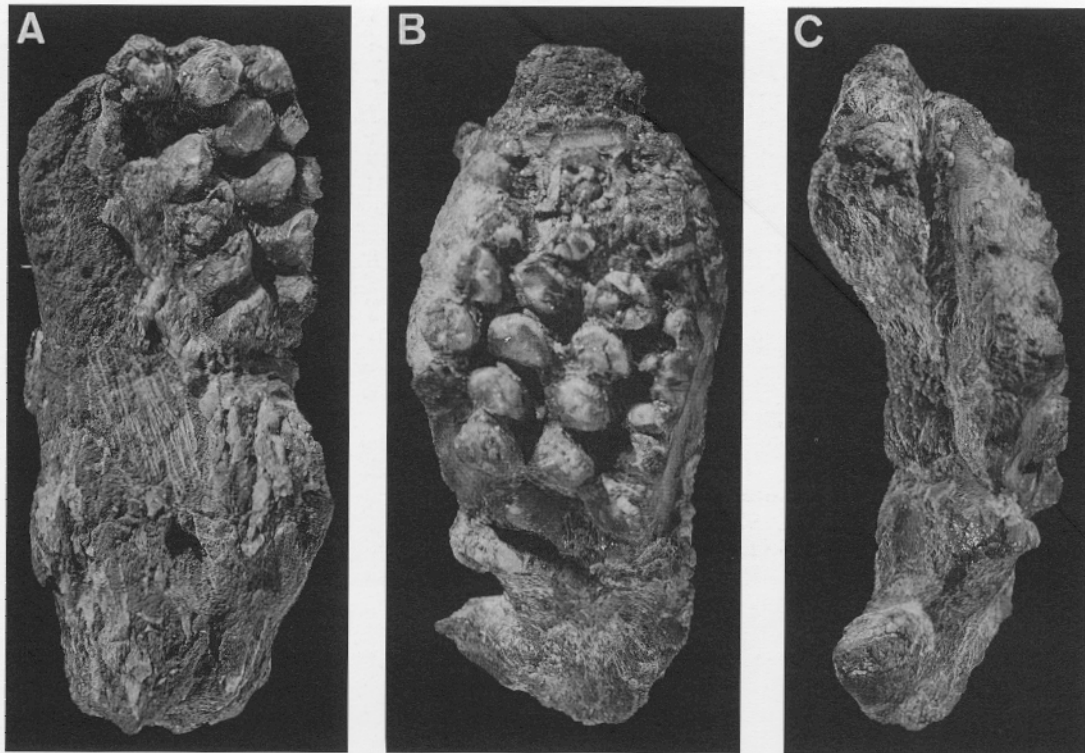
TEXT-FIG. 3. Moradisaurinae gen. et sp. indet.; Lower Argana Formation, Permian of Morocco. A, ARG 507, dental plate of right maxilla in occlusal view; B–C, ARG 508, dental plate of left maxilla in occlusal (B) and lingual (C) views. All ×2.
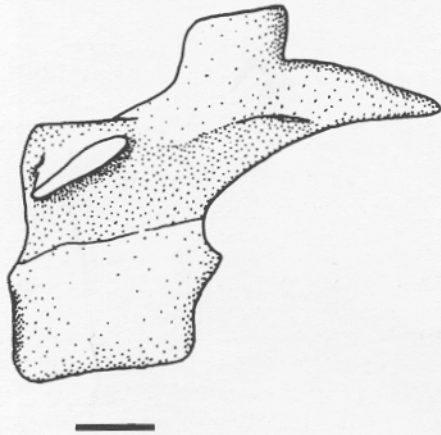
TEXT-FIG. 4. Moradisaurinae gen. et sp. indet.; Lower Argana Formation, Permian of Morocco. Reconstruction of dorsal vertebrae in lateral view (based on ARG 510 and ARG 511). Scale bar represents 10 mm.

the dental plate is missing in both ARG 507 and ARG 508. At least four tooth rows are present on ARG 508; on ARG 507 only three rows are preserved. As in all large, multiple-tooth-rowed captorhinids, the tooth-rows are longitudinal and parallel to each other and to the lingual border. In *Captorhinus aguti*, the rows are divergent (de Ricqlès and Bolt 1983). The size and shape of all preserved teeth are similar. The teeth are conical, sub-circular in cross section and are lower and stouter than those of *Acrodonta irerhi* (ARG 506). They are slightly bulbous at the base but the apex is pointed and posteriorly recurved as shown by a well-preserved tooth, broken at its base and lying at the posteriormost part of the dental plate (Text-fig. 3B). The pulp cavity

TEXT-FIG. 5. Moradisaurinae gen. et sp. indet.; Lower Argana Formation, Permian of Morocco. A–C, ARG 509, two caudal vertebrae in lateral (A), dorsal (B) and ventral (C) views; D, ARG 504, left humerus; E, ARG 505, proximal extremity of a femur. All ×0·5.

is large at the base of the teeth and narrows progressively towards the apex. The tooth implantation is subthecodont.

The dorsal neural arch is expanded laterally and is not completely fused to the notochordal centrum (as suggested by the isolated neural arches of ARG 511 (Pl. 1) and the longitudinal groove which separates the neural arches and the corresponding centra in ARG 510 (Text-fig. 4)). Unlike primitive reptiles, which have a centrum which is short relative to its diameter, the centra of ARG 510 are slender and are as long as high. The centra are hourglass-shaped in ventral view, with a ventral bevelling anteriorly and posteriorly for the accommodation of a large triangular intercentrum. The posterior bevelling is more pronounced, as shown by the large gap which was filled by an unpreserved intercentrum on ARG 510. There is no keel on the centrum. In ARG 510, the neural arches are noticeably swollen, but those of ARG 511 have a flat dorsal surface (Pl. 1). A swollen arch is known in all captorhinids in which the vertebrae have been studied (Dilkes and Reisz 1986; Sumida 1987, 1990). In *Labidosaurus*, the first presacral vertebrae are expanded but do not show any significant swelling (Sumida 1987, 1990). The apices of the neural spines are somewhat damaged but it is clear that they vary in height. When preserved, they are vertical and readily distinguishable from the ventrolaterally oriented surface of the neural arch (Pl. 1). A dorsal bifurcation seems to be present on the tip of the higher neural spine of ARG 511 as in *Labidosaurus* and to a lesser extent in *Captorhinus laticeps* (Dilkes and Reisz 1986, fig. 4; Sumida 1987). This bifurcation, also present in *Seymouria*, appears frequently and randomly anterior to the level of the pectoral girdle (Sumida 1987) and may have served for the attachment of supraspinal ligaments which supported the head (Dilkes and Reisz 1986). The pre- and postzygapophyses meet in a horizontal, large surface which extends laterally above the transverse process and the lateral side of the centra. A space filled by matrix separates the pre- and the postzygapophyses. This, along with the horizontal position of the zygapophyses, suggest the possibility of dorsiflexion in the vertebral column. A lateral constriction on the neural arch separates the pre- and postzygapophyses. The transverse processes project ventrolaterally and lie in the anteroventral border of the neural arch, just below the prezygapophyses (Text-fig. 4). The costal articular surfaces are badly preserved, but seem to be triangular, tapering anteroventrally.

The caudal centra (ARG 509, 512) are shorter than the dorsal centra. They are also hourglass-shaped in ventral view (Text-fig. 5). The transverse processes are well developed, and oriented posterolaterally. The neural arches are less expanded than those of the dorsal vertebrae. The neural spines are low and broad. The zygapophyses do not project laterally to the same extent as those of the dorsal vertebrae. They are tilted upwards from the horizontal plane and the articular surfaces are thus oblique.

ARG 513 is a poorly preserved pelvis (Text-fig. 6). The ilium, ischium and pubis seem to be indistinguishably fused, as in *Labidosaurus* (Sumida 1989). The ilium is lost and only its somewhat constricted base is preserved. The acetabulum is surmounted anterodorsally by a thickened bony buttress which may be interpreted as the dorsal part of the pubis. The acetabulum is hemispherical and deep. In *Captorhinus*, a large portion of the acetabulum is formed by the ilium (Fox and Bowman 1966). As in *Labidosaurus* (Sumida 1989), the fusion of the three elements of the pelvis in ARG 513 precludes direct comparisons. Anteroventral to the acetabulum is a large obturator foramen. Only the dorsal part of the ischium is preserved. It runs posteriorly from the acetabulum as a thickened ridge. The poor preservation precludes further description.

The proximal and distal heads of the humerus are orientated at 90° to one another (ARG 504, Text-fig. 5D). Its shaft is narrow by comparison to its expanded distal end. The proximal extremity is badly preserved, but seems to be less expanded than in *Captorhinus* and *Labidosaurus* (Holmes 1977; Sumida 1989). *Rhiodenticulatus* also has a more gracile humerus (Berman and Reisz 1986). A deep notch is present on the lateral border of the entepicondyle. The entepicondylar foramen was probably completely closed. The articular surfaces are not preserved on both proximal and distal ends.

Only the proximal extremity of the right femur is preserved (ARG 505; Text-fig. 5E). It is expanded (65 mm) relatively to its narrow shaft (19 mm). The internal trochanter, though incompletely preserved, appears to be well developed. It delimits a large and shallow depression, the intertrochanteric fossa. The shallowness of this depression and the thin bone in this region (6 mm) suggest that the puboischiofemoralis externus muscle was less developed than that of *Labidosaurus* (Sumida 1989) and *Rothianiscus* (Olson 1965). A bony projection is present dorsally, probably for the insertion of the puboischiofemoralis muscle (Sumida 1989).

Remarks. All three tooth-bearing elements (ARG 506–508) share one derived character state which is considered to be highly diagnostic within the Captorhinidae, namely the presence of multiple rows of marginal teeth. Consequently, ARG 506–508 are attributed to the Captorhinidae. Since the Lower Permian captorhinids *Romeria* (Price 1937), *Protocaptorhinus* (Clark and Carroll 1973), *Rhiodenticulatus* (Berman and Reisz 1986), *Labidosaurus* (Cope 1896), *Captorhinus laticeps* (Heaton 1979; Gaffney 1990) and probably also the Upper Permian (Ufimian) *Riabininus* (Ivachnenko 1990) have one row of marginal teeth, they are regarded as distinct from the Moroccan specimens and irrelevant to our comparison.

As described above, *Acrodonta irerhi* (ARG 506) shows character states which are significantly different from those observed on ARG 507 and 508. The smaller size, the low number of tooth-rows, the absence of an enlarged dental plate, and the size and shape of the teeth distinguish ARG 506 from ARG 507 and 508. Moreover, *Acrodonta* differs from all other captorhinids in possessing an acrodont tooth implantation. It is more primitive than *Labidosaurus*, *Captorhinus* and all other multiple tooth-rowed captorhinids in possessing sharply pointed, rather than blunt teeth, but this may be a more derived condition associated with diet.

ARG 507 and ARG 508 show more derived character-states (large size; blunt, rather than pointed, teeth; well-developed dental plate) and so fall within the Moradisaurinae of de Ricqlès and Taquet (1982) and de Ricqlès (1984), referred to as 'group 6' by Gaffney and McKenna (1979). The most noticeable postcranial characters are those of the dorsal vertebrae (slightly swollen neural arch; reduced neural spine; probably bifurcated neural spine; alternating neural spine height; large, spaced and horizontal zygapophysis).

Since first reported by Carroll (1968) in the microsaur *Pantylus*, the alternation of neural spine height has subsequently been described in such a large number of Permo-Carboniferous tetrapods (see Dilkes and Reisz 1986; Sumida 1987 for references) that its phylogenetic value is difficult to assess. More confusing is the fact that this character varies within the same family, the Captorhinidae (Heaton and Reisz 1980; Dilkes and Reisz 1986; Sumida 1987) and even in the same species, *Labidosaurus hamatus* (Sumida 1987). The bifurcation of the neural spine, which is present in *Labidosaurus*, is probably related to the presence of a massive head, as it is in the captorhinids
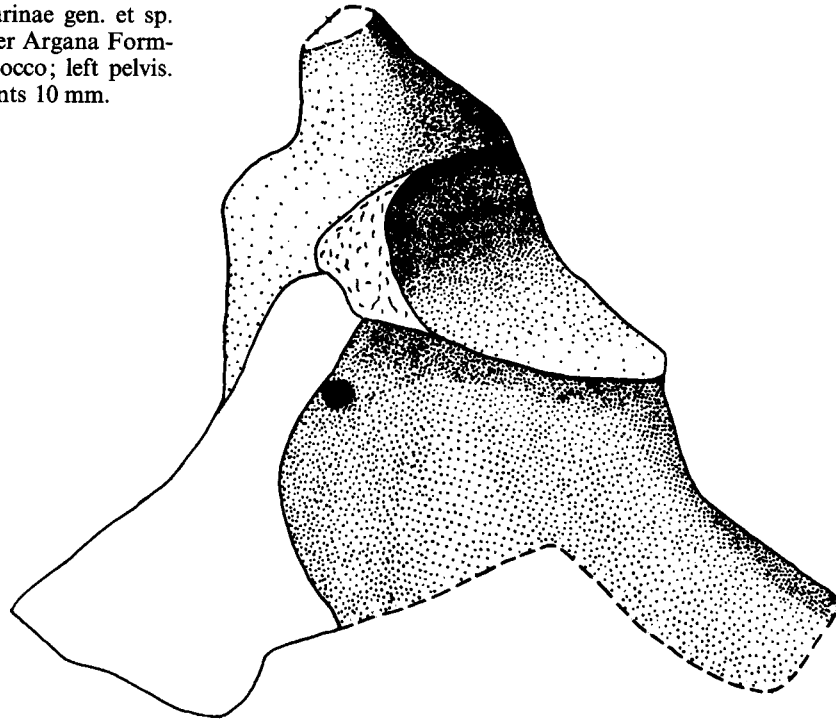
and may be a captorhinid character. Unfortunately, the vertebrae in our specimens are not sufficiently well preserved to show with certainty this character-state of the neural spine. Compared with other captorhinids, the dorsal vertebrae of ARG 510 and 511 are more similar to those of the Upper Permian moradisaurines *Kahneria* and *Rothianiscus* than they are to earlier smaller captorhinids. The neural arches are lower and broader relative to the centrum, the neural spines are lower and the zygapophyses are widely spaced and horizontal and suggest an attribution to a Moradisaurinae.

In recent studies on the interrelationships of captorhinids, the relationships of the basal genera have proved to be relatively uncontroversial, but the relationships of the Moradisaurinae (group 6 of Gaffney and McKenna 1979), have been neglected and are far from resolved. Until recently, it had been assumed that the multiple marginal tooth-rows represent a unique derived character-state within the Captorhinidae and that *Captorhinus aguti* is the primitive sister-group of all other multiple-rowed captorhinids (Gaffney and McKenna 1979; de Ricqlès and Taquet 1982; de Ricqlès 1984; Berman and Reisz 1986). Leaning on Olson's (1962) work, de Ricqlès (1984) proposed a cladogram depicting relationships of the moradisaurines. *Rothianiscus* (Olson and Beerbower 1953; Olson 1965) was linked to *Labidosaurikos* (Stovall 1950) on the basis of three character-states and together these two taxa were supposed to share one derived character-state (absence of pterygoidal teeth) with *Gecatogomphius* (Vjushkov and Chudinov 1957) and *Moradisaurus* (Taquet 1969; de Ricqlès and Taquet 1982). All the above cited genera formed an unresolved node with the other moradisaurines *Kahneria* (Olson 1962) and *Captorhinikos* (Olson 1954, 1970; Olson and Barghusen 1962).

The pterygoid is unknown in *Gecatogomphius*, and recent study has shown that small pterygoid teeth are present in *Labidosaurikos* (Dodick and Modesto 1995). Moreover, these authors have shown that *Labidosaurikos* is more closely related to the single tooth-rowed *Labidosaurus* than it is to other captorhinids, suggesting that the origin of multiple tooth-rows is diphyletic. The greatest

difficulty in studying the relationships of the Moradisaurinae lies in the fact that many taxa included in this clade are poorly known, from fragmentary material, and are distinguished from one another by their dentition or their size. All these taxa must be restudied before any phylogenetic analysis of the moradisaurines and other multiple-tooth-rowed captorhinids can be made. The Moroccan moradisaurines are too poorly preserved to be assigned confidently to an existing taxon or to be attributed to a new one and *Acrodonta* is considered as a Captorhinidae *incertae sedis*. Nevertheless, these taxa are important as indicators of the presence and the diversity of the Captorhinidiae in North Africa.

STRATIGRAPHY

All the material described here was found approximately 20 m above the diplocaulid-bearing level. However, such a difference is negligible because of the thickness of the level T2 in this region of the Argana Formation. The co-occurrence of these two taxa (diplocaulid nectrideans and a derived captorhinid) leads to two stratigraphical hypotheses.

1. Until now, it has been agreed that the upper part of the level T2 of the Argana Formation was Early Permian because of the presence of the diplocaulid nectridean (Dutuit 1976*c*, 1988; Milner 1993). This hypothesis is now weakened by two palaeontological records, namely the discovery by Olson (1972) of an Upper Permian diplocaulid, *Diplocaulus parvus*, and the discovery of the large derived captorhinids in level T2 (this study). Nevertheless, if we accept this hypothesis, the Moroccan captorhinids would be the earliest known non-North American captorhinids. Previously, the earliest record of a non-North American captorhinid was from the lower part of the Upper Permian (Ufimian, Ivachnenko 1990).

2. A scheme of the geographical and stratigraphical repartition of the captorhinids was given by de Ricqlès (1984, fig. 1). The captorhinids occur from the Lower Permian of North America (*Romeria*, Sakmarian, Texas; *Rhiodenticulatus*, Sakmarian, New Mexico; *Protocaptorhinus*, Upper Sakmarian–Lower Artinskian, Texas; *Labidosaurus*, Upper Artinskian, Texas; *Captorhinus*, Artinskian, Texas and Oklahoma; *Captorhinikos*, Kungurian, Texas and Oklahoma; *Labidosaurikos*, Kungurian, Texas and Oklahoma) to the Upper Permian (*Riabininus*, Ufimian, Tatarian, Zimbabwe; and a poorly known captorhinid from India). All the non-North American captorhinids are Late Permian (from the Ufimian to the Tatarian), the Gondwanan forms being the youngest (Upper Tatarian) (Vyushkov and Chudinov 1957; Kutty 1972; Gaffney and McKenna 1979; de Ricqlès and Taquet 1982; de Ricqlès 1984; Ivachnenko 1990). The character-states of the Moroccan captorhinids and the palaeogeographical distribution of this family rather suggest the Upper Permian. The upper part of level T2 could be correlated tentatively with the Chickasha Formation (Kazanian, Oklahoma) which yielded a large derived captorhinid (*Rothianiscus*, Olson and Barghusen 1962; Olson 1965) and a relatively small diplocaulid (Olson 1972), like level T2 of the Argana Formation. If we accept this hypothesis, *Diplocaulus minimus* is Late Permian (Kazanian) and the Moroccan captorhinid the earliest Gondwanan representative of the group.

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