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**GEOLOGY AND PALAEOBIOLOGY OF THE CENTRAL AND
SOUTHERN NAMIB**

**VOLUME 2:
PALAEOONTOLOGY OF THE ORANGE RIVER VALLEY,
NAMIBIA**

by

Martin Pickford and Brigitte Senut



Orangemeryx hendeyi

MEMOIR 19
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Director : Dr G I C Schneider

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NAMIBIA**

by

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Miocene Chelonians from southern Namibia

France de Lapparent de Broin

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Abundant remains of chelonians have been found at Auchas (Early Miocene) and Arrisdrift (basal Middle Miocene), two sites on the north bank of the Orange River, Namibia. Among the collection are several more or less complete carapaces which throw a great deal of light on these southern African Early Miocene tortoises and turtles and permit a systematic revision of the chelonians to be made. Two new genera are created for terrestrial tortoises. Freshwater turtles of the hyperfamily Pelomedusoides are represented by two genera, *Pelomedusa* and aff. *Erymnochelys*. At Arrisdrift, *Pelomedusa* is known by two fragments of hypoplastron which are typical of the genus. This record is important because until it was recognised at Arrisdrift, the earliest record of the genus was at Langebaanweg, South Africa (Early Pliocene). Aff. *Erymnochelys* is represented at Auchas and Arrisdrift by various pieces of xiphiplastron, hypoplastron, hyoplastron and pleurals which show derived characters of the Erymnochelyinae. Terrestrial tortoises of the family Testudinidae are represented by three taxa, *Namibchersus* (nov. gen.) *namaquensis*, *Mesochersus orangeus* (gen. and sp. nov.), and aff. *Psammobates-Homopus*. *Namibchersus* is represented by three almost complete carapaces and about 50 isolated pieces from Auchas (up to 82 cm carapace length) which are very close morphologically to the Elisabethfeld species described by Stromer as *?Testudo namaquensis*. New material from the latter site reveals that it belongs to a hitherto undescribed genus, *Namibchersus*, which is also present at Auchas. At Arrisdrift, a similar but not identical tortoise occurs, *Namibchersus* aff. *namaquensis*, based on several isolated pleurals, epiplastron, xiphiplastron, coracoid, humerus and tibia. Also from Arrisdrift is a second land tortoise (16-20 cm carapace length), *Mesochersus orangeus*, based on over 100 carapace and plastron fragments. Finally, there are four fragmentary specimens from Arrisdrift which indicate the presence of a third land tortoise at the site, aff. *Psammobates-Homopus*. The latter tortoise indicates that the presence of "small African endemics" in southern Africa, dates from at least the Early Miocene. The Auchas and Arrisdrift chelonians fill five distinct ecological niches, three of them terrestrial, one fully aquatic and one amphibious.

Version française abrégée

Les tortues fossiles du Tertiaire de Namibie étudiées ici proviennent de localités du Miocène inférieur de la région sud du pays: Arrisdrift (ca 17 Ma) et Auchas (ca 19 Ma) (Pickford *et al.*, 1995, 1996; Pickford & Senut, 2000; Senut & Pickford, 1995) (Tab. 1, S). Ces localités se situent à l'est d'Oranjemund, sur la rive droite de la rivière Orange formant frontière avec l'Afrique du Sud. Elles sont constituées de dépôts de terrasses, dans des boucles des méandres de la rivière Proto-Orange. Une partie du matériel d'Arrisdrift, récolté dans les années 1970 (Hendey, 1978), a déjà été étudiée (Meylan & Auffenberg, 1986). Le reste, ainsi que la plupart des spécimens provenant d'Auchas, a été récolté par l'équipe de B. Senut et M. Pickford (Expédition paléontologique de Namibie, 1991-2000). Le matériel d'Arrisdrift et d'Auchas est comparé avec les tortues fossiles précédemment connues et particulièrement les premières de Namibie à avoir été décrites, par Stromer (1926), en provenance de gisements (Elisabethfeld, Langental) situés dans la partie nord de la "Sperrgebiet", zone diamantifère de Namibie au sud de Lüderitz. Du matériel nouveau récolté dans ces mêmes sites par B. Senut et M. Pickford est mentionné et sera décrit par la suite. La liste des tortues fossiles de Namibie connues est donnée dans le Tab. 1. La présente étude comporte six taxons, avec deux genres de pleurodires d'eau douce (2 à Arrisdrift et 1 à Auchas) et trois genres de cryptodires terrestres (3 à Arrisdrift et 1 à Auchas).

Description Systématique

Chelonii Brongniart, 1800 (Latreille, 1800)
Pleurodira Cope 1864,
Pelomedusoides Cope, 1868
Pelomedusoidea Cope 1868,
Pelomedusidae, Cope 1868,
***Pelomedusa* Wagler, 1830**

Pelomedusa sp. est représenté à Arrisdrift (Pl. 1, Fig. 7) (partie médiale d'hypoplastron droit, éventuelle partie d'hypoplastron

gauche). Forme de tortue amphibie, semi-terrestre, semi-dulçaquicole, de petite taille (ca 14 cm de longueur de carapace) comparable aux petits représentants de l'actuelle *P. subrufa*, et appartenant à une nouvelle espèce qui sera définie par la suite sur la base de matériel plus complet que j'ai trouvé en 1998 à Langental (ca 19 Ma). La découverte de *Pelomedusa* au Miocène inférieur de Namibie est la plus ancienne du genre. Sa lignée est connue depuis au moins le Crétacé inférieur du Sahara. *Pelomedusa* est le groupe-frère plésiomorphe du genre *Pelusios* attesté depuis le Miocène inférieur de Napak, Ouganda, ca 19-20 Ma (Lapparent de Broin, 2000a).

Podocnemidoidea Cope, 1868,
Podocnemididae Cope, 1868,
Erymnochelyinae Broin, 1988a,
groupe *Erymnochelys* Baur, 1888

Aff. *Erymnochelys* sp. est représenté à Auchas (Pl. 1, figs 1-2) et Arrisdrift (Pl. 1, figs 3-6 et 8-9) par quelques pièces de carapace et plastron (mesures, Tab. 2). Grande forme dulçaquicole (carapace de ca 33 cm et plus), proche de l'actuelle *E. madagascariensis* par sa nucale mais moins dérivée par la position moins antérieure du sillon pectoroabdominal; le lobe postérieur est plus étroit (avec un étranglement fémoroanal marqué) que chez l'actuel et que chez les formes d'Erymnochelyinae d'Afrique suffisamment connues (Oligocène du Fayum à l'Actuel). La lignée Erymnochelyinae est connue depuis le Sénonien d'Ibeceten (Niger) (Lapparent de Broin, 2000a).

Cryptodira Cope, 1868

Testudinoidea Batsch, 1788,
Testudinidae Batsch, 1788,
Testudininei Batsch, 1788
***Namibchersus* nov. gen.**

Namibchersus n.g. *Namibchersus namaquensis* (Stromer, 1926) est représenté à Auchas par environ 65 spécimens dont trois carapaces (Figs 1-9, Pl. 2, Pl. 3 figs 5-6, Pl. 4, figs 10-13, Pl. 5, figs 16-18) et *Namibchersus* aff. *namaquensis* (Stromer,

1926) à Arrisdrift par environ 18 spécimens (Fig. 10): un nouveau genre est créé pour l'espèce de Stromer, d'Elisabethfeld, et un néotype semblable au spécimen-type (détruit pendant la guerre à Munich) est choisi parmi le nouveau matériel de la localité-type; le matériel d'Auchas lui est attribué. Le nouveau genre est une grande forme de tortue terrestre (carapace de 81.5 cm et plus), principalement décrite sur la base de l'espèce-type, avec: morphologie pygale-suprapygale du type dit (à tort) "*Geochelone*"; cervicale présente; petites pointes périphériques externes; coïncidence complète entre les sutures pleuropériphériques et les sillons costomarginaux; bourrelet cervicomarginal ventral long et à bord postérieur sinueux où non; protrusion gulaire modérée; bourrelet dorsal epiplastral élevé, atteignant où presque l'entoplastron, postérieurement élargi, avec une surface dorsale plate; axillaire en croissant; inguinale courte; pas d'étrécissement fémoroanal; recouvrement fémoroanal dorsal large sur le xiphiplastron; (autres caractères dans la version anglaise). La forme d'Arrisdrift diffère (dans la mesure où elle est connue) de l'espèce-type du genre par sa protrusion gulaire plus longue et légèrement plus étroite, ses gulaires ventralement plus courtes n'atteignant pas l'entoplastron et s'étrécissant dorsalement vers l'arrière au lieu de s'élargir.

Des mesures de comparaison générales de la carapace entre l'espèce *N. namaquensis* et les grandes espèces actuelles d'Afrique-Madagascar (Pl. 3, figs 1-4) sont données (Tab. 3). D'autres tableaux (Tab. 4 à 6) comparent les nouveaux genres fossiles de Namibie avec *Manouria impressa* d'Asie (considérée comme la plus primitive des formes actuelles de Testudininei terrestres), *Geochelone elegans* de Sri Lanka, espèce-type du genre, *Gigantochersina ammon* de l'Oligocène du Fayoum (le plus ancien Testudininei nommé d'Afrique) et les principaux taxons Africains actuels de Testudininei. Notamment les tableaux 5-6 permettent de comparer le stade évolutif des principaux caractères conservés sur la carapace des fossiles de Namibie. Ces caractères, ainsi que d'autres donnés dans le texte (telle la coïncidence entre sillons et sutures à la limite du disque pleural) montrent que *N. namaquensis* n. g. est morphologiquement le plus proche de l'actuel *Astrochelys* de Madagascar et a un grade évolutif plus proche de celui d'*A. yniphora* (plus évolué) que de celui d'*A. radiata*. Ces caractères se distribuent en mosaïque et, s'ils permettent de différencier les taxons, ils sont insuffisants pour définir les vraies relations parentales entre les divers taxons, en l'absence du crâne, des vertébrés, des os des membres des fossiles et de données non fossilisables. Toutefois certains donnent de claires indications sur les relations phylogénétiques possibles. La radiation de *Namibchersus* n.g. s'est faite avant la différenciation des grandes formes actuelles *Centrochelys* et *Stigmochelys*, et indépendamment de celle des petits à moyens endémiques africains incluant *Mesochersus* n. g. Son origine s'est produite le plus probablement grâce à une première vague d'immigrants qui a pu comprendre *Gigantochersina* (Oligocène basal) et ces petites à moyennes formes et sans relation avec la où les vagues qui ont apporté ensuite (Miocène inférieur) les lignées de *Centrochelys* et *Stigmochelys*. Une relation phylétique proche avec *Astrochelys* semble possible.

Mesochersus n. g. *Mesochersus orangeus* n. sp. est représenté à Arrisdrift par environ 150 éléments isolés de carapaces et d'os des membres (Fig. 11; Pl. 4, figs 1-9; Pl.

5, figs 1-15; Pl. 6, figs 1-7, 12). Plutôt petite forme de tortue terrestre (carapace de 16-20 cm); morphologie pygale-suprapygale de type "petits endémiques Africains" (incluant les actuels *Chersina*, *Kinixys* et le groupe *Psammobates-Homopus*, particulièrement présent en Afrique du Sud-Namibie, *Malacochersus* d'Afrique de l'Est et *Pyxis* de Madagascar), à pygale relativement large pour sa longueur avec une petite encoche antérieure suprapygale et extension de la vertébrale 5 sur la périphérique 11; coïncidence entre les sutures pleuropériphériques et les sillons costomarginaux excepté sur la périphérique 11 où se termine la vertébrale 5; nucale légèrement concave ventralement; cervicale présente; pointes externes périphériques présentes où absentes; bourrelet cervicomarginal ventral court et à bord postérieur rectiligne; bords latéraux du lobe antérieur nettement convergents vers l'avant; protrusion gulaire réduite; bourrelet epiplastral dorsal relativement élevé, en avant de l'entoplastron, s'étrécissant vers l'arrière, avec une surface dorsale légèrement convexe; pas d'axillaire où d'inguinale; lobe postérieur large antérieurement; pas d'étrécissement fémoroanal (ou rare?); large rebord dorsal fémoroanal sur le xiphiplastron; (autres caractères dans la version anglaise). A côté des caractères morphologiques distinguant le taxon, "*Mesochersus* n. g. diffère de *Namibchersus* n. g. par sa morphologie pygale-suprapygale qui indique clairement une relation privilégiée avec les petits endémiques africains; il partage aussi avec eux sa petite taille; l'absence d'inguinale peut aussi être mise en relation avec sa fréquente réduction chez ces derniers. Il a toutefois des caractères primitifs, comme chez *Namibchersus* n. g. où chez l'un où l'autre des petits endémiques, mais il n'est engagé dans aucune lignée particulière de ceux-ci en Afrique où à Madagascar.

Aff. *Psammobates-Homopus* est représenté à Arrisdrift au moins par 4 périphériques (Pl. 6, figs 8-11). Forme terrestre de taille moyenne (ca 30 cm de longueur), appartenant au groupe des petits endémiques africains par le recouvrement: 1) des périphériques antérieures et postérieures par les costales, et 2) de la périphérique 11 par la vertébrale 5. Elle appartient probablement au groupe *Psammobates-Homopus* par la forme large et courte des périphériques, tandis que celles-ci sont étroites et hautes chez *Mesochersus* n. g., *Namibchersus* n. g. et les autres endémiques africains.

Conclusion: Considérations paléocologiques et paléobiogéographiques

Les cinq genres de chéloniens présents à Arrisdrift et Auchas représentent cinq niches écologiques distinctes: trois niches terrestres d'herbivores en fonction de la taille des formes (petite, moyenne, grande) mais qui peuvent se recouper suivant l'âge; deux dulçaquicoles, l'une grande et bien aquatique (aff. *Erymnochelys*, l'actuel étant omnivore, principalement herbivore; Kuchling, 1988, 1993) et une petite plus amphibie (*Pelomedusa*, principalement carnivore). Leur capacité d'adaptation leur a permis de subsister au cours des temps géologiques au fur et à mesure de la détérioration du climat: sécheresse et refroidissement (hivernal où nocturne) compensé par un fort ensoleillement alterne.

Les pleurodires aff. *Erymnochelys* et *Pelomedusa* peuvent avoir été présents en Namibie où proximité longtemps avant le Miocène inférieur, date de leur première attestation, car leurs

lignées sont connues depuis le Crétacé inférieur d'Afrique. Les tortues terrestres ont pu être présentes depuis l'Oligocène, époque de leur première attestation d'arrivée en Afrique, avec *Gigantochersina*, en provenance d'Eurasie, et leur morphologie montre que les formes namibiennes du Miocène inférieur sont primitives par rapport aux actuelles. L'absence au Miocène inférieur de Namibie de taxons déjà présents au nord et à l'est de l'Afrique ne s'explique pas par une mutuelle exclusion: *Erymnochelys*, *Pelusios* et *Pelomedusa* sont souvent associés dans les eaux actuelles de Madagascar, où bien les deux premiers et les Trionychoidea (Cyclanorbiinae et Carettochelyidae) au Mio-Pléistocène d'Afrique de l'Est. L'absence en Namibie de *Pelusios* et *Kinixys*, présents ensemble bien au nord en Afrique de l'Est (Ouganda, Kenya) au Miocène inférieur, peut s'expliquer par le fait que leur différenciation dans ces pays à partir de lignées déjà présentes en Afrique (respectivement *Pelomedusa* et *Gigantochersina*) était encore trop récente pour leur avoir donné le temps d'arriver en Namibie à l'époque des dépôts étudiés ici. Mais il faut bien comprendre que les Trionychoidea et *Pelusios* n'ont jamais atteint l'extrémité sud de l'Afrique: c'est probablement dû à l'absence d'un réseau fluvial organisé - ils n'ont pas pu traverser les barrières terrestres entre les rivières orientales, les grands lacs et le Zambèze d'une part, et la rivière Orange et ses tributaires d'autre part. Ils n'ont pas non plus pu passer par l'océan entre les embouchures des rivières, à cause des courants marins dirigés vers le nord. Parmi les grandes formes de tortues terrestres des lignées de *Stigmochelys* et *Centrochelys*, probablement arrivées au Miocène inférieur en même temps que les Trionychoidea, seul *Stigmochelys* a atteint le sud où il a remplacé *Namibchersus* n. g., dont la cause d'extinction reste inconnue. Le groupe *Erymnochelys* a disparu d'Afrique durant le Pliocène, également pour une raison non connue (destruction de sa nourriture due à un changement climatique? Sécheresse excessive?), de même que les Carettochelyidae (pour la même ou pour une différente raison?). *Mesochersus* n. g. a été remplacé par des formes de son groupe *Psammobates-Homopus* tandis que *Kinixys* reste exclu.

Introduction

Location and age of localities

The fossil tortoises from the Tertiary of Namibia came from sites (Table 1) located in the southwest of the country in the diamond-bearing region between the latitudes of Lüderitz and Oranjemund. Some of the fossil localities (Table 1, SW areas) are in fluvial deposits in the coastal strip south of Lüderitz, while others are in aeolianites of Southern Namibia which are slightly younger. Others are located in the south (Table 1, S areas) on the right bank of the Orange River, which is the frontier with South Africa, east of Oranjemund. The latter represent terrace deposits of the proto-Orange, which accumulated in fossil meanders of the ancient river.

All the Namibian chelonian localities in the west and the south (Table 1) have been dated as Miocene, between ca 8 and 20 Ma (Pickford *et al.*, 1996; Pickford *et al.*, 1995; Senut & Pickford, 1995).

Extent of the study

Only the material from the southern localities of Arrisdrift

and Auchas (Table 1, S areas) are considered in this paper. It yields interesting new information.

Stromer (1926) was the first to study fossil tortoises from Namibia, comprising specimens from the northern part of the diamond area south of Lüderitz. His new species *?Testudo namaquensis* Stromer, (1926, Fig. 21) was created on the basis of a plastron from Elisabethfeld about 24 cm long, accompanied by diverse fragments of carapace of various sizes which he attributed either to this species or to the subfamily, and a femur of a "giant terrestrial tortoise". He mentioned a fragment of carapace from Langental, further south along the coast which he compared to his new species but which he left indeterminate within the Testudininae because there were no parts in common. Stromer's material was destroyed in Munich during the war.

New material from the type locality, Elisabethfeld, has been collected by B. Senut and M. Pickford and their team: It contains, among other specimens in preparation, a carapace with plastron EF x' 2000, identical to the lost holotype of the species *?T. namaquensis*, Stromer, 1926. It is here selected as the neotype of the species and it will be studied in detail with the rest of the sample from the northern sites (second monograph on Namibian tortoises). The material from Auchas, in the south of the country, attributed to the species *namaquensis*, is described under the new generic name *Namibchersus*. There is also an Erymnochelyinae.

At Arrisdrift, the team of B. Senut and M. Pickford extended the preliminary excavations of Hendey, (1978) and found additional chelonian fossils complementary to the sample described by Meylan & Auffenberg (1986). The latter authors studied the specimens mentioned by Hendey (1978) which used to be stored at the South African Museum, Cape Town (SAM), as part of a general revision of African Miocene terrestrial tortoises. This collection, together with unpublished pleurodires from Arrisdrift, was transferred to the Geological Survey of Namibia, Windhoek (MSGN) where I studied it and the new material collected by the "Namibia Palaeontology Expedition" at all the sites mentioned in Table 1. It is described in detail below and comprises a large species of *Namibchersus* nov. gen., and two small species of terrestrial tortoises, as well as *Pelomedusa* sp., and the same genus of Erymnochelyinae as that from Auchas.

Material from other localities has also been recovered by these two researchers (Tab. 1) notably samples from Langental comprising the most complete remains of the oldest known undoubted species of *Pelomedusa* from Africa. Unpublished fossil tortoises in the American Museum of Natural History were collected from Langental during the 1930s and I was able to study them in New York. It consists of an undetermined species of *Namibchersus* nov. gen. All this material will be studied in future.

For general information about extant taxa and their synonymy reference is made to Bour (1980), Loveridge & Williams (1957), Wermuth & Mertens (1961, 1977), Williams (1952) (among others) and for geographic distribution, to Iverson (1992).

Abbreviations

BM (NH) - Natural History Museum, London, UK.

MNHN - Muséum national d'histoire naturelle, Paris, France;
AC, Anatomie Comparée; H, Zoologie des reptiles et amphibiens, P, Paléontologie.

Table 1. Distribution of chelonians from Namibia; eol, eolianite deposits; fluv., fluvial deposits. N, North, SW, South-western area; S, Southern area (proto-Orange).

Namibia	Age	Area	Locality	Pleurodira	Cryptodira, Testudinidae, Testudinini	
Extant Fauna	Extant				African Endemics: <i>Chersina angulata</i> <i>Homopus</i> sp. "bergeri", ? <i>H. signatus</i> , <i>H. sp.</i> <i>Psammobates signatus</i> , <i>P. oculiferus</i> , <i>P. tentorius</i> , <i>P. sp.</i>	<i>Stigmochelys pardalis</i>
	Historical Site 1600 - 1750	N	Brandberg			<i>Stigmochelys pardalis</i>
Middle Miocene	ca 8 Ma, D. laini level	SW eol.	Rooilepel		<i>Namibchersus</i> n.g., sp.	
	ca 10-12 Ma, D. wardi level	SW eol.	Rooilepel		<i>Namibchersus</i> n.g., sp.	
	ca 10-12 Ma, D. wardi level	SW eol.	Karingarab		<i>Namibchersus</i> n.g., sp.	
	ca 10-14 Ma, D. wardi level	SW eol.	North of Gyp- sum Plate Pan		<i>Namibchersus</i> n.g., sp.	
Lower Miocene	ca 17- 17,5 Ma	S fluv.	Arrisdrift	Aff. <i>Erymnochelys</i> sp. <i>Pelomedusa</i> sp.	<i>Namibchersus</i> n.g. aff. <i>namaquensis</i>	<i>Mesochersus</i> <i>orangeus</i> n.g. n.sp. Aff. <i>Psammobates</i> - <i>Homopus</i> sp.
	ca 18 Ma	S fluv.	Auchas	Aff. <i>Erymnochelys</i> sp.	<i>Namibchersus</i> n.g. <i>namaquensis</i>	
	ca 19 Ma	SW fluv.	Glastal		<i>Namibchersus</i> n.g., sp.	
	ca 19 Ma	SW fluv.	Langental	<i>Pelomedusa</i> sp.	<i>Namibchersus</i> n.g., sp.	Aff. <i>Psammobates</i> - <i>Homopus</i> sp.
	ca 19-20 Ma	SW fluv.	Fiskus		<i>Namibchersus</i> n.g., sp.	
	ca 19-20 Ma	SW fluv.	Grillental		<i>Namibchersus</i> cf. <i>namaquensis</i>	
	ca 19-20 Ma	SW fluv.	Elisabethfeld		<i>Namibchersus</i> <i>namaquensis</i> (Stromer, 1926)	

MSGN - Museum of the Geological Survey of Namibia, Windhoek.

NHMW - Naturhistorisches Museum Wien, Austria.

NMK - National Museums of Kenya, Zoology, Nairobi.

OMS - Sperrgebiet Museum, Oranjemund, Namibia.

SAM - South African Museum, Cape Town, South Africa.

Systematic Descriptions

Ordo Chelonii Bronngniart, 1800 (Latreille, 1800)

Infraordo Pleurodira Cope, 1864

Hyperfamilia Pelomedusoides Cope, 1868

Introduction: Pelomedusids are aquatic, more or less amphibious. The texture of the external surface of the plates

of the carapace-plastron is smooth but with the naked eye one can generally observe small vascular dichotomising networks, especially on the dorsal carapace and the bridges, as in all aquatic forms, which don't occur in purely terrestrial forms, and are less visible in *Pelomedusa*, which is more terrestrial with denser bone. These networks are not visible in all the specimens figured herein, most of them having more or less eroded surfaces. Under the binocular microscope the microreticulation which occurs in the surface of the plates of all continental tortoises is visible. This microreticulation is large with sharp crests and rounded summits in the *Erymnochelyinae* from Auchas and extant *Erymnochelys madagascariensis* (not seen in the Arrisdrift specimens). The crests are finer and straighter in the plastron of extant *Pelomedusa subrufa* and *Pelomedusa* sp. from Langental (not seen at Au-

chas). The crests are wide as in *Erymnochelys* 'but are less closed, more or less distinct with rounded or flat summits, straight and above all punctuated in several specimens of terrestrial Testudinidae observed at Arrisdrift, Elisabethfeld and Langental, generally straight and punctuated in extant forms. Comparative material is in the MNHN (AC, H, P).

Superfamilia Pelomedusoidea Cope, 1868

Familia Pelomedusidae Cope, 1868

Genus *Pelomedusa* Wagler, 1830

***Pelomedusa* sp.**

Locality: Arrisdrift. Fossil meander of the proto-Orange, southern Namibia. Early Miocene, ca 17 Ma. (Hendey, 1978, Pickford *et al.*, 1996).

Material: MSGN. AD 475'98. Medial part of right hypoplastron (Pl. 1, Fig. 7).

Specimen AD 287'97 is probably also a fragment of left hypoplastron of *Pelomedusa*.

Description and comparison: AD 475'98: medial part of a hypoplastron. The lateral part of the bridge with the notch of the mesoplastron and the inguinal process are lacking.

Dimensions (cm): median length, 2.9; width at the femoro-anal sulcus: 2.6; anterior thickness: 0.6 cm. The specimen is small and thin, with a smooth surface (slightly irregular) and the bone is dense, well ossified right up to the edge of the sutures, indicating that it was an adult. The sulcus for the scutes is narrow and sinuous: It does not belong to a young terrestrial testudinid (see below). The rear dorsal border shows a strong spur near the external side of the hypo-xiphial suture. Immediately to the external side of the spur, the dorsal margin of the sulcus for the femoral scute is very narrow and its surface is rounded into a small ridge: these characters and the small size of the specimen are typical of *Pelomedusa*, a genus of small pelomedusid pleurodire which is widespread in Africa at present including Namibia (Iverson, 1992). The absence of any fontanelle in the medio-anterior corner (central plastral fontanelle) which persists for a long time even in extant adults, but is variably developed in different individuals, indicates that it was fully adult. A preliminary study of the measurements of the width of the femoro-anal sulcus compared with the median length in six extant specimens of *Pelomedusa* without their scutes (coll. MNHN, H, P), from diverse localities (Omo, Niger, Madagascar, two others without provenience), shows that the ratio of one on the other varies from 81.66% to 103.34% in the extant forms. The Arrisdrift specimen being 89.65% falls between a young male from Madagascar plus a juvenile of unknown locality and a series comprising an adult female, a juvenile, an adult male and a young male. This parameter does not seem to yield *a priori* any particular indication, although the very low figure for the Arrisdrift specimen could be due to a taxonomic factor independent of sex, by comparison with another specimen from the Early Miocene of Langental. In *Pelomedusa*, the male has a concave plastron in the central part and a narrower posterior lobe than in the female. The parameter showing the narrowing due to sex would be that of width at the abdomino-femoral sulcus or immediately behind it, where the hypoplas-

tron is narrowest, on the length of the entire plastron (the females retaining the greater percentage which is present in the juveniles). When the hypoplastron is complete, the stronger narrowing of the posterior lobe behind the femoro-anal sulcus is more evident in the male, but in this case the specimen is broken laterally just in front of the sulcus. The fragment does not show the incurving towards the middle, but the posterior lobe does not always show this in males, differing from the median hyo-hypoplastral part. It is thus not possible to determine the sex of the specimen.

AD 475'98 belongs to a species or variety of *Pelomedusa* in which the plastron was probably relatively narrow and of small size: the adult carapace was only about 14 cm long, as in extant specimens of *P. subrufa* (Lacépède, 1788) compared above (MNHN, H, P), and differs from the extant variety of the Cape which has a distinctly larger carapace. It is impossible to determine the species on this specimen alone. The genus *Pelomedusa* has already been reported from the Early Miocene of Langental (Namibia) (Lapparent de Broin, 2000a). These remains will be described in a forthcoming paper. They may represent a new species in which it will be possible to include the Arrisdrift specimen (of which no hint was known at the time that the above note was prepared).

The originality of this discovery is stressed. Up to now, *Pelomedusa* was doubtfully known in the fossil state in the Pliocene of Langebaanweg, South Africa, aged 4-4.5 Ma, and with certainty in the Plio-Pleistocene of Taungs, South Africa, about 2-2.5 Ma, in the Holocene of Ti-n Hanakaten, Algeria, about 7000 BP, and the Holocene of El Kadada, Nile Valley, Sudan, about 4800 BP, and in the Late Holocene of Haaskraal, South Africa. *Pelomedusa* is the plesiomorphic sister group of the genus *Pelusios* which is known from the Early Miocene with *P. rusingae* Williams, 1954a, Rusinga Island, Lake Victoria, Kenya, about 18 Ma and by *Pelusios* sp. of the Early Miocene of Napak, Uganda aged 19-20 Ma. *Pelusios* was also found in numerous other localities in Africa throughout the Neogene until the present (Lapparent de Broin, 2000a). *Pelomedusa* surely represents the most ancient African taxon still present at the generic and family level, the Pelomedusidae, and it still occurs in Namibia. The family has existed since the Late Aptian of Niger (at Gadoufaoua) and the absence of remains of early Tertiary age is due in part to the absence of continental fossil deposits. The only known Palaeogene localities are the Palaeocene ones of Morocco (poor in tortoise remains) which yielded an indeterminate form related to *Pelomedusa* (Gmira, 1995, material lost) and the Late Eocene-Early Oligocene localities of the Fayum (Egypt) and Oman, where the genus is not present in contrast to Podocnemididae which are. In the Mio-Pliocene, continental localities are abundant but the genus is still not known, as opposed to other Pelomedusoides, *Pelusios* or Podocnemididae (Lapparent de Broin, 2000a). Wood (1973) suggested that this absence of *Pelomedusa* in Mio-Pliocene localities may have been due to ecological reasons, taking into account the semi-terrestrial life of the genus. It is also possible that difficulty in recognising fragmentary remains of this fragile form has led to their being uncollected, or even if collected then they may have been confused with other taxa or have remained unidentified because of their fragmentary nature.

Superfamilia Podocnemidoidea Cope, 1868
Familia Podocnemididae Cope, 1868
Subfamilia Erymnochelyinae Broin, 1988a
Group Erymnochelys Baur, 1888
Aff. Erymnochelys sp.

Locality and age:

A. Auchas. Fossil meander of the proto-Orange River, Southern Namibia. Early Miocene, ca 18 Ma (Pickford *et al.*, 1995).

Material: MSGN. AM 11' 97, left hyoplastron fragment (Pl. 1, Fig. 1); AM 6' 97, right xiphiplastron (Pl. 1, Fig. 2).

B. Arrisdrift. Fossil meander of the proto-Orange River, Southern Namibia. Early Miocene, ca 17-17.5 Ma. (Hendey, 1978; Pickford *et al.*, 1996)

Material: MSGN. Old collections. PQ AD 1983, fragment of right xiphiplastron with part of the suture of the ischion; PQ AD 2078, medial part of a left hypoplastron and partial left xiphiplastron, (Pl. 1, Fig. 8); PQ AD 2096, left hyoplastron (Pl. 1, Fig. 9); PQ AD 2113 (Pl. 1, Fig. 5), fragment of even pleural; PQ AD 2115, nuchal (Pl. 1, Fig. 3); PQ AD xl and x2 fragments of odd and even pleurals (Pl. 1, Fig. 4 and 6).

Description and comparison: The portions of the posterior plastral lobe preserved in the Arrisdrift xiphiplastron PQ AD 1983 and the hypo-xiphiplastron PQ AD 2078 (Pl. 1, Fig. 8) and in the Auchas xiphiplastron AM 6'97 (Pl. 1, Fig. 2) are pleurodires by the presence of the pubic suture (obliquely elongated oval) and the ischion (medially extended triangle) on the dorsal surface of the xiphiplastra: the pelvis sutured to the carapace is a derived character of the infraorder Pleurodira.

Hyoplastra from Arrisdrift (PQ AD 2096, Pl. 1, Fig. C) and Auchas (AM 11' 97, Pl. 1, Fig. 1).

Dimensions (cm): Hyoplastron from Arrisdrift: maximum length and breadth: 11.4 x 11; width at the base of the auxiliary notch: 7.9; length and width of the postero-lateral notch for the mesoplastron which forms a quarter of a circle: 2.7 x 2.7. Hyoplastron from Auchas: width at the base of the auxiliary notch: 7 cm.

The Arrisdrift hyoplastron which is complete and quite large, possesses laterally at the rear the suture with the mesoplastron which was rounded laterally, about as long as large and located between hyo- and hypoplastron and two peripherals of the bridge. The rounded lateral mesoplastra are present from the beginning in the two extant families of pleurodires, Pelomedusidae and Podocnemididae (character of the Pelomedusoides); but in the pelomedusid genus *Pelusios*, they are resorbed into the hyoplastron and a suture forming a hinge cuts the hyoplastron behind the auxiliary notches, permitting the anterior part to fold (box turtle); in *Pelomedusa*, they are a little wider than long. These genera are thus distinguished by this feature of the mesoplastra and also by others present in the erymnochelyines. They are well represented from the Eocene onwards (and even from the Late Cretaceous with more archaic forms) in Africa (Lapparent de Broin, 2000a) notably by the *Erymnochelys* group, and at present are found only in Madagascar with *E. madagascariensis* (Grandidier, 1867).

There is no trace of the humero-pectoral sulcus traversing the Arrisdrift hyoplastra (Pl. 1, Fig. 9) and those from Auchas (Pl. 1, Fig. 1) behind the entoplastron or behind the epi-hyoplastral suture, across the hyoplastron and entoplastron. It is the mark of an evolved character acquired by the erymnochelyine podocnemidids: the humero-pectoral sulcus located in front of this epi-hyoplastral suture (humeral shortened at the expense of the pectorals) and, because of this not present here on the two hyoplastra (Broin, 1977; Lapparent de Broin, 2000). In *Pelomedusa* and *Pelusios*, the humero-pectoral sulcus, entirely on the hyoplastron, is primitively posterior to this suture, and is either always clearly posterior to the entoplastron (*Pelomedusa*), or posterior to the entoplastron or contacts it behind (*Pelusios*). The pectoro-abdominal sulcus, visible in the Arrisdrift specimen, secondarily is relatively separated a little bit medially from the hyo-hyoplastral suture, a bit less separated than in known erymnochelyines but clearly more than in *Pelomedusa*; it advances laterally before retreating completely laterally to cut the mesoplastron obliquely, more medially than in the known erymnochelyines. In *Pelomedusa* in which it is not advanced (longer pectorals) it cuts the mesoplastron transversely. The fragments of left hyoplastra from Arrisdrift and Auchas belonged to anterior plastrallobes which were wide at the base with an auxiliary notch that is wider and more open than in *Pelusios* and *Pelomedusa*, the lobe narrowing more towards the front as in most of the known Oligocene to Recent erymnochelyines, in a particularly concave curve, whereas the lobe has more rounded margins in the Pelomedusidae and several Erymnochelyinae. The Arrisdrift hyoplastron is almost the same size as that of the extant *Erymnochelys* such as specimen MNHN H, DD 67: 12.6 cm long, for a plastron of 33 cm and a carapace of 36 cm length.

Portions of posterior lobes of plastra (Tab. 2).

Part of the posterior lobe from Arrisdrift, PQ AD 2078, is very eroded and incomplete medially at the hypoplastron and laterally at the xiphiplastron. Its anterior margin corresponds to the placement of the abdomino-femoral sulcus. When reconstructed it appears to be relatively narrower than the specimen from Auchas, AM 6'97. The Arrisdrift fragment, PQ AD 1983, a right xiphiplastron with part of the suture for the ischion, is similar to the other specimen from Arrisdrift, but is smaller (lateral length of the suture of the ischion: 0.7 cm for 1.2 cm). Both are slim. The Auchas specimen is larger and thicker.

The dimensions of the fossil specimens are close to extant specimens of *Erymnochelys*. They represent large animals with plastra that would have been as large as, or larger than 33 cm long, the posterior lobes are neither enlarged, nor clearly rounded laterally and with a large suture for the ischion. The right xiphiplastron from Auchas and the part of the left posterior lobe from Arrisdrift are similar in their relative elongation to extant *Erymnochelys*, but the Arrisdrift lobe is narrower or relatively longer than that from Auchas. Complete carapaces would be necessary to determine the precise differences from the extant form, but it is possible to say that the posterior lobes of the two fossils were relatively longer and narrower right from the base and thicker at the point than in extant *Erymnochelys*. There is a more marked femoro-anal narrowing and the lateral borders of the xiphiplastra are parallel beneath the anals, whereas in *Erymnochelys* the lateral borders of the xiphiplastra converge towards the rear. The

Table 2. Comparative measurements of the posterior lobes of Erymnochelyinae from Arrisdrift, PQ AD 2078, Auchas, AM 6'97 and extant *Erymnochelys* from Madagascar, MNHN H, DD 67 (Pl. 1, fig. 8, 2 and 10).

Measurements in cm	PQ AD 2078	AM 6'97	MNHN H, DD 67
1) posterior lobe full length: hypoplastron, from the abdomino-femoral sulcus, and xiphiplastron	6	?	12.8
2) xiphiplastral length	7.3	9.2	8.5
3) xiphiplastral anterior width	4.6	5.5	6
4) width at the femoro-anal sulcus	3.3	4.7	5.4
% 4) / 3)	71.73	85.45	90
% 3) / 2)	45.2	59.78	70.58
5) thickness between pelvic sutures	not measured: thin	0.7	1
6) thickness at the xiphiplastral extremity	not measured: thick	0.8	0.4

dorsal margin of the anal scute is narrow laterally, moderately wide at the point on the edge and thinned in the anal notch as in *Erymnochelys*, but is relatively wider towards the point which is also thicker (preserved on the Auchas specimen).

In *Pelomedusa* the femoro-anal dorsal border bends upwards into a rounded ridge anteriorly (Pl. 1, Fig. 7b) and is narrow throughout, being barely enlarged at the anal point; in *Pelusios* the dorsal margin is often enlarged with the posterior lobe. Nevertheless, in extant *Pelusios gabonensis* (also known in the fossil state in the Pliocene of Afar, Ethiopia: Lapparent de Broin, 2000a), the xiphiplastron, with a relatively straight margin, not rounded laterally, resembles that of the Arrisdrift and Auchas pleurodire; but the dorsal border of the anal scute is wider and the sutures of the pubis and ischion are smaller; that of the pubis is more rounded and that of the ischion is less extended medially, not reaching the medial line. The sutures of the ischion and pubis of the two Namibian fossils which are more important than those of Pelomedusidae, are similar to those of *Erymnochelys*, as is the open and rounded V-shape of the anal notch, but this is not characteristic (individually variable to a certain extent).

The Arrisdrift nuchal (PQ AD 2115, Pl. 1, Fig. 3).

Dimensions (cm) compared to those of the *Erymnochelys* specimen: length on breadth, 6 x 6.2 cm; (5.1 x 5.6 cm in the specimen of *Erymnochelys*); thickness anteriorly and at the middle maximal part: 0.46 and 0.83 (3.3 and 6.6 for the specimen of *Erymnochelys*).

There is no cervical scute (character of Pelomedusoides). The nuchal resembles that of *Erymnochelys*, somewhat wider than long, and relatively great in length. This relative length is nevertheless less than that of *Pelomedusa* and *Pelusios* in which the anterior part of the carapace is secondarily more elongated than in Podocnemididae: in which the nuchal is clearly longer than the width and also longer in relation to the carapace. In the Arrisdrift nuchal as in *Erymnochelys*, there are fine striations in front of vertebral 1. The dorsal border of the marginals is a bit longer than in *Erymnochelys madagascariensis* (specifically variable character). As in this species, there is a small notch behind the two marginals 1 which extend laterally, being

more pronounced in the Arrisdrift nuchal than in extant *Erymnochelys*. This notch is variably present individually in *Pelusios* and in *Pelomedusa*. The ventral margin of marginals 1 is very short, as in *Erymnochelys* and *Pelomedusa*; it is longer in *Pelusios* (specifically variable). The important character of the nuchal is thus its relative width and its moderate length which aligns it with *Erymnochelys*.

Remains of pleurals: PQ AD2113 (Pl. 1, Fig. 5), fragment of even pleural, PQ AD xl (Pl. 1, Fig. 4) and PQ AD x2 (Pl. 1, Fig. 6), fragments of odd and even pleurals.

Dimensions (cm) of PQ AD xl and x2: length (from front to back): 3.1 and 2.2; thickness: 0.4 and 0.34.

The fragments have the texture and the fine and sinuous sulci which distance them from terrestrial tortoises (see below) and are similar to those of a podocnemidid of the size of the specimens represented by the other plates. These pleurals are too long and the bone is not dense enough to belong to *Pelomedusa* sp., which is also present in the Early Miocene of Namibia, notably at Arrisdrift (see above). Apart from these pleural fragments, all the other pieces studied above possess derived characters of Erymnochelyinae. They are not enough on their own to define a new genus to which they probably all belong, in view of the similarities of the hyoplastra and xiphiplastron from Arrisdrift and Auchas. The epiplastron is lacking, which would have the character of the gular-intergular schema of the *Erymnochelys* group: short intergular enclosed by the linked gulars behind.

Because of their great morphological differences the two forms of Erymnochelyinae present in the Eocene to Pliocene of Egypt and Arabia, *Stereogenys* Andrews 1901, and *Schweboemys* Swinton 1939 (Andrews, 1906; Lapparent de Broin, 2000a; Lapparent de Broin, 2000) are eliminated from consideration. *Kenyemys* Wood, 1983, of the Late Miocene of Lothagam 1, Kenya, an erymnochelyine of the *Erymnochelys* group because of its short intergular enclosed by the gulars, differs from the Namibian form by its narrow vertebral 1 which does not cover all the nuchal, the anterior lobe with parallel lateral margins and the rounded posterior lobe. Forms close to *Erymnochelys* from the Oligocene of the Fayum, of the, same group,

such as *Dacquémys fajumensis* (Andrews, 1903) (Dacqué, 1912; Reinach, 1903; Williams, 1954a, 1954b) and the Early Miocene of Moghara such as aff. *Erymnochelys aegyptiaca* (Andrews, 1900) could both be close to the Namibian one by the inclination of the lateral margin of the anterior lobe which could be identical to that of the Arrisdrift specimen in certain specimens of the former (Reinach, 1903, Pl. 1X Fig. 2; Dacqué, 1912, Text Fig. 11) and the specimen of the latter (Andrews, 1900, Pl. 1, Fig. 2), but in this one, the pectoro-abdominal sulcus is more advanced medially and laterally and the posterior lobe has a shorter, wider xiphiplastron (converging margins) as in *Erymnochelys* (cf. Andrews, 1906, Fig. 94; 1900, Pl. 1, Fig. 2; Dacqué, 1912, Pl. 1). For the same reasons, the Miocene specimens from Namibia resemble and differ from the indeterminate form represented by the carapaces from Lothagam 1 and 3 and from Kanapoi, Mio-Pliocene of Kenya (aff. *Erymnochelys* sp. A, meaning “*Podocnemis* sp. A” of Patterson *et al.*, 1970; Lapparent de Broin, 2000a). In addition, in this form, the nuchal is very wide (not preserved in the Egyptian forms close to *Erymnochelys*). But, if the Namibian fragments don't belong to the fossil forms or *Erymnochelys madagascariensis* it must be a new form of the same group of species.

In conclusion, the form was a pleurodire by the sutures of its pubis and ischion to the plastron, an erymnochelyine by the shape of its mesoplastron and the sutures of the pelvic bones and by the hyoplastron with convergent slightly concave lateral margins which are not cut by the humeropectoral sulcus which is advanced. It is close to *Erymnochelys* by the nuchal, but new by the moderately advanced pectoro-abdominal sulcus and the narrow xiphiplastra with narrowed latero-posterior borders and less convergent beneath the anals than in other Erymnochelyinae. It is possible that the Arrisdrift species was different from that from Auchas in view of the greater narrowness and the thinness of the posterior lobe in the former compared with the latter, the thinness equalling that of the xiphiplastron of *Erymnochelys*. In contrast, the Arrisdrift nuchal is thick relative to that of *Erymnochelys*.

Infraordo Cryptodira Cope, 1868
Superfamilia Testudinoidea Batsch, 1788
Familia Testudinidae Batsch, 1788
Infrafamilia Testudininei Batsch, 1788

Introduction

All the terrestrial Testudinidae examined differ from freshwater pleurodires by the surface texture of their bones which are smooth and dense. With the naked eye it is possible to discern the small points and narrow grooves (Pl. III, figs. 1-4) and not the fine dichotomising sulci that occur in freshwater chelonians. Under high power binocular microscope and Scanning Electron Microscope, all tortoises (terrestrial and freshwater) show microreticulation which varies in sinuosity and relief depending on the taxon, but it is always very punctuated (see introduction to Pelomedusoides above).

The diagnostic features are assembled in Tables 3 to 6 and permit the separation of two new Namibian taxa from other comparable African and Malagasy terrestrial tortoises.

The terrestrial Testudinidae are known in Afro-Arabia since the Early Oligocene (Thomas *et al.*, 1991). They arrived from

Eurasia in several waves. The most ancient form is named *Gigantochersina ammon* (Andrews, 1903) (in Andrews & Beadnell, 1903) from the Fayum, Egypt. They immediately diversified into forms endemic to the Afro-Malagasy continent before the later arrival (Late Miocene - Pliocene) of the palaeartic *Testudo* group in the northern part of Africa around the Mediterranean. This diversification occurred through the Oligocene and the base of the Miocene but we have no record on account of the absence of fossil sites of this age. Between the two waves the large extant forms *Centrochelys* and *Stigmochelys*, colonised the continent, remains being known from the Early Miocene onwards. From the summit of the Early Miocene about 19-20 Ma (corresponding approximately to the base of the marine Burdigalian) the three extant African endemic groups, *Centrochelys*, *Stigmochelys* and the small endemics, represented by the *Kinixys* group, are represented and partly described from East Africa. The Miocene species of *Kinixys* is without a name because it is by error that it was attributed to *K. erosa* by Meylan & Auffenberg (1986). This extant species has a very elongated anterior border with pronounced points, in contrast to the Miocene species which is less derived. Considered as related to *Kinixys* by the presence of supernumerary auxiliary scutes towards the front internally, is *Impregnochelys* Meylan & Auffenberg, 1986, of the Early Miocene of Rusinga Island, Kenya. The other described taxa of fossil Testudininei known from the African Miocene belong either to the *Stigmochelys* or the *Centrochelys* group (see Lapparent de Broin, 2000a).

As concerns the Early Miocene of Namibia, the two described taxa are based on insufficient material, which necessitates a systematic revision. One, previously described by Stromer, 1926, as a possible “*Testudo*” (i.e. ? *Testudo namaquensis*) was recently attributed (Meylan & Auffenberg, 1986) to a vague, poorly defined genus “*Geochelone*” and the other erroneously to *Chersina*. Thanks to new material, it is now possible to name two new genera for these taxa: *Mesochersus orangeus* n. g., n. sp., and *Namibchersus* n. g., with a different species at Arrisdrift (not named) from that of Auchas and Elisabethfeld, *N. namaquensis* (Stromer, 1926), and to determine the presence of a third genus at Arrisdrift, aff. *Psammobates-Homopus*.

Given the endemic nature of the fauna under study, I chose to make comparisons with a primitive member of the family, “*Manouria*” *impressa*, *Gigantochersina*, the oldest known African form from Egypt, the extant large African endemics *S. pardalis* and *C. sulcata*, and the small (to medium) extant African endemics: *Homopus* and *Psammobates*, species for which samples were available, *Chersina angulata* and *Kinixys erosa*, *K. homeana*, *K. b. belliana* and *K. b. nogueyi*. I did not include in the comparison the paedomorphic small specialised East African form *Malacochersus* (the “pancake tortoise”), *Pyxis* (*Pyxis*) and *P. (Acinixys)* from Madagascar. *Pyxis* are evidently (Bour, 1981) related to small African endemics and according to the envisaged apomorphic features, they closely approach one or other of the African genera (mosaic distribution of characters in the group). Neither did I include *Impregnochelys*, an extremely robust form considered as allied to *Kinixys*. The assemblage of all these taxa comprises the Ethiopian-African endemics (*sensu* Lapparent de Broin, 2000a, following Williams, 1952, *pro parte*, and the palaeotropical empire of Bour, 1980, *pro parte*). The study

shows that the smallest Namibian fossils, *Mesochersus* n. g. from Arrisdrift, seems to be related to the smallest extant African endemics: its ultimate relations to *Namibchersus* n. g., are not raised. Another small African endemic was present but is too poorly represented to be named. These new taxa show that the strictly African lineages of small and large endemics were in place well before the Miocene and the diversification of the large endemics *Centrochelys* and *Stigmochelys*. The large *Namibchersus* n. g., is an evolutionary grade quite close to that of the extant large form *Astrochelys yniphora* from Madagascar but a phyletic relationship of the two is possible with *G. ammon* from the Oligocene of the Fayum. For the small endemics, the basal parental relationship is unknown but it is surely older than the Miocene and distinct from that of the large forms.

Comparative sample

During this study, fossil specimens were compared with extant ones from which the scutes have been removed: collections MNHN, AC, H, P; BM (NH); NMK; Zoology Department, National Museum of Namibia, Windhoek; personal collections: Specimens with scutes often look different from osteological specimens prepared without their scutes. Scutes have a growth which extends beyond the subjacent plates, always or until advanced age. Under the points of the anals of *Psammobates*, for example, the xiphiplastra are not as well ossified round their edges and the anals thus appear to be longer in specimens with scutes. Similarly, the nuchal of *Kinixys erosa* is not completely ossified under marginals 1, such that the two nuchal notches on either side of the bony cervical projection are not visible in specimens with scutes which, on the contrary, may possess two marginal projections of scute on each side of an odd nuchal notch, apparently as in *Centrochelys*. The projection of the unique gular of *Chersina angulata* extends well beyond the projections of the epiplastra, as also occurs in *A. yniphora*. The gular lips and the femoro-anal narrowing may appear stronger in specimens with scutes than on those without, because the femoral scutes are wider than the parts of the subjacent hypoplastra and xiphiplastra, for example in *Kinixys*. But the extant ones often have sinuities and bony points less developed than fossils of the same size. This has been noticed in extant and fossil species such as *Pelusios sinuatus* (see Broin, 1969). This is considered to result either from a present day reduction of optimal ossification conditions, or to the animals being captured, (extant and fossil *P. sinuatus*. at Olduvai) are young individuals compared to those found as fossils which probably died of old age without being captured by humans (the case at Omo). One should therefore take into account the various factors during comparisons which include the anterior or posterior external borders of the carapace and plastron (percentages are given in the tables of the skeleton below) with extant specimens with their scutes. The reader is referred to data on small African endemics published by Broadley (1962; 1981; 1993; 1997a, b, c); Cooper & Broadley (1990).

Namibchersus n. g.

Synonymy: ?*Testudo*: ?*Testudo namaquensis* Stromer, 1926 - Stromer, 1926: 139.

Geochelone: *Geochelone stromeri* Meylan & Auffenberg,

1986 - Meylan & Auffenberg, 1986: 282, *pro parte*; Fig. 3, (Namib Desert). *Geochelone namaquensis* Stromer, 1926 - Meylan & Auffenberg, 1986: 281, Fig. 1 (Arrisdrift, Namib Desert).

Etymology of the genus name: “*Namib*”, from the Namib Desert where the specimens were collected, and the Greek “*chersos*” solid ground, continental.

Namibchersus namaquensis (Stromer, 1926)

Type species: ?*Testudo namaquensis* Stromer, 1926: 139.

Synonymy: ?*Testudo namaquensis* Stromer, 1926 - Stromer, 1926: 139.

Geochelone stromeri Meylan & Auffenberg, 1986 - Meylan & Auffenberg, 1986: 282, *pro parte*, p. 284, Fig. 3, SAM-PQ-N-140, 147 (Namib Desert).

Locality and age of the type species: Elisabethfeld, north-west part of Diamond Area 1, Namibia, Early Miocene, ca 19-20 Ma.

Combined diagnosis of the genus and species: Large terrestrial Testudinidae, the carapace substantially exceeding 80 cm in length, with the schema of the suprapygal-pygals and marginals 12 of the “*Geochelone*” type (but with the posterior sulcus of vertebral 5 crossing the lenticle in the arc of a circle towards the front) and peripherals 4 and 6 and the marginals of the bridge enlarged, rising as an arc of a circle at the expense of the pleurals; more evolved than *Gigantochersina* (at least where it is known) mainly by its constant peripheral points, its quadrangular neural 1 in all the cases, its dorsal epiplastral lip less projecting and always with convergent margins, dorsally more elevated and recurved into an overhang in front of or up to the entoplastron, and its complete pleuro-peripheral coincidence. Morphologically close to *Astrochelys yniphora* (more so than in *A. radiata*, which is less derived).

It is less specialised than *A. yniphora* by its unfused gulars and apparent absence of the gular spur present in the male of the latter, the dorsal plates are not thinned, the dorsal epiplastral lip is not concave from front to back and its form is less arched. It is more derived by the longer and more sinuous ventral lip of the nuchal plate with slight rounding of the marginals 1 border, and by the laterally shorter inguinals. It is derived following a different trend from *Astrochelys* by the slightly flat to convex dorsal epiplastral lip, widening behind with almost parallel gularo-humeral sulci. Other derived homoplastic features, but which are diagnostic when combined: pygal high and convex, especially in males; epiplastra elbowed in front of the moderate gular projection; gulars partly overlapping the entoplastron; entoplastron enlarged in the adult; elbowed humero-pectoral sulcus; the femoro-anal sulcus not notably narrowed; anal notch wide and moderately long; dorsal femoro-anal margin wide, in particular at the xiphiplastral points; the part of the femorals covering the xiphiplastra long in comparison to the anals; auxiliaries transverse triangular, big inguinals in an arc of a circle, from the posterior part of the marginals 7 to a small part of the femorals.

Bridge > anterior lobe > to < posterior lobe.

Abdominals > Femorals > Humerals > Gulars > Anals > Pectorals.

Species diagnosis of *Namibchersus namaquensis* (Stromer, 1926) in comparison with material from Arrisdrift: Moderate ventral gular projection, projecting compared with the slightly bent humeral margins, with convergent lateral borders and almost transverse anterior margin (slightly sinuous); elongated triangular gulars extending a little onto the entoplastron; dorsal epiplastral lip long, wider at the posterior margin than at the gular projection, moderately raised, recurved into a corniche in front of the entoplastron but eventually extending as far as it, with flat dorsal surface (or slightly convex); lateral borders of gularo-humeral sulci almost parallel. (Inguinal shortened at the contact of the femoral and the marginals).

Materiel: Neotype of the type species - MSGN. EF xl '2000, female carapace with plastron, still young, (cartilaginous spaces between sutures), carapace about 30 cm long, and plastron 24.4 long; from the northwest part of Diamond Area 1, Elisabethfeld, Namibia, Early Miocene, ca 19-20' Ma. Several other specimens from Elisabethfeld are being prepared including a young male, EF 68'00, several plastra and abundant isolated species. New specimens were collected in 2001 (not yet seen).

Referred material: Auchas, fossil meander of the proto-Orange, Southern Namibia, Early Miocene, ca 18 Ma (Pickford *et al.*, 1995). Auchas Mine was exploited on a large scale for several years. Several pits excavated in the fluvial sediments of the proto-Orange yielded fossils, of which one yielded the chelonians studied here.

MSGN. About 50 specimens recovered: one in 1993, eleven in 1995, thirty in 1998 and one in 1999, comprising the following pieces: AM 9'93, adult carapace with plastron lacking dorsal and right rear parts; AM 1'99 young adult carapace with plastron lacking the right rear part; AM x, large left peripheral 7; AM xa'98, fragments of suprapygal, pygal and peripheral 11; AM xb'98, fragments of suprapygal and pygal; AM xe, fragment of left peripheral 7 from the end of the bridge; AM 11'95, large neural 3 or 5; AM xf, elements of the posterior peripheral border of a very large carapace; AM 10'98, left epiplastron; AM 11'98, partial left epiplastron; AM 7'95, left xiphiplastron; AM 2'98, right xiphiplastron; AM xc, fragment of hypoplastron; AM xd, fragment of hypoplastron; various fragments of plastron, peripherals and pleurals. 1 humerus lacking the articulations; 1 fragment of humerus.

OMS. OMS xl, large dorsal carapace, probably female. OMS x: fragment of nuchal (13 cm of width preserved), three fragments of pleurals, a distal extremity of humerus (6 cm wide), a distal fragment of a very large femur, 2 fragments of radius and ulna, 3 fragments of plates.

A small number of specimens from the "Namib Desert" was described by Meylan & Auffenberg, 1986, and referred to "*Geochelone namaquensis* Stromer, 1926" (sic), Fig. 1B, or to *G. stromeri* Meylan & Auffenberg, 1986, Fig. 3, paratypes. According to the figures published by these authors (drawings), the pieces in their Fig. 3 conform to *Namibchersus namaquensis*, particularly by the moderate gular projection and the gulars ventrally covering the front of the entoplastron; the epiplastron of their figure 1 B with a long projection resembles their form from Arrisdrift, Fig. 3 A, C, which is attributable to another species (see below) but it has longer gulars. The genus to which the holotype specimen of the species

stromeri belongs is not defined (see below in the comparative remarks).

Description and comparison: Except in a few cases of individual variation mentioned below, the characters of the Auchas specimens are the same as those of *N. namaquensis* (Stromer, 1926) from Elisabethfeld, the species to which they are referred, in particular to the neotype.

Carapace, general characters: The maximum length of the carapace known at Auchas is about 81.5 cm, based on a posterior peripheral plate 10.7 cm long in specimen AM xf (part of the posterior peripheral border), which among the two large extant African genera, corresponds to one of the largest adults of *Stigmochelys pardalis* (ca 90 cm), and is smaller than the largest *Centrochelys sulcata* (ca 100 cm).

The morphology is completely known thanks to three of the most complete specimens: OMS xl, a large adult dorsal carapace, probably female, very eroded in places (imprint of plates visible) (Pl. 1V, Fig. 11), AM 9'93, a large adult female dorsal carapace lacking dorsal and right rear parts (Pl. 1V, Fig. 12; Figs. 2-3) and AM 1'99, sub-adult male carapace, with plastron, lacking the right rear part and the posterior borders (Pl. 11, Fig. 1; Pl. 1V, Fig. 13; Fig. 1) (measurements, Tab. 3a). The morphology of the isolated fragments adds to information available from the above specimens.

The shape is elongated with sub-parallel lateral borders, moderately high: the height is from 40 to 55 % of the length and it is higher in the young male AM 1'99. The pleural disk is bulging and slightly dilated, more in the young male AM 1'99 than in the large adult AM 9'93 (Pl. 11, Fig. 1c; Fig. 3). It is more bumpy in AM 1'99 under the vertebral and costal scutes less in the preserved females (bumps are common in all the large forms of Testudininei, both males and females). The ventral lateral margin of the carapace is underlined by a crest at the curve of the peripherals of the bridge, sharper in the young individual (the neotype) than in the large adult (the two large carapaces from Auchas). The marginal sulci terminate at the edge of the anterior and posterior peripherals preserved by a small more or less marked point (eroded specimens) at Auchas, more marked in some specimens from Elisabethfeld (Tabs 5a-6, character 5), without any direct relationship to the long points in certain endemics such as *Kinixys erosa*. The carapace does not have the posterior dorso-lateral hinge contrary to *Kinixys* (Tabs 5b-6, character 21), nor the ventral hinge on the anterior lobe, in contrast to *Pyxis* (*Pyxis*) from Madagascar. The females have a flat plastron which is wider at the abdomino-femoral sulcus whereas the males have a concave plastron which is narrower, as in *Astrochelys radiata*, *S. pardalis* and *C. sulcata* (Pl. III; Tab. 3). The plastron may also be concave in females of insularized forms (Indian Ocean, Madagascar; Bour, 1985, 1994) but rarely in continental forms (*Testudo marginata* in the palaeartic; Bour, 1987). In *Namibchersus* n. g., both sexes have a posteriorly convex pygal but in males (Pl. 11, Fig. 3b; Fig. 5a) it is clearly more convex than in the females (Pl. 11, Fig. 2a; Fig. 4a) as in *S. pardalis*. Old males of Testudininei generally have extroverted anals and a posterior ventral xiphiplastral depth (Pl. III, Fig. 4b; Broin, 1977, Pl. XXVII, Figs 7 and 9; Gmira, 1995, Pl. XV etc.; Andrews, 1906, Fig. 89, "*Testudo ammon*"). Thus they may have a narrowing at the femoro-anal sulcus which is absent in females (Andrews, 1906, Fig. 91, "*Testudo beadnelli*"). There is no large male preserved here and the young males

Table 3a. Measurements of some specimens of *N. namaquensis*. Compare with Table 3b the relative plastral narrowness in the male. Ab-Fe, abdomino-femoral; HP, humero-pectoral; P-Ab, pectoro-abdominal; hypo, hypoplastron; xiphi, xiphiplastron.

Measurements in cm	<i>N. namaquensis</i> Neotype Elisabethfeld, young female, EF x1'2000	Auchas, AM 1'99, young male	Auchas, AM 9'93, large adult female	Auchas OMS x1, large adult, female?
1- carapace length	ca 30	ca 25.4	47 (on ca 50)	ca 47
2- carapace width	21.5	19.5	ca 29	ca 33
3- carapace height	ca 13	13.9	19.5	ca 24
4- plastral length	24.4	ca 22.5	40.6 sur 41	
5- width at the HP sulcus	11.2	9.9	17.8	
6- width at the P-Ab sulcus	16.2	14	29.2	
7- width at the Ab-Fe sulcus	11.5	10.8	19	
8- length up to the hypo-xiphi suture	19	19.7	32.2	
% 6/4	66.39	62.22	71.21	
% 3/1	ca 43.33	ca 54.72	41.48 (à 39?)	ca 51

Table 3b. Measurements of some specimens of extant Testudininei. Compare with Table 3a the relative plastral narrowness in the male. P-Ab, pectoro-abdominal.

Measurements in cm	<i>C. sulcata</i> female	<i>C. sulcata</i> male	<i>S. pardalis</i> female	<i>S. pardalis</i> male	<i>A. radiata</i> female	<i>A. radiata</i> male
1- carapace length	33	ca 36	34.8	20.4	28	28
2 - carapace width	26.2	?	24.2	13.7	21.2	20
3- carapace height	14.2	?	18	11.2	17.2	17
4- plastral length	33.3	36.2	29.5	19	24.2	25.4
6- width at the P-Ab sulcus	24.4	25.3	21.8	11.5	17.4	15.3
% 6/4	73.27	69.88	73.89	60.52	71.9	60.23
% 3/1	43	?	51.72	54.9	61.42	60.71

do not have this femoro-anal narrowing.

In several large individuals, the bony plates are thinned between the sulci for the scutes which are raised in relief. This is particularly striking on the dorsal margin of the xiphiplastron (Pl. III, Figs 5, 6), but also at the epiplastral symphysis of the neotype. Such a thinning of bony plates is also present in *A. yniphora* (see Broin in Allibert *et al.*, 1990) where it is also strongly present on the pleural disc. Raised sulci at the summit of the crest with a median groove bordered by sharp crests are a characteristic of Testudininei among cryptodires, being almost always present even though attenuated in places. Here, the relief is very marked. This relief also exists rarely in pleurodires (*Pelusios sinuatus* see Broin, 1969; the Dortokiidae *Dortoka* Lapparent de Broin & Murelaga, 1996, 1999, and *Ronella* Lapparent de Broin in Gheerbrant, *et al.*, 2000).

Dorsal carapace: The anterior dorsal peripheral border is moderately elongated in comparison with the primitive condition, but the nuchal is not elongated and there is no notch at the anterior border (Tabs 5a-6, characters 2, I), as in *Mesochersus* n. g. The sulci between the scutes of the border and those of the

pleural disc and the sutures between the peripherals and plates of the pleural disc, coincide from peripheral I up to the pygal, as in *A. yniphora*, *Stigmochelys* (except sometimes at the medial corner of peripheral I) and *Centrochelys* but also as in *Manouria emys*. "*M.*" *impressa*" and *Malacochersus* have retained the most primitive position: the sulcus of the marginals with the costals overlaps the peripherals as in freshwater forms of the family, the edges of the marginal scutes being clearly more external on the bony margin of the peripheral. The sulcus which separates the marginals and the pleurals approaches the suture but probably remains separated from it in *Gigantochersina ammon* (see Andrews, 1.906, Fig. 88B but not the other figures which are too stylised), *Homopus*, most of the specimens of *Psammobates* observed (but not all, only at the front in a specimen of *P. t. tentorius* from the Karoo). It zigzags mostly along the suture in *Kinixys* (more or less closely depending on the species). They approach each other in the middle part, remaining further apart at the front in *Astrochelys radiata*; they are separated at the front and the back in *Chersina angulata*.

The state of the character is thus even more primitive in the endemic Afro-Ethiopian endemics with cervicals, from which *Namibchersus* n. g., is distinguished by this fact, except *A. yniphora*. In *Mesochersus* n. g., the sulcus is separated from the suture on peripheral 11 (Pl. VI) but not on the others. In primitive forms of fossil Eocene Testudininei of Europe (Broin, 1977, figs 104-105) and several North American fossils (Hay, 1908), the sulcus of marginals 1-2 with costal 1 is still located on peripherals 1 or 1-2, at the front of the carapace, and not at the peripheral-pleural suture as for the succeeding marginals. All these examples of specific or sub-specific variation, even within monophyletic groups, show that as for other characters evolution towards coincidence is homoplastic and responds to a common tendency in the infrafamily, with amplifications and eventual secondary particularities (*Kinixys* and second indeterminate form of small African endemic from Arrisdrift, see below).

The peripherals of the bridge and with them the marginal scutes elongate between peripherals 3 and 7, being greatest between peripherals 4 to 6, moderately (Pl. IV, Figs 12b and 13), at the expense of the corresponding pleurals (the pleuro-peripheral limit in the arc of a circle in lateral view) and this even in the smallest specimens. This elongation is almost the same as in *S. pardalis* (arched form) *C. sulcata* (flatter form) and *Astrochelys* from Madagascar (very arched form, well defined character): it appears that, among Testudininei, elongation of the plates and scutes of the bridge is more marked in the largest forms. But in the tabular forms reaching large dimensions, such as *Chelonoidis* from South America, and *Indolestudo elongata* from Asia, and in the medium to small Ethiopian endemics, elongation is minimal, as in *Manouria emys*. It is not present in "*M. impressa*".

The nuchal is wider than long (AM 1'99: 7.3 cm x 5.1 cm), not reduced in width or length, without a notch either side of the cervical and without cervical projection (Tabs 5b-6, character 23) as in *Mesochersus* n. g., and *Astrochelys*. In "*M. impressa*" and *M. emys*, the nuchal is relatively wider, with a rounded notch at the cervical (wide) and a rounding towards the front of each side of the cervical which is shorter. The retreat of the nuchal in comparison with peripherals 1 can vary a bit, if one examines, for example, *Gigantochersina ammon* (Andrews, 1903) (see Andrews 1906), but this is not the case in *Namibchersus* n. g., according to specimens from Auchas AM 1'99 and AM 9'93, the neotype and other specimens from Elisabethfeld. The anterior margin of the nuchal itself may be more or less sinuous, for example more in *Manouria*, less in *Gigantochersina* and *A. radiata* but this is not the case for the preserved specimens of *Namibchersus* n. g. The ventral surface of the nuchal of *Namibchersus* n. g. has a long ventral depth supporting the ventral border of the cervical and the medial portion of marginals 1. This depth terminates behind by an overhanging margin compared to the back of the plate which is concave ventrally. Among the compared taxa (ventral surface of the plate not known in *Gigantochersina*), the nuchal may have a short depth ("*M. impressa*", *M. emys*, *Malacochersus*, *Psammobates*, *Homopus*, *Mesochersus* n. g.), a bit elongated (*A. yniphora*, *A. radiata*), or clearly elongated (*Centrochelys* and *Stigmochelys*, as in *Namibchersus* n. g.). The depth is much more elongated in extant *Kinixys* and *Chersina* because the nuchal is more elongated and its anterior margin narrowed above all in *Kinixys* where, among

other things, the nuchal projects in front at the cervical level. The posterior margin is somewhat sinuous in the neotype of *Namibchersus* n. g., with a slight marginal rounding towards the rear of each side of the posterior margin of the cervical, as in the extant species of *Kinixys* and a bit like *Ch. angulata* but much less than in the latter where the rounding is very pronounced and characteristic. Another very large specimen from Elisabethfeld also has a sinuosity as in the neotype. The young male from Auchas (AM 1 '99) shows a long margin and the sinuosity barely marked on the left side (Pl. 11, Fig. 1 b, to the right of the cervical); the other specimens are not cleaned ventrally. The ventral border of the cervical and marginal 1 scutes is flat in *Manouria*. It is barely raised but not overhanging in *A. radiata*. It is raised and more or less overhanging in all the others, as in *Namibchersus* n. g., (ventral part not known in *Gigantochersina*). The posterior sinuosity of the border cannot exist in forms without a cervical (*Centrochelys* and *Stigmochelys*).

The cervical is well represented (Tabs 5a-6, character 3), longer than wide (AM 1'99: ca 1.7 x 1.1 cm), with straight anterior margin and moderately long on the nuchal (about 1/3 of its length) which is not elongated (different from *Chersina* and *Kinixys*). In "*M. impressa*" and *M. emys* it is wider and shorter (primitively) and has a notched and rounded anterior margin (may be an apomorphy of the two taxa).

Dorsally, the posterior border of the marginals 1 lengthen from the cervical to rejoin the corner of the nuchal, between its two lateral sides (Figs. 1c, 2a). Vertebral 1 either extends beyond the corners of the nuchal (Fig. 1 c), or coincides (or nearly so) with the borders of the nuchal (Fig. 2a). The primitive condition such as in *Manouria*, is that vertebral 1 is a bit wider to somewhat less wide than the nuchal, as in *Namibchersus* n. g.

The neural series is well differentiated into plates: elongated quadrangular (neural 1), octagonal, quadrangular, octagonal and quadrangular (neurals 2 to 5) and hexagonals with small anterior sides (neurals 6-8) (Tabs 5-6, characters 17, 18).

The suprapygal/pygal schema and that of vertebral 5 / marginals 12 (Tabs 5a-6, characters 6, 7) is of the so-called "*Geochelone*" type, *sensu* Auffenberg (1974), with suprapygal 1 anteriorly enclosing the lenticular second one, and the posterior sulcus of vertebral 5 crossing the lenticular plate (Figs 4-5). It was thus named at the time that almost all the large Testudininei of the World were phenetically assembled under this generic name, agreeing with authors such as Williams, 1952, following the attribution of *Testudo sulcata* Miller, 1779, to *Geochelone* by Fitzinger (1838), before its attribution to the genus *Centrochelys* Gray, 1872, an identification which is justified but which was not followed by all researchers. Remember that the genus *Geochelone* has as its type species the small Asiatic *Testudo elegans* Schoepff, 1795, which has no phyletic relationship with the large forms included in the genus (Lapparent de Broin, 2000a), and not *Centrochelys sulcata*, the large African form. The so-called "*Geochelone*" schema, occurring in *Centrochelys* and *Stigmochelys*, is however, only partly present in *Geochelone elegans*, the type species of the genus (Indian subcontinent) (see remark 6, in the conclusion of this chapter). This schema is not present in "*M. impressa*" and *M. emys* which still have the goemydinian one, in which the suprapygals are transversely separated

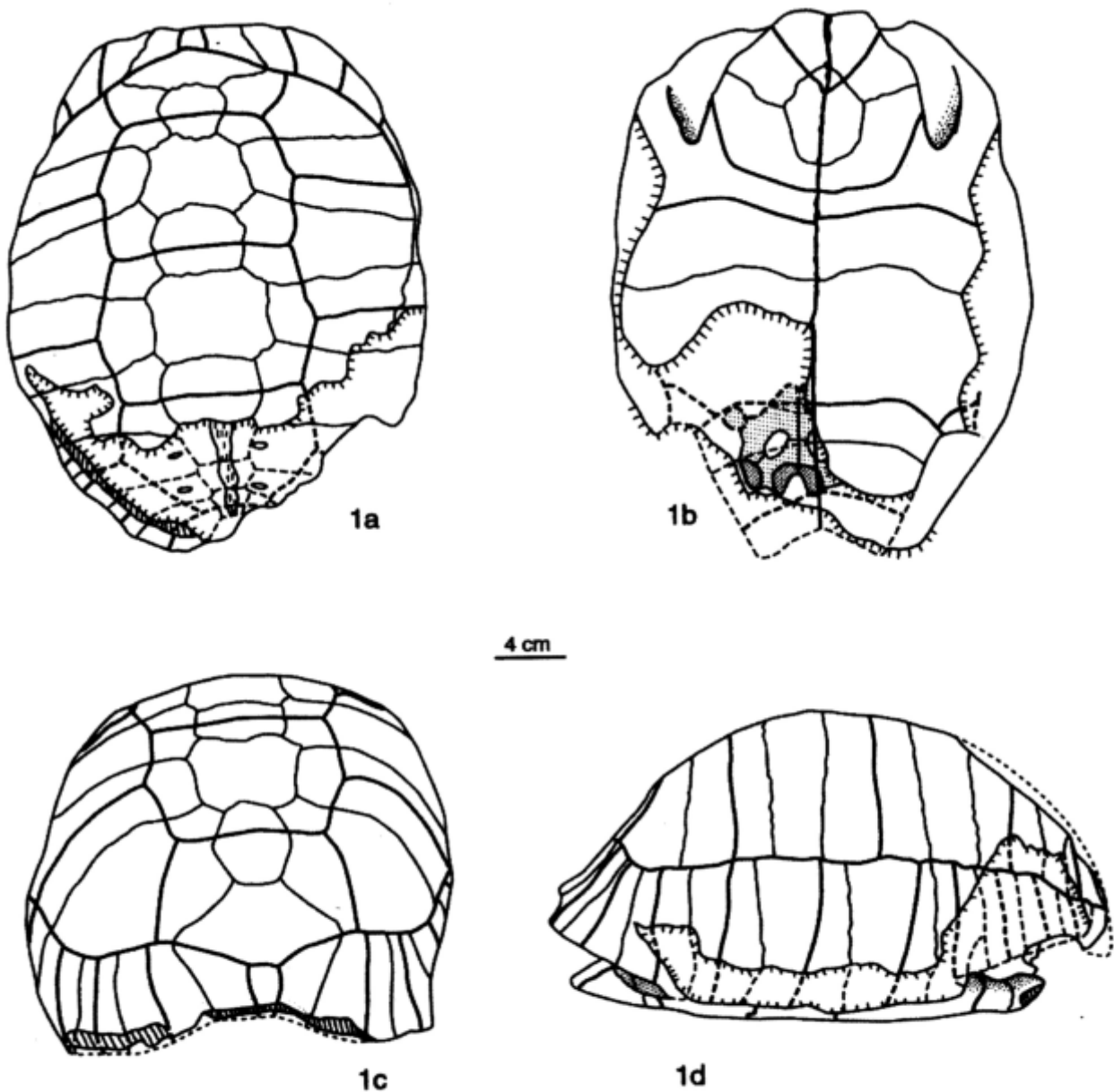


Figure 1 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 1'99, carapace, young male, a, b, c, d, dorsal, ventral, anterior, left lateral views.

and the second one diverging from the former is wider. In several of the large American fossil and extant forms, suprapygals 2 is anteriorly enclosed by suprapygals 1; it is not lenticular but simply semi-circular; its posterior border is transversal without a posterior circular arc, and the sulcus of vertebral 5 follows the suprapygals 2 - pygal suture instead of traversing suprapygals 2. In contrast, several other South and North American forms (Hay, 1908) and European ones ("*Ergilemys*" from France, *Cheirogaster*) have the so-called "*Geochelone*" schema, with variations in the course of the sulcus on vertebral 5 and the degree of reduction of the posterior part of the lense of suprapygals 2. The pygal of *Namibchersus* n. g., is noticeably elongated with respect to its width, as in *Stigmochelys*, whereas it is relatively less elongated in *Astrochelys* and *Centrochelys*, and even less so in *Manouria emys* and not at all in "*M. impressa*". *Namibchersus* n. g., has the "*Geochelone*" grade, separately evolved with respect to the grade of the *Testudo* group,

and that of the small African endemics in the Testudinini (to which grade belongs *Mesochersus* n. g.). The elongation of the pygal is here at a maximum in the "*Geochelone*" grade (Tabs 5a-6, character 6). In *Namibchersus* n. g., (specimens from Auchas and Elisabethfeld) after having traversed the lense of suprapygals 2, forming an arc anteriorly, the sulcus of the vertebral 5 - marginal 12 scute follows exactly the suture, between suprapygals - peripheral 11 (Pl. 1V, Fig. II; Figs 4 and 5) then that of the pleurals-peripherals, as in the large African forms and *A. yniphora* differing from *A. radiata*, *Mesochersus* n. g. and the small-medium endemics in which the sulcus for the border scutes does not coincide everywhere with the suture between the border plates and the pleural disc.

The posterior pygal border of the carapace is subvertical in the female (neotype included) with the pygal somewhat arched (Pl. 1V, Fig. 12b; Fig. 4). It is clearly recurved towards the front in the male (Pl. 1V, Fig. 13; Fig. 5). In Testudinini, the pygal

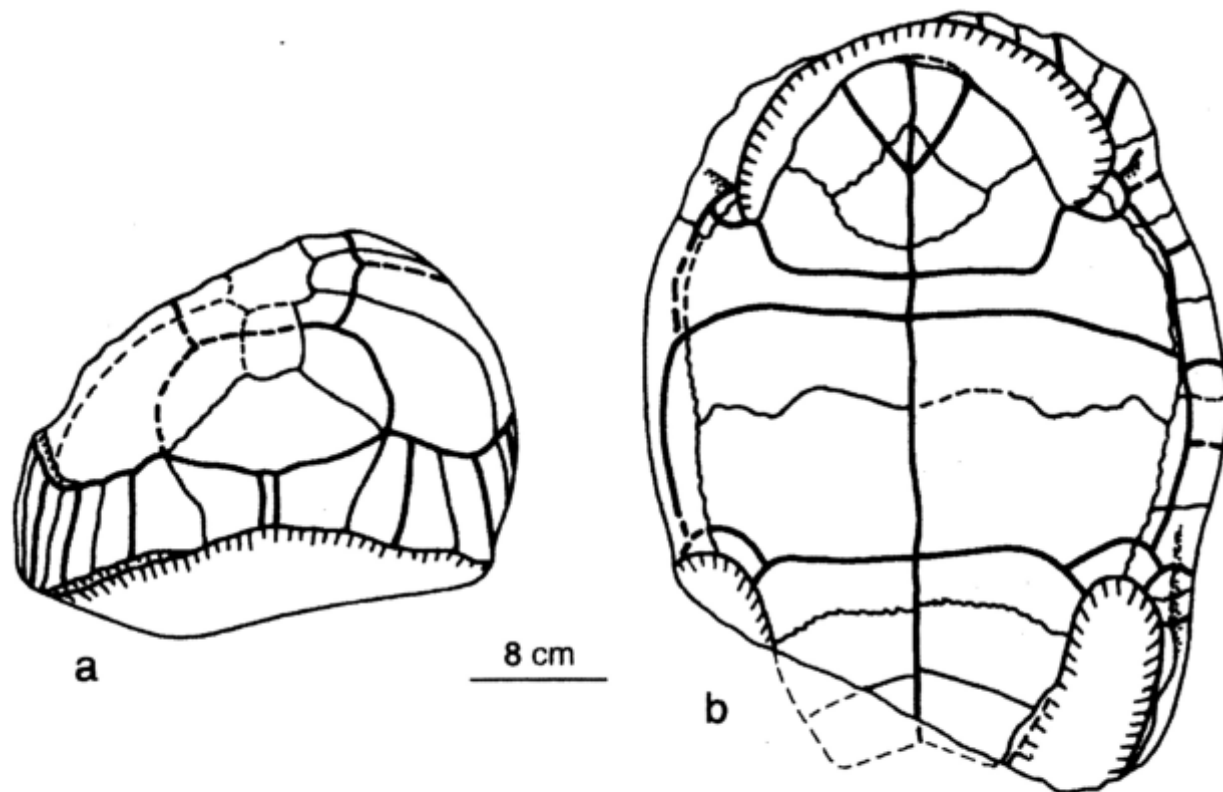


Figure 2 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 9'93, carapace, adult female, a, b, anterior, ventral views.

is: - either recurved towards the interior in the male only, and vertical (*K. belliana nogueyi*) or upright (*K. homeana*) in the female; - or recurved in the female as in the male, but less so, for example in *S. pardalis* and *Astrochelys*, or in *Paleotestudo canetotiana* from the Miocene of France (Lapparent de Broin, 2000b); - or spread out towards the rear and more (male) or less (female) convex and recurved downwards as, for example, in *Psammobates*. The posterior margin of peripherals 10-11 adjacent to the pygal may be raised up or not according to sex. It is barely uplifted in the female neotype of *Namibchersus namaquensis*, from Elisabethfeld, as is the

large female from Auchas AM 9'93 and in the isolated peripherals from Auchas AM xf. It is unknown in the young males from Auchas and Elisabethfeld, which are poorly preserved at the rear. This border rises in *Gigantochersina ammon*.

The bridge extends between peripherals 3 and 7 and it is long in comparison with the plastron as in other Testudininei (AM 1'99: 13 cm for ca 22.5 cm of plastron; AM 9'93: ca 20.6 for ca 41 cm; neotype from Elisabethfeld: 13.2 cm for 24.4 cm).

Plastron: Measured at its limit with the peripherals of the bridge, to the pectoro-abdominal sulcus, the plastron is somewhat narrower in males than in females (Tab. 3a) as in the extant forms used for comparison (Tab. 3b) although the dorsal carapace of the young male is relatively wider due to its globosity.

The plastron of the specimens from Auchas agrees with the figured holotype of *?Testudo namaquensis* Stromer, 1926, and to the neotype from Elisabethfeld: almost all the relative proportions conform, except for differences due to sex and age; the morphology of the margins, in particular of the gular projection, from the epiplastrallip and the posterior lobe, decisive for the diagnosis, are the same. The posterior lobe seems to be relatively longer in the very large, presumed female, specimen AM 9'93, whereas it is shorter in the neotype.

The anterior lobe is globally trapezoidal narrowed forwards. The convergent lateral margins are bent towards the front at the epiplastra, after which they close up by forming a slight posterior concavity at the gularo-humeral sulcus.

The gular region is very important from the taxonomic and phyletic points of view (Tabs 5a-6, characters 8 to 12) (Pl. 11, Fig. 1e, 1f, 1g, 4; Pl. 1V, Fig. 12a; Figs 1b, 2b, 6 and



Figure 3 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AL 9'93, carapace, adult female, anterior view.

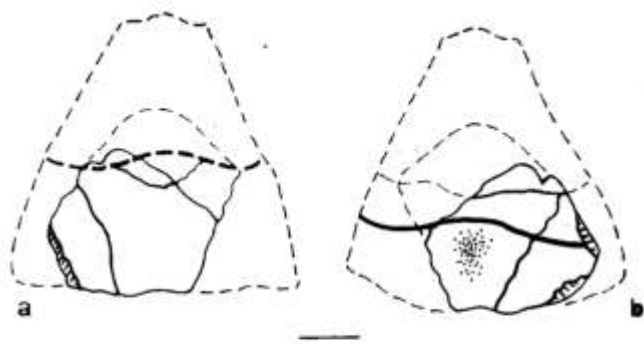


Figure 4 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM xa'98, fragment of suprapygal 2, pygal and left peripheral 11, female, a, b, dorsal, ventral views. (scale - 4 cm)

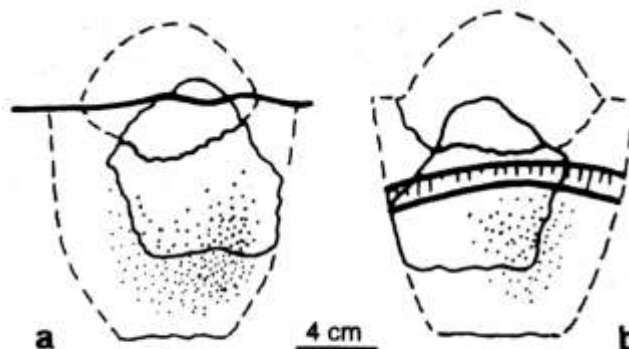


Figure 5 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AMxb'98, fragment of suprapygal and pygal, male, a, b, dorsal, ventral views.

7). The gular projection and the dorsal gular lip in the specimens from Auchas and Elisabethfeld are the same as those in the destroyed holotype of *?Testudo namaquensis* figured by Stromer, 1926, from Elisabethfeld: the moderate ventral gular projection has anteriorly converging lateral borders, with modest individual variation in length. It is a point by which the Auchas and Elisabethfeld specimens differ from the Arrisdrift one figured by Meylan & Auffenberg, 1986 (Fig. 1 A): In the latter, the ventral projection is much longer, which must constitute one of the diagnostic characters of the species. In *N. namaquensis*, the dorsal gular lip is long, wider towards the back than at the front of the projection, moderately raised (more or less depending on the individuals), recurved towards the rear forming an overhang above the epiplastron, in front of the entoplastron or just above it (a reconstructed specimen from Auchas, Fig. 6a; a specimen from Elisabethfeld). and with a flat dorsal surface.

The gular projection (character 9) is moderate in comparison with that seen in extant Asian forms: "*M.*" *impressa*, considered to be the basal taxon of the Testudinini (in some ways their sister group or their plesion) and *M. emys*, a form considered to be the most primitive of the extant Testudinini (but not the most primitive if we include some of the fossil species of the Laurasiatic *Hadrianus* s.l.), and in the first African form, *G. ammon* from the Oligocene of the Fayum. It was an error (Auffenberg, 1974) that the North American Eocene genus *Hadrianus* was put into synonymy with *M. emys*, on the basis of symplesiomorphies such as this, and because the marginals 12 are still separated (character 7). The suprapygal-pygal schema is different, still geoemydinian in "*M.*" *impressa* with vertebral 5 overlapping a long way over the pygal and peripherals 11; in *M. emys*, the posterior sulcus of vertebral 5 follows the suprapygal 2-pygal suture to the rear. In *H. corsoni* (Leidy, 1871) (the type species of the genus, see Hay, 1908) marginals 12 are always separated, but suprapygal 2 is surrounded by the first, with a semi-circular suprapygal 2 behind the first, bordered behind by the pygal and with the sulcus of vertebral 5 at the pygal-suprapygal limit. This is a schema intermediate between that of *M. emys* and that of so-called "*Geochelone*" in which a lenticular suprapygal 2 is traversed by the vertebral 5.

All these primitive forms share the pronounced gular projection, a derived character in comparison to the state present in freshwater forms but which appears here as primitive within

the terrestrial group. The projection is less pronounced in *Centrochelys* and *Stigmochelys*, among others, secondarily in my opinion, as in *Namibchersus* n. g. In contrast it is secondarily sometimes even more pronounced in one or another species such as African *K. erosa* and *Ch. angulata*. A more pronounced projection than in *Namibchersus* n. g., is present in *A. radiata*. The bony projection may be prolonged by an even stronger projection of the scutes, with fusion of the gulars (*A. yniphora*, *Chersina angulata*) or without fusion, or even well separated into two forks in the large male (*Centrochelys*).

The projection is primitively wider in freshwater forms and "*M.*" *impressa* in comparison to most of the other Testudinini, including *Namibchersus* n. g., where it is restricted in width. But it is also relatively wide in juveniles of all forms and in the small African *Homopus*, *Malacochersus* and *Psammobates*, where the character appears to be pedomorphic. The lateral margins of the projection are sub-parallel in "*M.*" *impressa*. They are either convergent or parallel in *M. emys*, as in the first African form, *G. ammon* from the Oligocene of the Fayum and sub-parallel (male) to convergent (females) in *A. radiata* but they are always convergent in the other African forms observed here, including *Namibchersus* n. g., both male and female. They are parallel in *H. corsoni*. They are parallel or divergent in the Eocene European forms attributed to this genus (s. l.). At the front, the gular margin may be slightly sinuous in *Namibchersus* n. g., (neotype from Elisabethfeld, AM 1'99 from Auchas, Pl. 11, Fig. 1 e) recalling the deep anterior indentation in every epiplastron that one sees in *Manouria* and

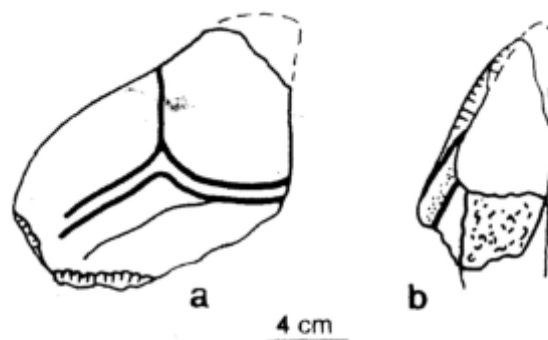


Figure 6 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 11'98, left partial epiplastron, a, b, dorsal and symphyseal views (the displaced fragment visible on Pl. II, fig. 4, is here withdrawn).

the primitive Asian fossil forms (see *Kansuchelys tsiyuanensis* Yeh, 1979), and in extant juveniles from Africa, occasionally up to the adult stage (*Centrochelys*, *Stigmochelys*) (no juveniles of *Namibchersus* n. g., are preserved).

Dorsally, we have seen that the epiplastral-gular lip which is relatively wide at the front in *Namibchersus* n. g., widens a bit towards the rear (character 12) in comparison with the front of the gular projection (Pl. 11, Fig. 1g; Figs 6-7) as in *S. pardalis* and in contrast to *Mesochersus* n. g. In the neotype, on each epiplastron there is a small longitudinal dorsal depression on each side of the symphysis, more raised with its crest for the sulcus between the gulars being well marked. Dorsally, on all the specimens, the gularo-humeral limit is displaced laterally in comparison to its ventral contact point at the front and the gulars are wider dorsally than ventrally, as in most of the forms *Mesochersus* n. g., *A. yniphora*, *Centrochelys*, *Stigmochelys*, *Chersina*, and *Kinixys* but not *A. radiata*, *Psammobates* and *Homopus*. In the specimen of *Namibchersus* n. g., from Arrisdrift, the gulars narrow towards the rear instead of having the borders sub-parallel to widened, probably another specific difference. The posterior margin of the lip is recurved into an overhang; its dorsal surface is raised above the rear of the epiplastron and is relatively flat (character 11), as in certain specimens of *S. pardalis* (where, with others, it can be clearly convex) and as in *A. radiata* (but in the latter the lip is narrowed at the back and is very projecting at the front). The dorsal surface is not as low as in *Centrochelys* and *A. yniphora*. The margin of the recurved lip does not extend rearwards as far as the edge of the entoplastron (Pl. 11, Fig. 1f, g; Fig. 6; neotype of *N. namaquensis*) or perhaps a bit above it (Fig. 7a) (character 10), as in *S. pardalis*. It is always more anterior in *C. sulcata* (see Lapparent de Broin & Van Dijk, 1999; Roset *et al.*, 1990) and *A. radiata*. Primitively ("*M. impressa*"), the dorsal epiplastral lip is barely medially raised, low in front from the posterior part of the epiplastron and is not recurved; its dorsal surface is concave from right to left between two pronounced flanges located at the limit of the gularo-humeral sulci; this morphology is that of Geoemydinei such as *Geoclemys hamiltoni* or certain fossils of the European Tertiary group *Ptychogaster* (Murelaga *et al.*, 2002). In the primitive Palaeogene forms (Broin, 1977), the dorsal lip rises a little, either remaining concave or flat-

tening. In *Gigantochersina* from the Fayum, the dorsal lip is flat and not recurved, as in *M. emys* (where it is more or less concave depending on the individual), the ventral epiplastral surface being concave in the male. The grade reached by all the extant African forms and the Namibian fossil ones later than *Gigantochersina*, is that of a lip that is at least somewhat raised, and not concave from right to left and recurved towards the entoplastron (which it either reaches or not); its dorsal surface is flat to convex, or a little concave from front to back (*Centrochelys*, *A. yniphora*) but not in the two Namibian genera.

The entoplastron (Tabs 5b-6, characters 19, 20; Tab. 4) is wider ventrally than dorsally. In the young it is longer (primitive youthful character) (AM 1'99; EF 68'00) and in the large specimens, females here (neotype EF x1'00 included) it is wider (Pl. 11, Fig. 1 e, Fig. 1 b; Figs 2b, 7) conforming to the holotype figured by Stromer, 1926, and as in *Astrochelys*, *Centrochelys* and *Stigmochelys* (Pl. 111, Fig. 1-4). With respect to the plastron it is big (young) to moderately big (Tab. 4). The elongated triangular gulars cover it a bit, relatively less in the young specimens (Fig. 1 b) than in the large adult (Fig. 2b). The rate of elongation of the gulars is specific; for example in extant *C. sulcata*, the gulars do not cover the entoplastron whereas they cover them a little or not in *S. pardalis*; the amplitude of variation in covering of the entoplastron by the gulars is not yet defined in *Namibchersus* n. g., but there is always a covering. In the specimen of *Geochelone namaquensis* in Meylan & Auffenberg, 1986, from Arrisdrift (Fig. 1 A), the gular does not reach the entoplastron. Even less in the holotype specimen of *G. stromeri* Meylan & Auffenberg, 1986, from Langebaanweg, South Africa. By this and other characters (see below) these two specimens belong to two species different from *N. namaquensis*, which is, in contrast, represented by the paratype specimens of *G. stromeri* Meylan & Auffenberg, 1986, Fig. 3, from the Namib Desert.

Under the hyoplastra, the humero-pectoral sulcus is located well behind the entoplastron, with a more or less marked angle laterally. The pectoro-abdominal sulcus, moderately advanced, is well separated from the humeropectoral sulcus (short pectorals but abdominals shorter than the distance separating them from the anterior gular border). The auxiliaries are clearly visible, differing from *Mesochersus* n. g., each

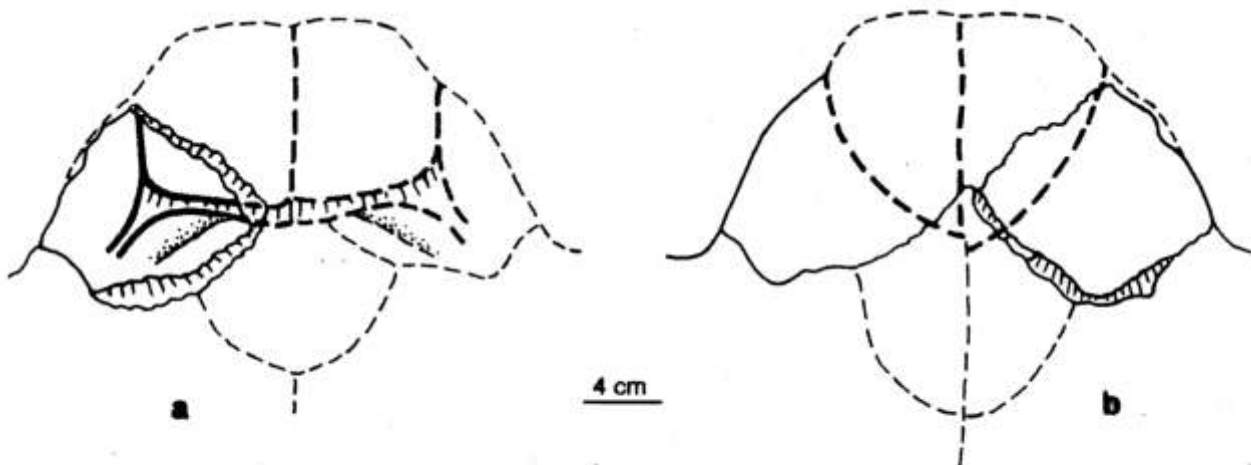


Figure 7 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 10'95, left partial epiplastron, a, b, dorsal and ventral views with reconstructed missing part of the right epiplastron and entoplastron.

Table 4. Relative proportions of the entoplastron (ento): width (w), length (L) in comparison with the anterior lobe width at the epi-hyoplastral suture (a, b) and between them (c); ento, entoplastron; epi, epiplastron. Auch, Auchas; Elis, Elisabethfeld. La, large size, M, middle, S, small species.

	a) ento w/epi w (cm)	%	b) ento L/l epi w (cm)	%	% L/L ento
" <i>Manouria</i> " <i>impressa</i> M	2.5/5 (female)	50	3.3/5	66	2.5/3.3: 75.75.
<i>Gigantochersina</i> La	2.5/4.9 (male)	61.53	2.5/4.9	61.53	2.5/2.5: 100
<i>A. radiata</i> M	4.5/9 (male)	50	3.9/9	43.33	4.5/3.9: 115.38
	5/8.4 (female)	59.52	4.35/8.4	51.78	5/4.35: 114.94
<i>A. yniphora</i> M	3.2/5.7 (young female)	56.14	3.1/5.7	54.38	3.2/3.1: 103.22
<i>S. pardalis</i> La	6.3/11.5 (female)	54.78	6/11.5	52.17	6.3/6: 105
	3.4/7 (young male)	48.57	3.4/7	48.57	3.4/3.4: 100
	5.2/9.5 (male)	54.73	4.9/9.5	51.57	5.2/4.9: 106.12
<i>C. sulcata</i> La	1.4/3.2 (juvenile)	43.75	1.55/3.2	48.43	1.4/1.55: 90.32
	8.1/15 (female)	54	5.5/15	36.66	8.1/5.5: 147.27
	8.1/14.5 (male)	55.86	5.7/14.5	39.31	8.1/5.7: 142.10
<i>G. elegans</i> MS	2.11/5.11 (female)	41.29	2.11/5.11	41.29	2.11/2.11: 100
<i>Namibchersus namaquensis</i> n.g. n.sp. La	5/9.2 (female. neotype Elis)	54.34	4.7/9.2	51.08	5/4.7: 106.38
	8.82/14.4 (female Auch 993)	61.11	7.2/14.4	50	8.8/7.2: 122.22
	3.7/8.9 (male Auch 199)	<41.57	4.55/8.9	51.12	3.7/4.55: 81.31
	3.3/6.6 (male Elis)	50	3.5/6.6	52.03	3.5/3.6: 97.22
<i>Mesochersus orangeus</i> n.g. n. sp. MS	2.5/4.8	<52.08	2.5/4.8	44.64	2.5/2.5: 100
	2.2/4.4	50	2.3/4.4	52.27	2.2/2.3: 95.65
<i>Homopus areolatus</i> S	1.1/3.35	37.50	1.2/3.35	35.82	1.1/1.2: 91.66
<i>Psammobates tentorius</i> S	1.8/3.8	47.36	1.3/3.8	34.21	1.8/1.3: 138.46
	0.5/2.7	18.51	0.5/2.7	18.51	0.5/0.5: 100
	0.7/2.7 (female)	25.92	0.8/2.7	29.62	0.7/0.8: 87.50
<i>Psammobates geometricus</i> S	0.6/4	15	0.9/4	22.5	0.6/0.9: 66.66
	0.6/2.6	23.07	0.7/2.6	25.92	0.6/0.7: 85.71
<i>Psammobates oculifer</i> S	1.2/3.5	34.28	1.5/3.5	42.85	1.2/1.5: 80
<i>Chersina angulata</i> M	1.2/4.4 (male)	27.27	1.65/4.4	37.50	1.2/1.65: 68.57
	1.25/6.2 (male)	20.16	1.75/6.2	28.22	1.25/1.75: 71.42
<i>Kinixys belliana</i> M	2.8/5.6 (female)	50	3.15/5.6	56.25	2.8/3.15: 88.88
<i>Kinixys homeana</i> M	2.5/5.9 (male)	42.37	2.95/5.9	2.37	2.5/2.95: 84.74
<i>Kinixys erosa</i> M	2/4.8 (female)	41.66	2.4/4.8	50	2/2.4: 83.33

one a transverse triangle in the depth of the notch (visible in AM 9'93, Pl. 1V, Fig. 12a, Fig. 2b).

The hypoplastra are a little longer (in total length) than the hyoplastra in specimen AM 1'99 (as in the young male from Elisabethfeld EF 68'00) but slightly shorter in the large AM 9'93 and the neotype from Elisabethfeld, as is general in the compared Testudinidae; perhaps they are relatively longer than in *Mesochersus* n. g. (Fig. 11). The inguinals are clearly visible, differing from *Mesochersus* n. g., they form an arc of a circle in the depths of the inguinal notch; they are moderately reduced medially at their contact with the femorals (Pl. 11, Fig. 1e; Pl. 1V, Fig. 12a; Pl. V, Fig. 17; Fig. 1 b; Fig. 2b) as in *A. yniphora*, *S. pardalis* and *C. sulcata* but differ from *A. radiata* where the contact is longer. But they are reduced laterally, contacting only the rear of marginals 7 at the back of the peripherals 7, as in *C. sulcata*. (Pl. 11I, Figs 1-4) (Tabs 5b-6, characters 14, 15, 16). These possibilities of specific variations of the contact of the inguinals with the femorals and marginals exist also in the other Anicano-Ethiopian endemics. Nevertheless, the inguinals are particularly reduced in certain *Psammobates* and *Homopus* and are totally absent in *Mesochersus* n. g.

The posterior lobes appear to be relatively narrow in comparison with *Mesochersus* n. g. They are not particularly

shortened and the posterior margin is not rounded in contrast to *Pyxis*, *Kinixys* and *Chersina* (Tabs 5b-6, characters 22, 24). The posterior lobe is thus not spread out in length and breadth to hide the legs and tail during rest, in contrast with that of these genera. The posterior anal part is missing in the three most complete carapaces from Auchas, such that the comparison of the ratio posterior lobe length/ plastron is difficult; it is known to us by isolated xiphiplastra and in the neotype from Elisabethfeld. The margins of the lobe are convergent from the inguinal notch towards the xiphiplastral points, with a weak narrowing either in front of the femoro-anal sulcus (neotype and other specimens from Elisabethfeld, AM 9'93) or behind it (Pl. 11I, Fig. 6; Figs 8-9), or at the level of the sulcus (another specimen from Elisabethfeld) (character 13). In *Namibchersus* n. g. from Auchas and a specimen from Elisabethfeld, the narrowing displaced in front of the sulcus is similar to that of *A. yniphora*. The anal narrowing at the femoro-anal sulcus is a character that is present not only in *Manouria* but also in the other large forms. It is very pronounced in *C. sulcata* (low, wide form), quite strong in *Stigmochelys brachyularis* (Meylan & Auffenberg, 1987), from the Pliocene of Laetoli and even stronger in extant *S. pardalis* (males and females). A moderate narrowing (as in *Stigmochelys*) is also present in the European fossil *Cheirogaster*, envisaged as the possible sister group of *Centrochelys* (figures

in Broin, 1977; Lapparent de Broin, 2000a, b; Lapparent de Broin & Van Dijk, 1999). The narrowing, moderate, is less in female *A. radiata* than in the male. There is a possible case of narrowing in *Mesochersus* n. g. (Pl. V, figs 7, 8, 15).

As in the figure of the holotype of *?Testudo namaquensis* Stromer, 1926, and of the neotype, the anals are short in comparison with the part of the femorals covering the xiphiplastra, above all medially, in contrast to *Mesochersus* n. g., where they are equal to this part which is shortened. Dorsally, the anals have a hint of a division at the level of the xiphiplastral point, a primitive character preserved in the specimens of numerous fossil and extant Testudininei (including *Stigmochelys*, *Centrochelys* and *Astrochelys*) but absent in the small to medium African forms and *Mesochersus* n. g.

The dorsal margin of the scutes of the posterior lobe form a high relief, greatest at the sulcus of the scutes with the skin, higher towards the inguinal notch and lower at the level of the xiphiplastral points. This border is narrowed in the zone of the femoro-anal sulcus, but wide in front and behind, particularly towards the points (Figs 7b, 8b; Pl. III, 6b), more than in other forms. This notable width is clearly visible in the figure of the holotype of *?Testudo namaquensis* Stromer, 1926, as in the neotype from Elisabethfeld.

Limbs: The only remains of the limbs are fragments of humerus without heads, a fragment of distal end of a humerus 6 cm wide (corresponding to a carapace about 73 cm long), a fragment of distal end of a much bigger femur, 2 fragments of radius and ulna. It is impossible to find useful characters. The remains of limbs will be studied in the second part of this work thanks to the remains of much better quality that have

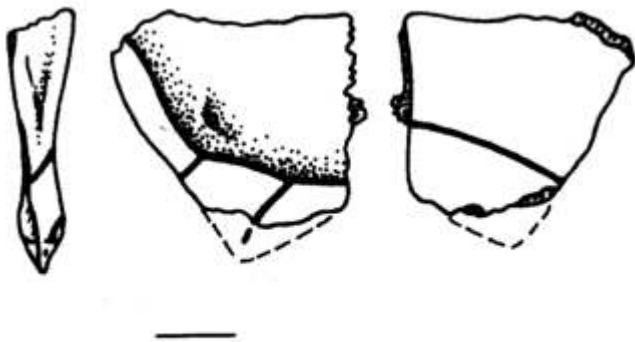


Figure 8 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 795, left xiphiplastron, a, b, c, lateral, dorsal, ventral views.

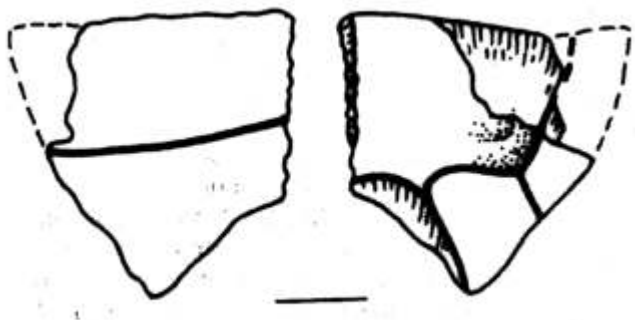


Figure 9 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 298, right xiphiplastron, a, b, ventral, dorsal views.

been recovered from other localities on the Atlantic coast, including, Elisabethfeld.

Their only contribution (femur fragment) is to show that *Namibchersus* n. g., could be larger than 81 cm. Recall that Stromer (1926) also mentioned the existence of a giant tortoise at Elisabethfeld based on a very large femur.

Comparative remark

Geochelone stromeri Meylan & Auffenberg, 1986, was based on a holotype from Langebaanweg, South Africa, E Quarry, 104 km NNW of Cape Town, Varswater Formation, Pelletal Phosphate Member, Pliocene, ca 4-4.5 Ma (see the catalogue in Lapparent de Broin, 2000a). The paratypes (two bits of a plastron) came from the "Namib Desert" and correspond in morphology to *Namibchersus namaquensis* (see above).

In contrast, the holotype (Fig. 2 of the authors) is difficult to identify generically. It consists of fragments of a dorsal carapace, with remains of a plastron, about 35 cm long. The peripherals of the bridge are raised into an arc of a circle. It does not belong to *Geochelone* because of the presence of a cervical. The latter, short dorsally and ventrally, with a short ventral margin, and incurved laterally on its dorsal surface, does not have the morphology of that of *Namibchersus* n. g., but more like that of *Mesochersus* n. g., without it being really similar. The pygal is short in comparison to that of *Namibchersus* n. g. The dorsal epiplastral lip is shorter and very convex. The relatively short gular projection has the margins almost parallel. The gulars end well in front of the plastron ventrally. No diagnostic piece corresponds to *Namibchersus* n. g. Perhaps it is more likely an ally of *Mesochersus orangeus* n. sp. This material belongs to a good species of an undefined genus and could be closer to the small African endemics than to *Namibchersus* n. g.

Conclusion

Tables 5-6 and the description given above show that *Namibchersus* n. g., differs as much from the small endemics and *Mesochersus* n. g., because its nuchal, of the suprapygal-pygals and vertebral 5 schema, and of the complete coincidence of sutures-sulci, as from the two large African endemics, mainly because of the absence of the cervical and the v-shaped nuchal notch present in the latter. The outline of the latero-anterior borders of vertebral 1 of *Mesochersus* n. g., also show that this scute was more reduced in width, as in small endemics, than it is in *Namibchersus* n. g.

Namibchersus n. g., is more evolved than *Gigantochersina* (where its morphology is known) by the features indicated above and in the diagnosis, and it is morphologically close to *Astrochelys yniphora*. The attribution of the two extant species of *Astrochelys* to the same genus is sometimes questioned. *A. radiata* has more primitive features than *A. yniphora* and *Namibchersus* n. g. The two extant species do not have many derived characters in common among those studied here, applicable to the Namibian fossils, except for the arched form and the same geographic and temporal distribution (Madagascar, extant)!. At the best we can consider the existence of a super-taxon incorporating *Namibchersus* and the two species attributed to *Astrochelys*. But parallel evolution of the characters shared by these forms is just as possible. A more comprehensive cladistic analysis, taking into account more characters and more taxa (including the other

Table 5. Some discriminant characters of the terrestrial turtles examined. They show the principal morphological differences between the new Namibian taxa and the other principal African taxa and some comparable Malagasy and Asiatic taxa. These characters are adapted to the present study taking into account the preserved skeletal parts, and could not be sufficient for a generalized study of the phylogenetic relationships of the infrafamily. State 0 is primitive for the group; the others are derived and alternative. Some of them may be primitive or reversed (1, 9, 12) at state 0, or primitive in the juvenile of large-middle forms or in the adult of small African endemics by paedomorphosis (11, 12). In some taxa, characters may present successive states according to element growth (19, *Namibchersus* n. g.). A better sample of each taxon ought to yield some other examples and the state of several characters has always to be considered taking into account the growth state. Character 20, see details in Table 4.

1- V shaped nuchal notch	no 0	yes 1	strong 2		
2- elongated anterior peripherals/ nuchal	weak 0	moderate 1	much 2	much more 3	
3- cervical	yes 0	at least dorsally reduced in width and + or - in length 1	at least dorsally absent 2	fully absent 3	
4 - vertebral 1/nuchal	at least as wide to wider 0	slightly wider to slightly narrower 1	always narrower 2		
5- marginal sulci ending externally by protruded points or incisions	no 0	points 1	points or incisions 2	incisions 3	
6- suprapygals/pygal and vertebral 5/ marginals 12	Geoemydinae type 0	" <i>Geochelone</i> " type 1	small african endemics type (<i>Kinixys</i> , <i>Psammobates</i> , <i>Homopus</i> , <i>Chersina</i>) 2	mixed 1 + 2 types: 3	
7- marginals 12	not fused 0	fused 1			
8- upwards elongated (lateral view) bridge peripherals and marginals	no or weakly 0	yes			
9- gular protrusion	long 0	few protruded 1	very long 2	reduced 3	
10- dorsal epiplastral lip / entoplastron	anterior 0	at anterior limit 1	above prolonged 2		
11- dorsal epiplastral lip relative to entoplastron and dorsal face	not elevated and concave dorsal face 0	slightly elevated, flattened 1	elevated, moderately convexe 2	elevated, flattened to concave 3	elevated, flattened to much convexe 4
12- posterior border of dorsal epiplastral	as wide as gulars	narrower than gulars	wider than gulars		
13- anals narrowing	no to weak (straight border) 0	pronounced 1	much pronounced 2	no, rounded border 3	
14- inguinal	triangular (laterally long) 0	rectangular or in arc (laterally short) 1	apparently absent 2		
15- anterior inguinal + marginals contact	+ anterior part of marginal 7 : 0	+ posterior part of marginal 7: 1	+ marginal 6: 2	+ posterior marginal 7 or 8: 3	absence 4
16 - inguinal +femoral contact	long 0	short 1	much reduced 2	absent 3	
17-first neural	hexagonal +short posterior sides 0	quadrangular or hexagonal 1	quadrangular 2		
18- neural series	few differentiated compared with Geoemydinae 0	variably differentiated (hexagonals, octogonals/quadrangulals/hexagonals) 1	well differentiated 2		
19-entoplastron shape	longer than wide 0	widened, length = width 1	more widened: wider than long 2		
20 :entoplastron size (w and L) with regard to epi-hyoplastral suture. % at least in one dimension:	large 0 50%	large to moderate 1 40 to 50%	reduced (at least in width) 2 30-40%	much reduced (w and L) 3 < 30%	
21- dorsal hinge	no 0	yes 1			
22- xiphiplastral posterior border contacts carapace posterior border	no 0	yes 1			
23- cervical protrusion	no 0	yes 1			
24 - rounded posterior lobe	no 0	yes 1			

Testudininei but also the Geoemydinei) and with a redefinition of the extant genera, will provide a test for this hypothesis.

Remarks on the characters in tables 5 and 6: Study of the characters shows a strong capacity for homoplasy and a mosaic distribution. The taxa are easy to distinguish but, with so

few elements, their phyletic relations are not, even within the monophyletic group of "African-Ethiopian endemics".

1 * and 2*: *Chersina angulata* may possess a secondarily completely elongated nuchal like the anterior peripherals, attenuating the nuchal notch. Its secondary elongation and that of the

anterior peripheral plates which surround, them is clear from the relationship to the rest of the carapace.

6: Five extant specimens' of *Geochelone elegans* (type species of the genus) from Sri Lanka, the presumed type locality of the species, were observed in Vienna (NHMW) during submission of this article to the publishing committee. The suprapygal-pygals schema is not that of *Centrochelys* and *Stigmochelys*, so-called "Geochelone". The schema, more primitive as a whole, presents individual variations that occur in African endemics and *Testudo* s. s. : suprapygal 1 and 2 are separated transversely; suprapygal 1 elongated on only one side as far as peripheral II or on both sides, its posterior margin being either straight or rounded in the pygal but smaller than the anterior one, as in *Mesochersus* n. g. (Pl. VI, Fig. 6), or as in certain *Chelonoidis carbonaria* from South America. The sulcus of vertebral 5 traverses suprapygal 2 or follows the straight suprapygal 2 - pygal suture. Other characters of the nuchal, vertebral 1 and the neural series of *G. elegans* recall the African endemics. The epiplastral lip is similar to that of *Psammobates oculifer* and *P. geometricus* (narrower and longer than in *P. tentorius*). Two specimens of *G. elegans* and *G. platynota* observed in London (BM NH) present the so-called "Geochelone" schema (lenticular suprapygal 2 traversed by the V 5), but they possess a more primitive pygal, which is still short and wide as in the African endemics and *Manouria*, differing from the large extant African forms and *Namibchersus* n. g. It is definitely necessary to distance the latter from extant *Geochelone elegans* the lineage of which could either be close to that of *Mesochersus* n. g., and the African endemics, or have evolved in parallel.

In the small Ethiopian-African endemics, the suprapygal block has four sides, as in the so-called "Geochelone" schema, posterior to *Manouria emys*; it may be subdivided transversely (primitively or secondarily) into 2 suprapygals (*Pyxis*) or secondarily into three suprapygals (*Kinixys*); it can retain a wide posterior expansion (*Pyxis* (*Pyxis*)) or a narrow one in the elongate pygal, slightly notched at the front (the case with *Mesochersus* n. g.), or suprapygal 1 can encircle the second at the front, but without posterior expansion in the elongated pygal. These cases parallel the situation that one finds in palaeartic Eurasian forms (*Testudo* group; Bour, 1987) except the posterior expansion of the suprapygal 2 in the pygal and the limited posterior expansion, which does not occur in Eurasia except in *Agrionemys horsfieldii*. Furthermore, in the African ones, the fused vertebral 5-marginals 12 sulcus is much more variable in its trace, either at the height of the pygal-suprapygal suture, or more to the rear, or with a slight expansion of the marginal 12 on the suprapygal (single or double). There may be variations in the straightness or otherwise of the margins of the pygal (straight or angulated borders), as in the Euro-Asiatics. But when the suprapygal block is of the kind that is found in the *Testudo* group in the Africans, the vertebral 5 - marginals 12 schema is different and vice-versa. There is always a small difference between them to which we add the greater verticality of the suprapygal block (*Kinixys*, *Homopus*, *Pyxis*, certain *Psammobates* with protuberances of the group *tentorius*) and the concavity and convexity of the elements in the Ethiopian endemics (in particular see *Kinixys*, *Psammobates* with protuberances or with points of the *oculifer* group). For example, *Ch. angulata* like "*Testudo*" *hermanni* has a pygal with angular lateral

margins and there is almost identity when the sulcus between the scutes come into contact with the suture which separates the plates (a possible variation in *Ch. angulata*), but in the former the marginals 12 are fused and they are not in the latter. It was this that was demonstrated by Gmira (1995) but too schematically and with only a part of the possible variation.

9: 1*3, the presence of a poorly developed projection of the gular lip (*Centrochelys*, *Namibchersus*, *Mesochersus*, *Stigmochelys*) or its absence (*Stigmochelys*, *K. belliana* and *K. homeana*) show that the slightly developed stage is not homologous to the supposed primitive state 0 of the Geomydinei but is secondary and is even accentuated in the case of absence (state 3).

11: 2*, *Psammobates geometricus*: dorsal epiplastral lip varying between low and clearly concave medially (young) to raised and slightly concave medially.

12: gular lip wide and enlarged at the rear in comparison with the gulars, is not necessarily homologous in all cases; it could be primitive in some ("*M. impressa*"), pedomorphic (*Homopus* and *Psammobates*) or secondarily derived (*S. pardalis*). The morphology of the lip is specific and its parameters are more numerous than those in the table (see text). The lip is particularly wide and short in *Homopus* and *Psammobates* where quite frequently, with its dorsal concavity, it appears as pedomorphic. The dorsal epiplastral lip of *Pyxis* is closer to that of *Homopus*, and a bit longer than that of *Psammobates*.

16: a young *Homopus* sp., the flattened *Homopus* sp.-like *Malacochersus* from Namibia observed at Windhoek and *Homopus signatus cafer*, the type of *Testudo cafra* Daudin, 1801, have a short inguinal-femoral contact.

17*: the *S. pardalis* observed (BM, NH; MNHN; NMK; Windhoek) all have a quadrangular neural 1. *S. pardalis* with a hexagonal neural I with small posterior sides was noted by Cooper & Branch (1999) in Namibia.

17 **: hexagonal neural I with enlarged posterior sides like the anterior ones instead of being short (derived character from state 0).

19, 20 (Tab. 6): the long entoplastron of *Psammobates oculifer* and *H. areolatus* as in a "*M. impressa*" is narrow in comparison with that of "*M. impressa*". It is reduced. The reduction in size can be accomplished in two stages: firstly by narrowing in *Homopus* and *Psammobates* then by shortening in *P. geometricus* and *P. tentorius*. The long entoplastron is primitive and in some ways pedomorphic: the longer entoplastron is more frequent in the young of the large forms (and becomes wider in the adults such as in *Namibchersus*) and in the medium sized forms (*Chersina*, *Kinixys*) and the small forms (pedomorphy). In *Kinixys*, it seems wide in the anterior lobe because of the narrowing of this towards the front of the epiplastra, particularly in *K. b. belliana* and *K. b. nogueyi*. The narrowing of the entoplastron is equivalent to that of *Mesochersus*, but this one has a more shortened entoplastron than in *Kinixys* and young *Namibchersus*, as in certain *P. tentorius* from Namibia. The entoplastron of *Pyxis* is reduced as in *Homopus*, *Psammobates* and *Chersina*.

22 ***: a specimen of *P. tentorius*, from Namibia has a particularly elongated posterior margin of the carapace (male) and thus the posterior lobe does not touch the margin.

24*: In a young *Homopus* sp., from Namibia, the posterior lobe may be rounded under the scutes as in a female *Ch.*

angulata; it is bifid in the adult of *Homopus areolatus* as in the male of *Ch. angulata*. The short and rounded posterior lobe of *Chersina* and *Kinixys* is also present in *Pyxis* (Bour, 1981).

Namibchersus* aff. *namaquensis (Stromer, 1926)

Synonymy: *Geochelone namaquensis* Stromer, 1926 - Meylan & Auffenberg, 1986: 281; Fig. 1 A, C, SAM-PQAD-2789 (Arrisdrift); ?, Fig. 1 B, SAM-PQ-N-141 (Namib Desert).

Locality and age: Arrisdrift. Early Miocene, ca 17 Ma. (Hendey, 1978, Pickford *et al.*, 1996). ?, "Namib desert". Age probably Early Miocene, and unidentified locality.

Material: MSGN. Old collections from Arrisdrift (see Hendey, 1978, Chelonia, gen. and sp (spp). indet.); 1 fragment of carapace with two and a half neurals and the adjacent extremity of the pleurals, PQ AD 73; 1 proximal fragment of right pleural 1, PQ AD 1293; 1 right epiplastron, PQ AD 2789, Meylan & Auffenberg, 1986, Fig. 1 A, C; 1 left xiphiplastron, PQ AD 3478; 1 tibia, PQ AD 2108; 1 coracoid, PQ AD 608. New collections (1994-1998). Pleurals: 7 remains; 2 peripherals; 2 partial humeri including AD 160'94; 1 partial tibia, AD 225'94.

Description and comparison: The specimens from Arrisdrift

correspond to a large species of tortoise. The xiphiplastron PQ AD 3448 (Fig. 10), median length 6.6 cm, corresponds to a plastron about 40 cm long, in comparison with the neotype from Elisabethfeld. The epiplastron PQ AD 2789 (Meylan & Auffenberg, 1986, Fig. 1 A, C), 9.5 cm wide, corresponds to a plastron about 50 cm long, in comparison with the neotype from Elisabethfeld.

The limb bones do not permit comparison, other than to show that there were some very large specimens. A tibia is 14 cm long, which would correspond to a carapace 110-115 cm long by comparison with *Cheirogaster perpinina* from the Pliocene of Perpignan (France).

The xiphiplastron conforms to that of *Namibchersus* n. g., by the triangular form of the two xiphiplastra at the anals (short anal notch in an obtuse angle) and above all by its dorsal surface (Fig. 10a). It shows the same great width of the dorsal margin of the anals as in *Namibchersus* n. g. In contrast there is no hint of the dorsal division of the anals.

The epiplastron conforms to *Namibchersus* n. g., by the gular morphology with convergent margins and by the dorsal epiplastral ridge moderately raised, with a flat dorsal surface. It terminates just in front of the entoplastron. The epiplastron differs ventrally from that of *N. namaquensis* by the clearly longer ventral projection of the gulars and the gulars not covering the entoplastron. Dorsally, the gularo-humeral sulcus bends from front to back in a curve before ending at the posterior border of the lip clearly medially in comparison with the anterior margin of the projection, instead of laterally in

Table 6: Distribution of character states 1 to 24 of Table 5 in: a, "*Manouria*" *impressa* (extant Southeastern Asia) considered to be the basic extant representative of the Testudininei (fossil forms not taken into account); *Gigantochersina*, lower Oligocene from the Fayum, the oldest named terrestrial African testudinineine; the middle-large and large "Ethiopian" forms and *Namibchersus* n. g.; and the extant Indian *Geochelone elegans*, type of the genus, incorrectly attributed to the large African forms. b, *Mesochersus* n.g. and the medium-small African endemics. Excluded: insularized modified forms from the Indian Ocean. La: large adult; M, middle adult; S, small adult ; y, young; ju, juvenile.

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
"M". <i>impressa</i> M	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Gigantochersina</i> La	0	1	0	0	3	1	1	1-	0	0	1	?	0-1	?	?	?	1	1	1	0	0	0	0	0	0
<i>A. radiata</i> M	0	1	0	0	3	1	1	1	0	0	2	1	0	0	0	0	2	2	2	1	0	0	0	0	0
<i>A. yniphora</i> M	0	1	0	0	1	1	1	1	0	1	3	0	0	0	1	1	2	2	1+	0	0	0	0	0	0
<i>S. pardalis</i> La	1	2	3	1	2	1	1	1	1	2	4	2	1	0	1	1	1*	2	1+	0	0	0	0	0	0
<i>C. sulcata</i> La	1	1	3	1	3	1	1	1	1	0	3	0	2	1	1	1	2	2	0	ju	0	0	0	0	0
<i>Namibchersus</i> n.g. La	0	1	0	1	1	1	1	1	1	0-2	2	0	0-1	1	-1	1	2	2	0-2	1	0	0	0	0	0
<i>G. elegans</i> S-M	1	1	3	2	3	3	1	1	1	1	2	1	1	1	3	3	1	1	1	1	0	0	0	0	0
Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
<i>Mesochersus</i> n.g. n.sp. MS	0	1	0	2	2	2	1	0?	1	0	2	1	0	(1)	2	3	3	1	1	1	0	0?	0	0	0
<i>H. areolatus</i> S	2	1/2	1	2	1	2	1	0	1	0	0	0	0	0	1	3	2	2	0	2	0	10	1	0	*
<i>P. tentorius</i> S	1	1	0	2	3	2	1	0	1	0	2	0	0	1	1	1/0	0*	1	2	1	0	1	0	0	0
<i>P. geometricus</i> S	0	2-	0	2	2	2	1	0	1	0	2*	0	0	0	1	1	0	1	0	3	0	0	1	0	0
<i>P. oculifer</i> S	0	2-	0	2	2	2	1	0	1	2	2	2	0	1	1	2	0	1	0	2	0	0	1-	0	0
<i>Ch. angulata</i> M	1	2*	1/+-	1	1	2	1	0	2	2	3	1	3	1	1	2	1	2	0	3	0	1	0	0	1*
<i>K. belliana</i> M	1	2	0	2	1	2	1	0	1*	2	3	0	3	0	2	0	0	0	0-	0	1	1	1	1	1
<i>K. homeana</i> M	0	3	1	0	1	2	1	0	1	2	3	1	3	0	2	2	0	0	0-	1	1	1	1	1	1
<i>K. erosa</i> M	0	3	2	0	1	2	1	0	2	0	3	1+	3	0	2	2	0	0	3	1	1	1	1	1	1

comparison with this margin in *N. namaquensis*.

It must belong to the same genus *Namibchersus* n. g., but to a new species which requires more elements for it to be properly characterised.

***Mesochersus* n. g.**

***Mesochersus orangeus* n. sp.**

Synonymy: *Chelonia*, gen. and sp(p). indet. - Hendeby, 1978: 2, *pro parte*.

Chersina sp. - Meylan & Auffenberg (1986): 288.

Etymology: Genus, from the Greek: "Meso", by allusion for the size of the tortoise, and "chersos", earth, continental. Species: from the name of the River Orange.

Type locality and age: Arrisdrift. Fossil meander of the proto-Orange, north bank of the present day Orange River, southern Namibia, Early Miocene, ca 17 -17.5 Ma. (Hendeby, 1978, Pickford *et al.*, 1996)

Diagnosis of the genus and species: Medium sized form of terrestrial Testudinidae with carapace from 16 to 20 cm long, elongated and probably moderately arched. Pygal rather wide, slightly convex and high, with short anterior notch for the suprapygal 2 and an overlap of the sulcus of vertebral 5 on the front of the peripherals 11 (small African endemic schema). Points or entries to the extremities of the marginals on the peripherals. Morphologically close to *Namibchersus* n. g., by the peripherals of the bridge and posteriors high and narrow, by the anterior border and the proportions of the nuchal with a cervical, differing by its ventral margino-cervical border slightly elongated under the nuchal, terminating in a weak overhang above the rest of the ventral slightly concave surface of the plate, with a totally transversal posterior border of the marginals and cervical; vertebral 1 narrower. Anterior pi astral lobe clearly but moderately narrowed towards the front, trapezoids, with lateral margins regularly convergent towards the gular projection. Ventral gular projection moderate with convergent lateral margins and rounded anterior border (slightly sinuous), with the triangular gulars elongated and encroaching more or less onto the entoplastron; dorsal epiplastrallip long, with dorsal surface barely convex narrowing to the rear, moderately raised, recurved into a small overhang well in front of the entoplastron; gularo-humeral sulcus incurved and not elbowed; entoplastron almost as long as wide, big; humero-pectoral sulcus regularly curved behind the entoplastron. Posterior lobe wide with lateral borders convergent towards the xiphiplastral points without femoro-anal narrowing, or with a clear narrowing at the femoro-anal sulcus in one individual (if it belongs to the species). Rather wide dorsal femoro-anal margin. Wide moderately long anal notch. Anals particularly short. Neither auxiliaries nor inguinals visible.

Bridge > Anterior lobe ca= Posterior lobe

Abdominals > Gulars > to < Humerals > Femorals > Anals > Pectorals.

Material: Holotype: MSGN, AD 389'96, Pl. 1V, Fig. 2 and Pl. V, Fig. 1, left epiplastron.

Referred material: MSGN. Referred material figure in Meylan & Auffenberg, 1986: PQ AD: 1984; Fig. 5G (here Pl. V,

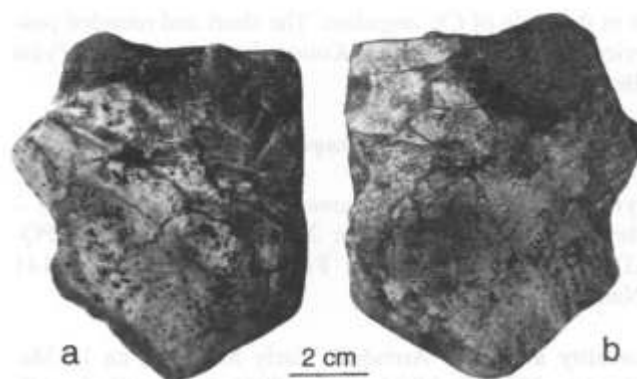


Figure 10 - *Namibchersus* aff. *namaquensis* (Stromer, 1926), Arrisdrift, PQ AD 3448, right xiphiplastron, a, b, ventral, dorsal views.

Fig. 10) and 1294, Fig. 5H, nuchals; 1436, neural 1, Fig. 5 D; 898, neural octagonal, Fig. 5 C; pygal reconstituted on the basis of 1527 and 3084, partial pygals, Fig. 5 E (here, Pl. VI, figs. 6 and 7); 1505, left peripheral 3, Fig. 5 F; 73a, right hyoplastron, Fig. 5 B; 832, right hyoplastron, Fig. 5A. Mentioned but not figured: 1251, right hypoplastron. Not mentioned: 1521, right hypoplastron; 73e, right peripheral 9. Mentioned but not found: PQ AD 512, hyoplastron; 2501, entoplastron; 876 and 2262, hypoplastra; 1141 and 1148, xiphiplastra. *Inventoried material and identified to body part in the new collections AD# 94-98:* 1 nuchal, 533'97; 1 neural 1, 72'98; 5 pleurals 1, right 563'94, right 606'97, part of left 474'98, partial left 165'95; left 208'95; pleurals 1-2 and fragments of neurals 1-2, 207'95; 3 pleurals, one even pleural 487'95, 5 right (7) 832'97 and 6 right, 290'95; 13 peripherals: 1 left 429'95 (7); 1 right, 564'94; 3 left, 12'97 and 479'98; 4, 5 or 6, 347'95; 4e (7) left, 592'98; 7 right, AD 339'95; 9 right, 345'96 and 471'98 (7), 97 562'97; 10 left, 478'98; 11 right, 159'98 and 564'94; 1 epiplastron (holotype) 389'96; 4 entoplastra, 66'95, 320'95, 363'96, 469'97; 5 hyoplastra: 6'94, 185'95, 368'86 (partial), 651 '97, left, 472'98, right; 9 hypoplastra: 485'94, 257'97 (partial), 715'97, 42'98, 156'98 (partial), 480'98, 407'95, right; 361'96, 477'98 (partial), left; 3 xiphiplastra, AD 468'98 and AD x, right, AD 470'98, left; including AD 339'95, right peripheral 7 and AD 407'95, right hypoplastron, found together, coming from the same individual. *Total pieces seen* (preliminary examination), AD # 94-98 and PQ AD: about 100 pieces located on the skeleton, 30 unlocalised, 9 limb bones: 8 femora and humerus more or less fragmented (AD # 94-98); 1 phalanx (AD 256'95).

Description and comparison: This new taxon is almost entirely represented by isolated elements. The locality is in a fossil meander of a river and the surface extent is limited (about 300 m² by about 40 cm thickness). Even though the specimens were recovered over several years we consider it likely that the material corresponds to a certain biological homogeneity.

The specimens belong to individuals with carapaces some 16-20 cm long.

In comparison with a specimen of *Psammobates tentorius* from Namibia the carapace of which is 12cm long and the plastron 10A cm long, the specimens in Pl. 1V-V - VI are:

carapace 16 cm: peripheral 11, Fig. 12; carapace 18 cm long: nuchal Fig. 1; carapace 20 cm: pygal Fig. 6. Plastron Fig. 11, reconstituted from similar sized individuals, is 18 cm long, which corresponds to a carapace with the same approximate length (18 to 20 cm). The holotype, an epiplastron 2.9 cm maximum width, compared to an extant epiplastron 1.9 cm, would correspond to a plastron about 15.5 cm long for a carapace about 18 cm long.

The elements of the dorsal carapace are insufficient for reconstruction. Only the plastron is easy to reconstruct to a good resemblance and on its own is sufficient to define a new taxon. The problem with the dorsal part is that there is an ensemble of four plates, of which three were found conjointly in 1998, which do not correspond to the rest of the material: AD 429'95, left peripheral 1, Pl. VI, Fig. 9; AD 592'98, left peripheral of the bridge (4e?), Pl. VI, Fig. 8; AD 471'98, right peripheral 9, Pl. VI, Fig. 10; AD 159'98, right peripheral 11, Pl. VI, Fig. 11. The first three are wide (antero-posteriorly) and short (dorso-ventrally) and belong to a carapace about 30 cm long, whereas the other small peripherals from the site are dorso-ventrally high and antero-posteriorly narrow, such as peripheral AD 339'94, Pl. V, Fig. 14, and belong to a smaller species (18 to 20 cm). Peripheral AD 339'94 belongs to an ensemble of plates of several individuals, found together and with the same appearance, of which a hypoplastron of the same individual as the peripheral, left pleural 1 and right pleurals 1 and 2 and a pleural 5 make the link with the other isolated pieces and reveal that they belong to the same taxon, distinct from that of four plates questioned above.

Among these, the anterior peripheral 1 and the posteriors 9 and 11, show the scutes of costals 1 and 4 and of vertebral 5 overlapping the plates instead of coinciding with the pleuro-peripheral suture. The preserved nuchals PQ AD 1984 and AD 533'97 (Pl. V, Figs 10a, 11) do not coincide with the peripheral 1 AD 429'95, because they indicate a costal 1 which does not encroach the nuchal whereas this peripheral 1 AD 429'95 shows the contrary. The wide and short peripheral of the bridge AD 592'98 indicates a coincidence of the sutures of pleurals and the sulci as do the narrow and high plates at the level of the bridge. Peripherals 11 AD 564'94 (Pl. VI, Fig. 12a), concord with the pygals preserved (Pl. VI, Fig. 6 and 7) and the high peripherals, revealing a coincidence of sulci and sutures of the front and rear borders, except for a small prolongation of vertebral 5 centrally in front of this peripheral 11. On the contrary, the other peripheral 11, AD 159'98, (Pl. VI, Fig. 11a) shows a marginal border which is longer and wider than the peripheral one, as in the other wide and short peripherals at the front and back (Pl. VI, Fig. 9 and 10) and the vertebral 5 covering the front of the pygal, contrary to the two preserved pygals (Pl. VI, Figs 6-7).

These four plates differ from all the others by proportions (greater width, reduced height) and their scutes (overlapping onto the peripherals at the front and back and on the pygal) must on this basis belong to another form, closer to *Psammobates* and *Homopus* (see below). The wider form of the plates and the covering by the scutes of the pleural disc are more primitive (geoemydinian characters) or are reversal.

There are also two types of neural I, one with four sides,

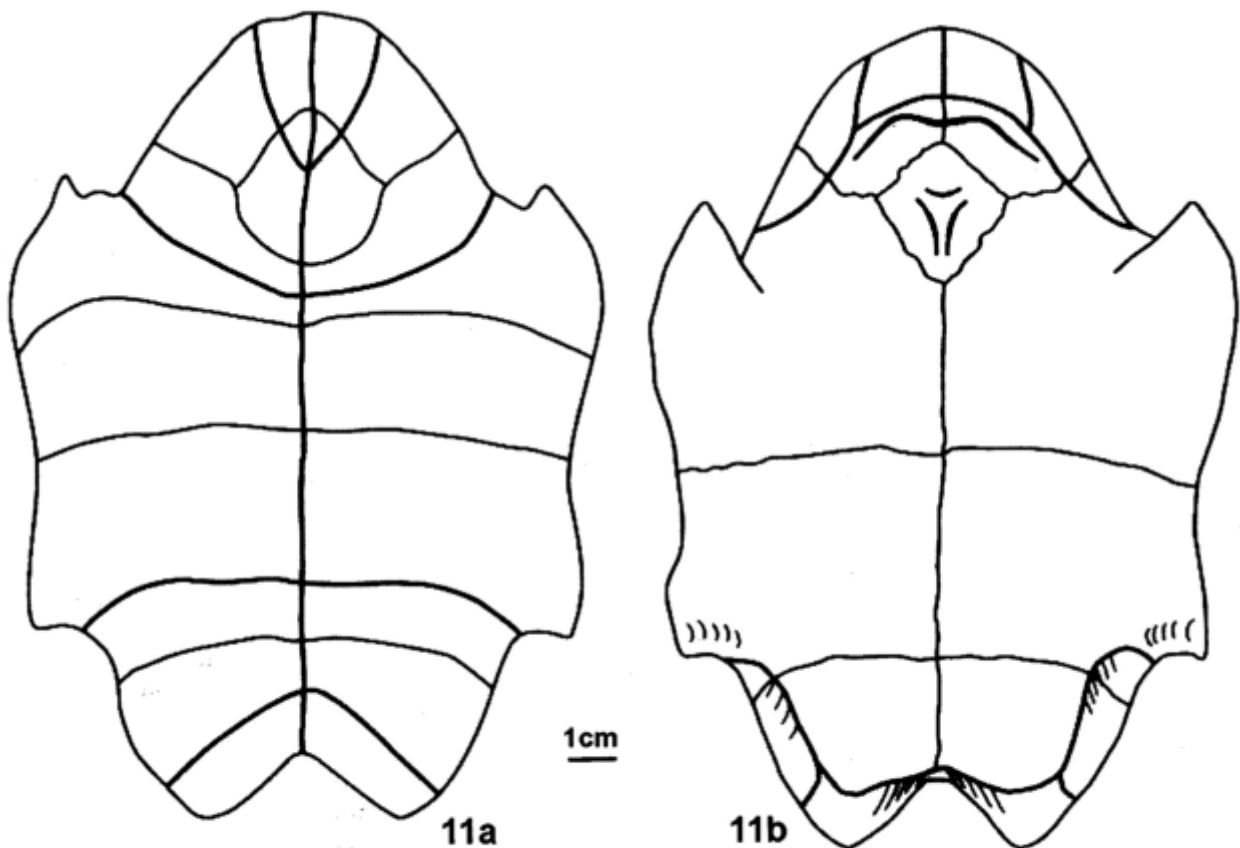


Figure 11 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, plastral reconstruction from the figured specimens Pl. 4 and 5: AD 389'96, epiplastron; 469'97, entoplastron; 185'95 and 472'98, hyoplastra; 407'95, 42'98 and 361'96, hypoplastra; 470'98 and 468'98, xiphiplastra; a, b, ventral, dorsal views.

which is more derived (Pl. VI, Fig. 3), the other hexagonal with small posterior sides (more primitive) (Pl. VI, Fig. 5). In the extant small African endemics, neural 1 is hexagonal with small posterior sides or with the posterior sides almost equal to the anterior ones (derived character), except sometimes in *Homopus* in which it is quadrangular. This difference between 4 and 6 sides may also well be an individual variation than a specific difference within the African endemics.

Dorsal carapace: Several plates have very marked growth annuli (Pl. IV, Fig. 6; Pl. V, Figs 12, 14) and because of this the material appears to be heterogeneous. This character exists within extant species as a function of differing environment.

In *Mesochersus orangeus* n. g. n. s., (Pl. IV, V, VI; Fig. 11), there is no dorsal hinge between pleurals 4 and 5 and peripherals 6 and 7, contrary to only *Kinixys* (box tortoise) (Tab. 5, character 21). The anterior border of the nuchal is straight (character 1) and not notched nor sinuous, as in certain specimens of *P. oculifer* and as in *Namibchersus* n. g. The anterior border can't be elongated considering the moderate length of the nuchal, as in *Namibchersus* n. g., *Homopus* and *Psammobates* in comparison with *Chersina* and *Kinixys* in which the border is elongated (character 2). The nuchal is wide and short, slightly curved, with a short cervical (character 3), not narrowed, a bit wider than broad, without medial projection (character 23). The ventral surface of the nuchal is slightly concave, with a moderately long scute border and a slight overhang above the rear of the plate, as in *Homopus* and *Psammobates*. Nuchal PQ AD 1984 (identical to nuchal AD 533'97) was attributed to *Chersina* by Meylan & Auffenberg, 1986. The major difference from *Chersina* is its weak length, the transverse anterior border which is neither projecting nor notched, and the ventral margin not more elongated and not notched at cervical, without rounding of each side. There are points or re-entrants in the preserved peripherals (from the bridge to the back) (character 5). These peripherals are raised, as in *Chersina* and *Kinixys*, but are relatively narrower as is common in the large forms; they don't have the border raised towards the rear as in diverse *Kinixys* and *Psammobates*: they descend vertically as in *K. belliana nogueyi* and the large African forms including *Namibchersus* n. g. It is not possible to know whether there was an elevation of the medial border of the peripherals and marginals of the bridge in an arc of a circle (character 8). The pleural disc is preserved by several pleurals 1, all similar to each other, several other pleurals and some neurals: there is a neural series which is clearly differentiated (character 18) (Pl. VI, figs 1,3,5) and an alternation of narrower even plates and wider odd ones, medially (character of the terrestrial tortoises Testudinidae). Neural 1 is either hexagonal with small posterior sides, or quadrangular (character 17) as in *Gigantochersina* and *Stigmochelys* and certain *Homopus*, if the two neural 1 plates conserved do indeed belong to the same taxon. Vertebral 1, which is relatively narrow, does not cover all the nuchal laterally. According to the trace of the lateral anterior border vertebral 1 on the nuchal and the latero-posterior border of this vertebral 1 on the pleural, the posterior sulcus of marginal 1 with costal 1 follows the suture of peripheral 1 with pleural 1 (coincidence of the anterior pleuro-peripheral): costal 1 does not encroach onto peripheral 1 differing from most of the small African endemics and the large primitive forms as we saw above. The pygal is wide and high, with a short median notch

for the posterior border of suprapygal 2 (not preserved). The sulcus of marginals 12 is absent, the two scutes being fused (character 7). The posterior sulcus of vertebral 5 (Pl. VI, Figs 6, 7 and 12) does not cut the pygal but the suprapygal or suprapygals, incurving towards the rear on peripheral 11 (as in a *P. tentorius* from the Karroo and certain *P. geometricus* from South Africa in Broadley, 1997, Fig. 1A, differing from other *P. geometricus* preserved in the Paris Museum) or it follows the pygal-suprapygal suture (as in certain *Pyxis arachnoides*), then climbs upwards laterally towards the suprapygal or the limit of pleural 8 (Pl. VI, Fig. 12a). This is a schema typical of "small African endemics" (character 6), principally because of the sinuosity of the posterior sulcus of vertebral 5 and the form of the pygal.

Plastron: *Mesochersus orangeus* n. g. n. s., is mainly established on its plastron formed of plates which are homogeneous in size and proportions and adult on the basis of their thickness and size, without traces of ligaments between the sutures (Pl. IV, Figs 1-9, V Figs 1-9; Fig. 11).

The plastron is massive, relatively wide and short.

The anterior lobe is trapezoidal narrowing at the front but less than that of *Kinixys*. Its lateral borders are clearly more inclined towards the middle (convergent) than in *Namibchersus* n. g., and without an elbow or epiplastral narrowing in front of the gular. The gular projection is weak (character 9), its borders convergent and rounded in front, with just a very limited sinuosity recalling the primitive anterior gular division. Dorsally, the dorsal epiplastral lip is elongated and raised into an overhang but it remains well anterior of the entoplastron; its dorsal surface is barely rounded, regularly from right to left and from front to back; the posterior margin is narrower than the gular projection at the front, to the gularo-humeral sulcus; the lateral dorsal margins of the gularo-humeral sulcus are a bit divergent towards the rear. This morphology of the lip is different from that of all the African endemics, small and large. Notably, there is no marked crest medially at the dorsal gularo-humeral sulci, with a medial flattening, in contrast to *Kinixys* and *Chersina*. As in *Namibchersus* n. g., it is less derived than in any of these forms, but all the same is different from the lip of this one by the narrowness of its posterior border and its smooth lateral rounding. The entoplastron is large in the anterior lobe, almost as wide as long (Tab. 5b, characters 19-20), neither enlarged in the adult thereby differing from *Namibchersus* n. g., nor reduced in length and/or width, thus differing from the smallest African endemics, nor elongated as in *Kinixys* (in certain *K. belliana*, the anterior lobe is very narrowed which makes the entoplastron apparently wider). The gulars overlap by a quarter (Pl. VI, Fig. 1b) to more than a third (Pl. VI, Fig. 3) of the entoplastron, which means that the gulars are above or below the humerals in length; they are relatively narrow (specifically variable characters). The humero-pectoral sulcus is also more separated from the entoplastron than the abdominals, and its lateral trace is regularly incurved in all the specimens, less elbowed than in *Namibchersus* n. g. There is no apparent axillar in the depths of the auxiliary notch, but a slight depression in width where one ought to find thin, lightly corneous skin replacing it.

The bridge is long.

Posterior lobe. It is short, about equal to, the anterior one, but wide compared to *Namibchersus* n. g., almost the same

as in *Psammobates oculifer* from Namibia. The anals are relatively shorter than in *Namibchersus* n. g., and *P. oculifer* (generally specific character). The xiphiplastra are variably short and wide in the African endemics but in certain ones they are clearly rounded (character 24), and thus wider, touching all the posterior border of the carapace recurved to this effect (character 22) in order to better cover the posterior space and protect the legs and the tail (*Chersina*, *Kinixys*) whereas in others, the margins of the posterior lobe are convergent, giving a more narrowed aspect (certain *P. tentorius*) or in contrast they are less, as in *Mesochersus* n. g., and *P. oculifer*. In *Homopus* and *Psammobates*, these characters vary specifically. The anal notch is wide, almost as in *Namibchersus* n. g., but a bit longer. Dorsally, the margin of the scutes is wide but more regularly than in *Namibchersus* n. g. The femoral dorsal margin of the xiphiplastra and the rear of the hypoplastra rise strongly towards the inguinal process. There is no hint of a subdivision of the anals in front of its points, not more than in the small African endemics. There is no femoro-anal narrowing except in the right xiphiplastron AD x, (Pl. V, Fig. 15): this could be due to a sexual difference as in *G. ammon* and *Astrochelys radiata* unless the specimen does not belong to the species.

There is no inguinal apparent on any of the 9 hypoplastra preserved, but a slight depression is visible on specimens AD 715'97 (Pl. V, Fig. 9) and AD 407'95 (Pl. IV, Fig. 6) and a residual scute, very latero-ventral in position, is present against marginals 7 and 8 visible only on peripheral 7 (Pl. V, Fig. 14) as in *Homopus areolatus* (MNHN, H). On the hypoplastron of the same individual (Pl. IV, Fig. 6), there is also a short depression, in the arc of a circle in the depths of the notch, in contact with the femoral but without contact with the residual lateral scute. The reduction of the inguinal scute into a short arc of a circle occurs in certain *Psammobates* and *Homopus* as in *Namibchersus* n. g., sometimes barely visible ventrally in certain specimens of *P. tentorius*.

Meylan & Auffenberg (1986) studied part of the material of *Mesochersus orangeus* n. g. n. s. They made useful comparisons with the small African endemics, to which the reader is referred. They understood the phyletic relations of this taxon with this group but they selected an attribution to *Chersina* sp. It is curious that these authors gave at the outset of the chapter a diagnosis of the genus in formal contradiction with the description of the specimens such as the nuchal. Thus, while they envisaged the existence of a new fossil genus for the Miocene of Kenya (*Impregnochelys*), they did not also see the existence of a new fossil genus in the Miocene of Namibia and they chose *Chersina* as having the most characters in common with this fossil, despite the formal incompatibilities of certain characters. It was comprehensible not to create a new genus given the nature of the material, at the time quite restricted. The presence of new elements permits the better discernment of the question and to eliminate *Chersina* as well as the other small African endemics.

Aff. *Psammobates-Homopus* sp.

Locality and age: Arrisdrift. Fossil meander of the proto-Orange, north bank of the present day Orange River, southern Namibia, Early Miocene, ca 17-17.5 Ma. (Hendey, 1978, Pickford *et al.*, 1996).

Material: MSGN. AD 592'98, left peripheral of the bridge (4e?), Pl. VI, Fig. 8; AD 429'95, left peripheral 1, Pl. VI, Fig. 9; AD 471'98, right peripheral 9, Pl. VI, Fig. 10; AD 159'98, right peripheral 11, Pl. VI, Fig. 11.

Description (see above, its comparison with *Mesochersus orangeus* n. g., n. sp.) (Pl. VI, Fig. 8-11).

A form of "small African endemic" of medium size (carapace about 30 cm long) of the *Psammobates* or *Homopus* type by : - its wide and short plates; - its costal 1 encroaching on the nuchal and the peripheral 1 at the front, with pleuro-peripheral and margino-costal coincidence at the level of the bridge and costal 4 and vertebral 5 encroaching on the corresponding peripherals and the pygal. The sulcus of vertebral 5 traverses the pygal (of which we have no specimen) behind the pygal-suprapygal suture and followed on peripherals 11, as in a *P. tentorius* from Namibia and certain *P. oculifer* from Botswana, (in Broadley, 1997, Fig. 1D), differing from other *P. oculifer*, from Namibia. These characters are variably present in these two genera depending on the species. They are also present in *Chersina* and *Kinixys* but here the peripheral plates are not elongated in contrast to the latter ones.

Conclusions on the Testudinidae from Namibia

1 - Relations of *Namibchersus namaquensis* (Stromer, 1926) and *Mesochersus orangeus* n. g., n. sp.

M. orangeus n. g. n. s., resembles *N. namaquensis* by the absence of a nuchal notch, of a cervical projection, the moderate elongation of the anterior peripherals, the presence of the cervical, the fused marginals 12, the weak to absent femoro-anal narrowing (except one possible case), the absence of a dorsal hinge and of a rounding of the posterior lobe contacting the posterior border of the carapace and a certain neural differentiation, all characters present in the family before the grade of *Gigantochersina*; the presence of moderate points at the peripherals, the raised dorsal epiplastral lip and the reduction of the gular projection are acquired posteriorly by both and by other Africans (Tabs 5-6) as throughout the world in diverse lineages.

M. orangeus n. g. n. s., differs from *N. namaquensis* on the one hand by the re-entrants at the peripherals accompanying the points on other plates (more primitive character), and on the other by its clearly narrower vertebral 1 anteriorly, its reduced dimensions, the type of schema vertebral 5-pygal-suprapygals with non complete coincidence of the pleuro-peripheral sutures and scute sulci to peripherals 11, the absence of the dorsal anal subdivision on the xiphiplastral points and the reduction (here complete) of the inguinals (derived characters of small African endemics).

The so-called "Geochelone" type of schema of vertebral 5 and suprapygal-pygal prevents us from establishing a relation between *Gigantochersina* and *N. namaquensis* on the one hand with the small African endemics on the other unless the passage is possible from the type of the "small African endemics" to that of the "Geochelone" type (a question that needs to be studied).

Other differences may be specific and are independent of the lineages: the dorsal epiplastral lip in front of the entoplastron, the entoplastron not widened in the adult (character of large forms), the narrower posterior margin of the dorsal epiplastral lip, the gular projection in continuity with the epiplastral margin, the posterior lobe wider with short anals (although this

character could also be a generic one), the gulars variable in their extension.

2 - *Namibchersus* n. g., *Mesochersus* n. g. and aff. *Psammobates-Homopus* sp.

If the differences listed above indicate the presence of two small species, in both cases as well as in *Namibchersus* n. g.

- the anterior margin should not have a notch (primitive character) because there is no specimen of peripheral 1 and nuchal with an oblique margin indicating the possibility of such a nuchal notch,

- several of the peripherals preserved have external points at the junction of the marginal sulci in *Mesochersus* n. g., all of them have them in *Namibchersus* n. g., and the character is variable in the extant small endemics: present or not depending on the species in *Psammobates* (paedomorphic form), present and more or less developed depending on the species in *Homopus*, *Kinixys* and *Chersina*: more or less marked development of this character in the group shows that it is independently developed in *Namibchersus* n. g., and the other large extant forms from Africa (derived character acquired independently in several stages in several lineages).

In the two small forms and in contrast to *Namibchersus* n. g.

- there is at least a small overlap of the vertebral 5 on peripheral 11 and absolutely no sulcus-suture coincidence at this level, as in the small African endemics *Homopus*, *Psammobates*, *Kinixys* and *Chersina*: on the point of the coincidence, *Namibchersus* n. g., is at the maximum stage of development of the character in its group and *Mesochersus* n. g., is not far off in its one; among the small endemics, *Mesochersus* n. g., is primitive by its high peripherals (like *Kinixys* and *Chersina*) and by its entoplastron not being reduced.

The terrestrial tortoise fauna of the Miocene of Namibia is a relatively primitive one: *Namibchersus* nov. gen., in comparison with *A. yniphora* on the one hand and in comparison with the extant large forms from Africa *Stigmochelys* and *Centrochelys* on the other; *Mesochersus* n. g., seems to be derived prior to the divergence of the extant small African endemics.

It is too early to establish the phyletic schema of these taxa. The main problem is the vertebral 5 and suprapygal-pygals schema: how did the two schemes derive from the “geoemydian” one? Is *Gigantochersina* related to *A. radiata* then to *A. yniphora* and *Namibchersus* n. g.? It is quite possible. But where does *Mesochersus* n. g., and the small African endemics fit? When we follow the evolution of the palaeartic forms from Europe which present so many parallelisms with each other, we don't see how to derive the small African ones: we must consider that they evolved independently in several common directions, from an unknown Eurasian ancestor. Whatever the case, *Centrochelys* and *Stigmochelys* do not fit into these schemes and must have come from other waves of immigrants: *Cheirogaster* from Europe (known from the Bartonian, MP 19) was proposed as the sister group of *Centrochelys* (of which the lineage is known from the Early Miocene, as is *Namibchersus* n. g.) (Lapparent de Broin 2000a,b, 2001). What are the relations of *Stigmochelys*? Study of characters in all the species of fossil and extant Testudinini will provide clearer answers to the questions.

Conclusions

Palaeoecological and biogeographic considerations: The tortoise fauna from the Early Miocene of Namibia is a continental one, including:

1- three terrestrial genera of Testudinidae

- the large form *Namibchersus* n. g., replaced in Namibia at present by the big *Stigmochelys* which clearly belongs to a separate lineage. The extant *Stigmochelys pardalis* (carapace 80 cm long) does not attain the possible size of *Namibchersus* n. g., from the Miocene of Namibia nor the gigantic size of tortoises of the Mio-Plio-Pleistocene of East Africa including the genera *Stigmochelys* and *Centrochelys*. *Namibchersus* n. g., resembles *Mesochersus* n. g., in primitive characters but a true derived relationship between these two and between *Namibchersus* n. g., and the small African endemics is not established;

- *Mesochersus* n. g., is represented today in Namibia by the medium and small forms *Chersina*, *Homopus* and *Psammobates*. The latter ones belong to the same South African group as *Mesochersus* n. g., and are part of the small “Ethiopia-African endemics”;

- another medium sized form must be present, related to the small African endemics *Psammobates* and *Homopus*;

2 - a quite large truly aquatic form:

- the fossil Erymnochelyinae of Namibia, of a similar size to those of the Mio-Pliocene of East Africa and the extant *Erymnochelys madagascariensis*;

3- a small amphibious genus (semi-aquatic semi-terrestrial):

- the Pelomedusidae *Pelomedusa* sp., similar in size to most of the extant forms, including those from Namibia.

These tortoises occupied four or five distinct ecological niches in the same region, depending on their size, habitat and diet. Terrestrial tortoises are mainly herbivores (occasionally eating small invertebrates). The aquatic genera *Pelomedusa* and *Erymnochelys*, which can be sympatrically associated with *Pelusios*, today occupy different ecological niches in the same region of Madagascar. *E. madagascariensis* is very aquatic, living in calm and deep open waters, lakes and large rivers, with vegetation. It is mainly omnivorous: large quantities of plants, gastropods, diverse arthropods, fish remains etc. (Kuchling, 1988, 1993). *Pelomedusa* and *Pelusios* are principally carnivores (prey varies with size of the individuals). *Pelusios*, more or less aquatic depending on species and locality, has a life style close to that of *Pelomedusa* but the latter is more terrestrial and can disperse more easily. In case its water body dries up, it can traverse dry ground to find another one, whereas *Pelusios* normally buries itself in the mud and waits for the next rainy season, which *Erymnochelys* also does when necessary (Bour, com. pers.; Loveridge, 1941; Loveridge & Williams, 1957; Pritchard, 1979). There is no competition between the three genera in Madagascar (Kuchling, 1993).

Pelusios is absent from Namibia as are Trionychoidea with paddles (Carettochelyidae, Trionychidae), other turtles that inhabit open waters. The Trionychoidea have coexisted with the Podocnemididae throughout the Miocene-Pliocene in Africa, but there does not appear to be coexistence between *Erymnochelys* and *Pelusios*, and particularly the large *Pelusios sinuatus*, which is widespread in large lakes and rivers of

East Africa during that time period.

However, the respective distribution of the genera over the course of time is not well established due to the fact that many of the Miocene fossil tortoises remain unidentified, notably in Kenya (Baringo Basin), so that their possible coexistence during the Miocene is not definitively excluded (Lapparent de Broin, 2000a, tab. 3).

The terrestrial Testudinidae are not good indicators of temperature because today they are adapted to extreme conditions for short periods interspersed with favourable seasons: they can either survive very cold winters (steppe tortoises *Agrionemys horsfieldii* in Afghanistan) or dry and hot seasons and cold nights (*Centrochelys sulcata* of the Sahel and Sahara, Gopherus in North America), digging deep burrows if necessary. One of the extant species of *Homopus* (*Homopus* sp. indet.) from Namibia is flattened, with paedomorphic fontanelles giving it great suppleness, similar to the "pancake tortoise" *Malacochersus* in East Africa, which permits it to protect itself from predators and high temperatures by entering narrow cracks. Today, depending on where they live, the various forms of terrestrial tortoises in Namibia show adaptations to heat, cold and above all drought. If the ambient humidity was higher during the Early Miocene, it is not this family which would indicate it. The persistence of tortoises in Namibia until the present reveals that desertification and climatic cooling, if they took place, did not pose any real problems for them, save for their relative growth which became weaker, just as occurred in the rest of the World.

The problem posed by the Testudinidae of the Miocene-Recent transition is the replacement of *Namibchersus* n. g., by *Stigmochelys*: during the Miocene, the absence of *Stigmochelys* in Namibia must be explained. In effect, the hypothesis is that '*Stigmochelys* and *Centrochelys*, lineages which had just arrived from Eurasia, developed in the north and East and *Namibchersus* n. g., and *Mesochersus* n. g., evolved in the south from ancestors which arrived much earlier, probably the Oligocene, such (as *Gigantochersina* of the Fayum, the possible plesion of *Namibchersus* n. g., It is necessary to postulate that *Namibchersus* n. g. disappeared, leaving its place to *Stigmochelys*. Another absence from the Miocene (until now) is that of *Kinixys*, known from the Early Miocene of Kenya and Uganda and well represented in sub-sahelian Africa today, but still not known in Namibia. Perhaps *Kinixys* was in the process of diversifying in the north-east but had not had time to reach Namibia, just as with *Pelusios*, *Stigmochelys* and *Centrochelys*. Once *Mesochersus* n. g., disappeared, its replacement by *Kinixys* did not occur, probably because the other small African endemics, *Homopus* and *Psammobates* (and eventually *Chersina* the presence of which in Namibia is weak) took over from *Mesochersus* and prevented the implantation of *Kinixys*.

Pelomedusa has a present day distribution from the Sahel to the southern tip of Africa. It requires small water courses or swamps, including temporary ones and an inter tropical temperature even if variable, at least warm for part of the year or during the day; the dry season can be survived by aestivating in the mud. Since the humid tropical period of the Cretaceous, *Pelomedusa* (its lineage) also adapted to dry seasons and to the cold African nights. Its presence in Namibia today is not a good example for the climate of the Miocene. As in the terrestrial Testudinidae its presence until today shows its extreme suppleness for adaptation during climatic changes

(Loveridge, 1941), as long as the total amount of annual insolation does not drop too far.

If there were environmental changes after the Miocene it is Erymnochelyinae which would demonstrate it. These changes must have affected the fluidity and size of water courses, vegetation and fauna sufficient for their diet and relative heat. But the Erymnochelyinae also disappeared from East Africa during the Late Pliocene, and only survive today in Madagascar. This regression in East Africa, a region which remained more humid than present day Namibia, is difficult to correlate with that of Namibia. It corresponds to the disappearance of the Carettochelyidae from East Africa, also during the Pliocene.

Today, the Erymnochelyinae have disappeared from Africa, including Namibia. But *Pelomedusa* is still present in Namibia whereas *Pelusios* and the Trionychoidea are still absent from Namibia, just as they are from the entire region drained by the Orange River and its tributaries. The Trionychoidea, open water turtles with paddles, (above all the Carettochelyidae), which came from Laurasia and are represented in Africa since the Early Miocene, are associated in other parts of Africa, with either *Pelusios* or the Erymnochelyinae: their absence in Namibia is thus not a question of competition. The present day absence of *Pelusios* and Trionychoidea in the south, which are so abundant in East and Northern Africa in sites of Early Miocene and later times, could be considered to indicate a barrier to their penetration southwards.

Their absence in Namibia during the Early Miocene like that of *Stigmochelys* and *Centrochelys*, could be explained by the fact that the Trionychoidea had just arrived in the north from Eurasia. *Pelusios* had also just started to diversify in the north-east, where it is only known from the Early Miocene of East Africa (Kenya, Uganda) such as the Trionychoidea, *Stigmochelys* and *Centrochelys*. After the Early Miocene, the barrier preventing the arrival of Trionychoidea in Namibia could have been the absence of a suitable fluvial network between the great lakes of East Africa and the Zambezi and its tributaries and the southern part of Africa drained by the Orange River and its tributaries. In addition, eastern coastal currents were probably not favourable for their penetration; "along the sea and into river mouths, in contrast to the penetration of *Trionyx* along the west coast of Africa from the north, as far as south as Angola. Even though they have articulations in the autopodia, these tortoises have paddles which incorporate all the fingers (and not just interdigital membranes as occur in fresh water amphibious turtles) and they travel with difficulty across the ground. Competition with the Erymnochelyidae may have been an obstacle to the penetration of *Pelusios*, because the latter can move across the ground; but not over extended distances far from water, thus differing from *Pelomedusa*. As with *Pelomedusa*, crocodiles, because of their amphibious habits (Behler, 1999; Cogger & Zweigel, 1993), can also easily travel across the ground and cross dry land between river courses, if necessary. They could thus have reached the proto-Orange without there being a permanent fluvial network between it and that of East Africa and the Zambezi, in contrast to the Carettochelyidae and Trionychoidea.

In contrast, *Pelomedusa*, the most primitive of the Pelomedusidae (family present in Africa since the Early Cretaceous) and the Podocnemididae of the group *Erymnoche-*

lys (attested in Africa since the Late Cretaceous) (Lapparent de Broin, 2000a) of much more ancient origins, was perhaps already largely distributed in the proximity of Namibia (at the time more or less emergent) in the basal Miocene, even if the fluvial networks of the east and south were not connected permanently to each other during the Early Miocene. *Pelomedusa* and the Erymnochelyinae, could thus have had the advantage of their ancient differentiation to be represented in the region of the proto-Orange and its surrounding margins during the Early Miocene. In terrestrial forms, the same was achieved by *Namibchersus* n. g., and *Mesochersus* n. g., descendants of lineages (such as that of *Gigantochersina* of the Oligocene of the Fayum for the former) appeared well in advance of those of *Stigmochelys* and *Centrochelys*, known only from the Early Miocene.

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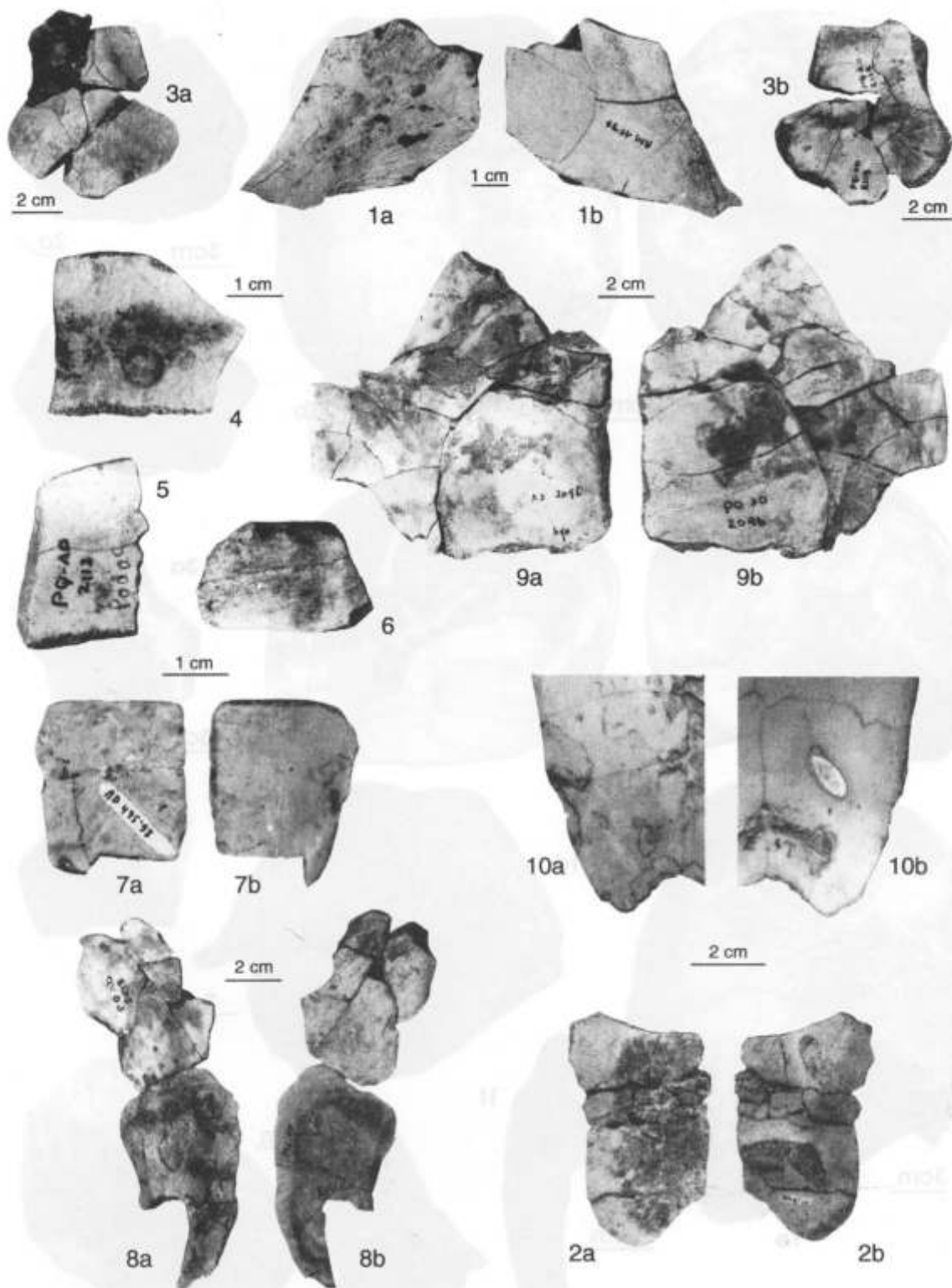


Plate I

- Figure 1** - Aff. *Erymnochelys* sp., Auchas, AM 11'97, left hyoplastral fragment; a, b, dorsal, ventral views.
Figure 2 - Aff. *Erymnochelys* sp., Auchas, AM 6'97, right xiphiplastron; a, b, ventral, dorsal views.
Figure 3 - Aff. *Erymnochelys* sp., Arrisdrift, PQ AD 2115, nuchal; a, b, dorsal, ventral views.
Figure 4 - Aff. *Erymnochelys* sp., Arrisdrift, PQ AD x1, fragmentary even pleural; dorsal view.
Figure 5 - Aff. *Erymnochelys* sp., Arrisdrift, PQ AD 2113, fragmentary odd pleural; dorsal view.
Figure 6 - Aff. *Erymnochelys* sp., Arrisdrift, PQ AD x2, fragmentary even pleural; dorsal view.
Figure 7 - *Pelomedusa* sp., Arrisdrift, AD 475'98, right partial hypoplastron; a, b, ventral, dorsal views.
Figure 8 - Aff. *Erymnochelys* sp., Arrisdrift, PQ AD 2078, partial left hypoplastron with xiphiplastron; a, b, dorsal, ventral views.
Figure 9 - Aff. *Erymnochelys* sp., Arrisdrift, PQ AD 2096, left hyoplastron; a, b, dorsal, ventral views.
Figure 10 - *Erymnochelys madagascariensis* (Grandidier, 1867), Madagascar, extant, MNHN H DD 67, part of plastral posterior lobe with the right xiphiplastron; a, b, ventral, dorsal views.

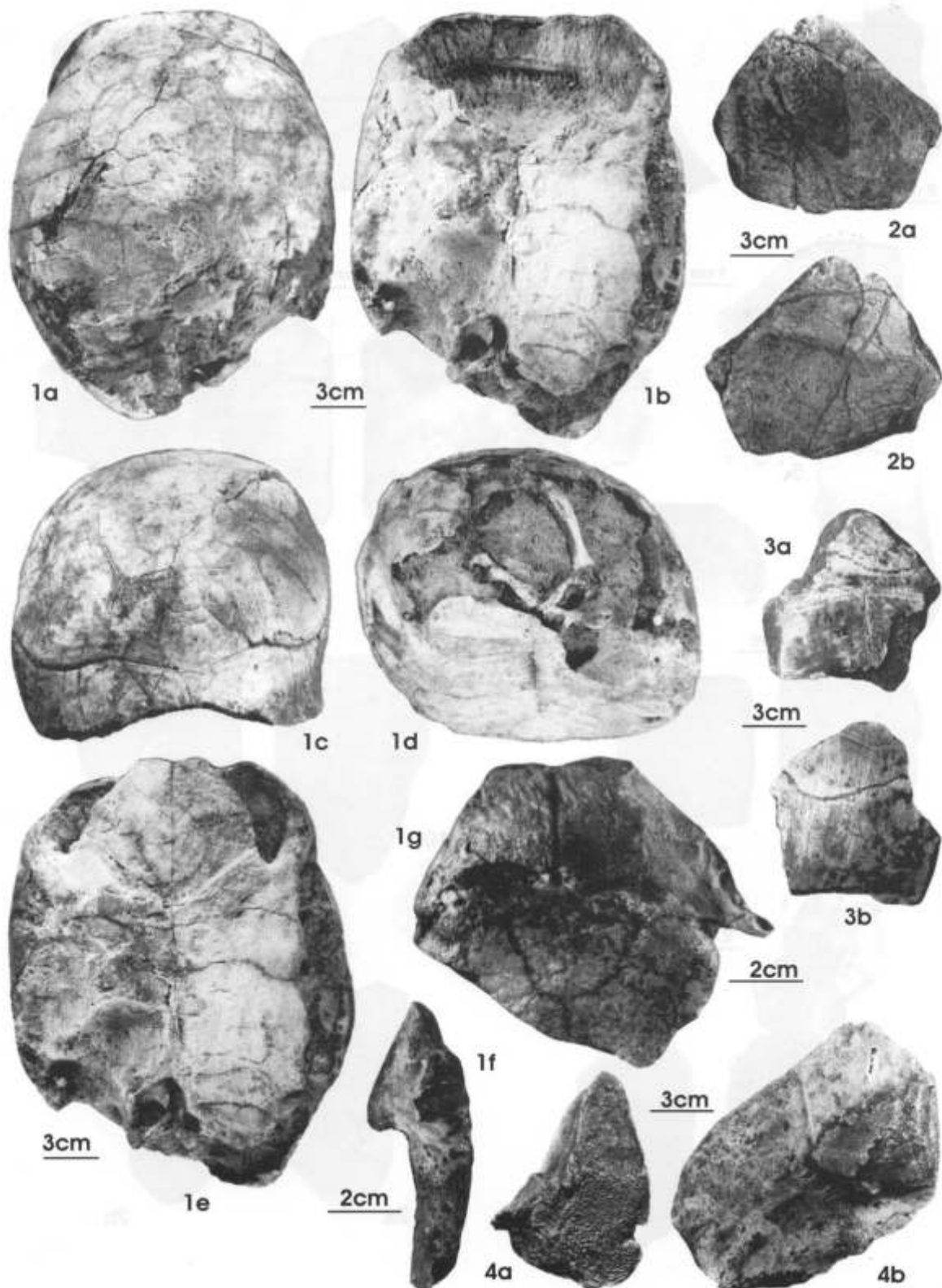


Plate II

Figure 1 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 1'99, carapace, young male; a, dorsal view, b, ventral view, anterior lobe withdrawn to show the long inferior border of the anterior scutes; c, anterior view; d, infero-posterior view on the right side of the pelvis; e, ventral view with the anterior lobe; f, anterior lobe, left lateral view; g, anterior lobe, dorsal view.

Figure 2 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM xa'98, fragments of suprapygal 2, pygal and left peripheral 11, female, a, b, dorsal, ventral views.

Figure 3 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM xb'98, fragments of suprapygal 2 and pygal, male, a, b, ventral, dorsal views.

Figure 4 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 11'98, partial left epiplastron, a, b, symphyseal and dorsal views with a medial fragment laterally displaced.

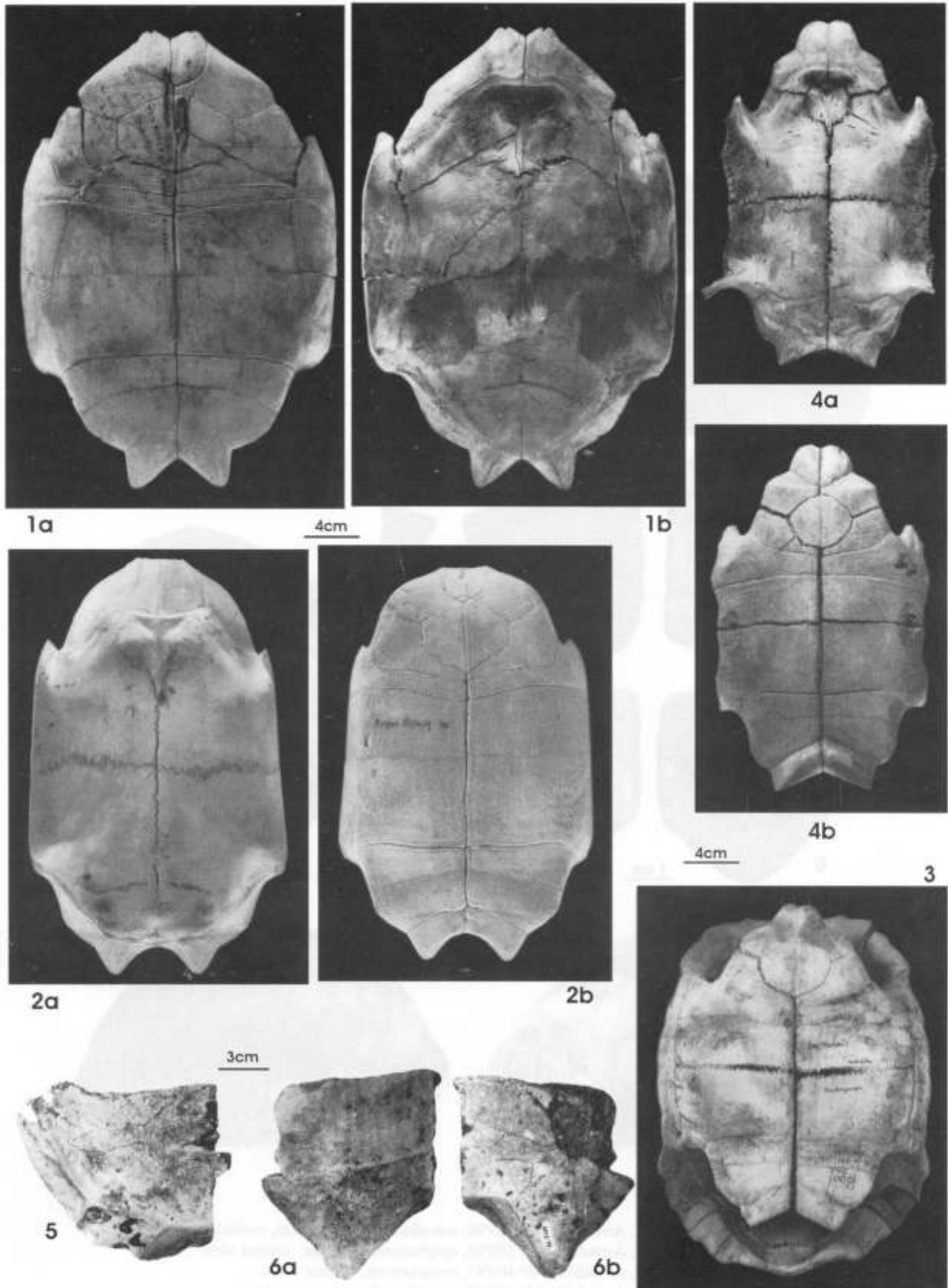


Plate III

- Figure 1 - *Centrochelys sulcata* (Miller, 1779), extant, Africa (Niger), MNHN, P, REP 37, plastron, female, a, b, ventral, dorsal views.
 Figure 2 - *Stigmocheilus pardalis* (Bell, 1828), extant, Africa, R. Bour coll., plastron, female, a, b, dorsal, ventral views.
 Figure 3 - *Astrochelys radiata* (Shaw, 1802), extant, Madagascar, MNHN, P, REP 38, carapace with plastron, female, ventral view.
 Figure 4 - *Astrochelys radiata* (Shaw, 1802), extant, Madagascar, MNHN, P, REP 39, plastron, male, a,b, dorsal, ventral views.
 Figure 5 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 795, partial left xiphiplastron, dorsal view.
 Figure 6 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 298, partial right xiphiplastron, a, b, ventral, dorsal views.

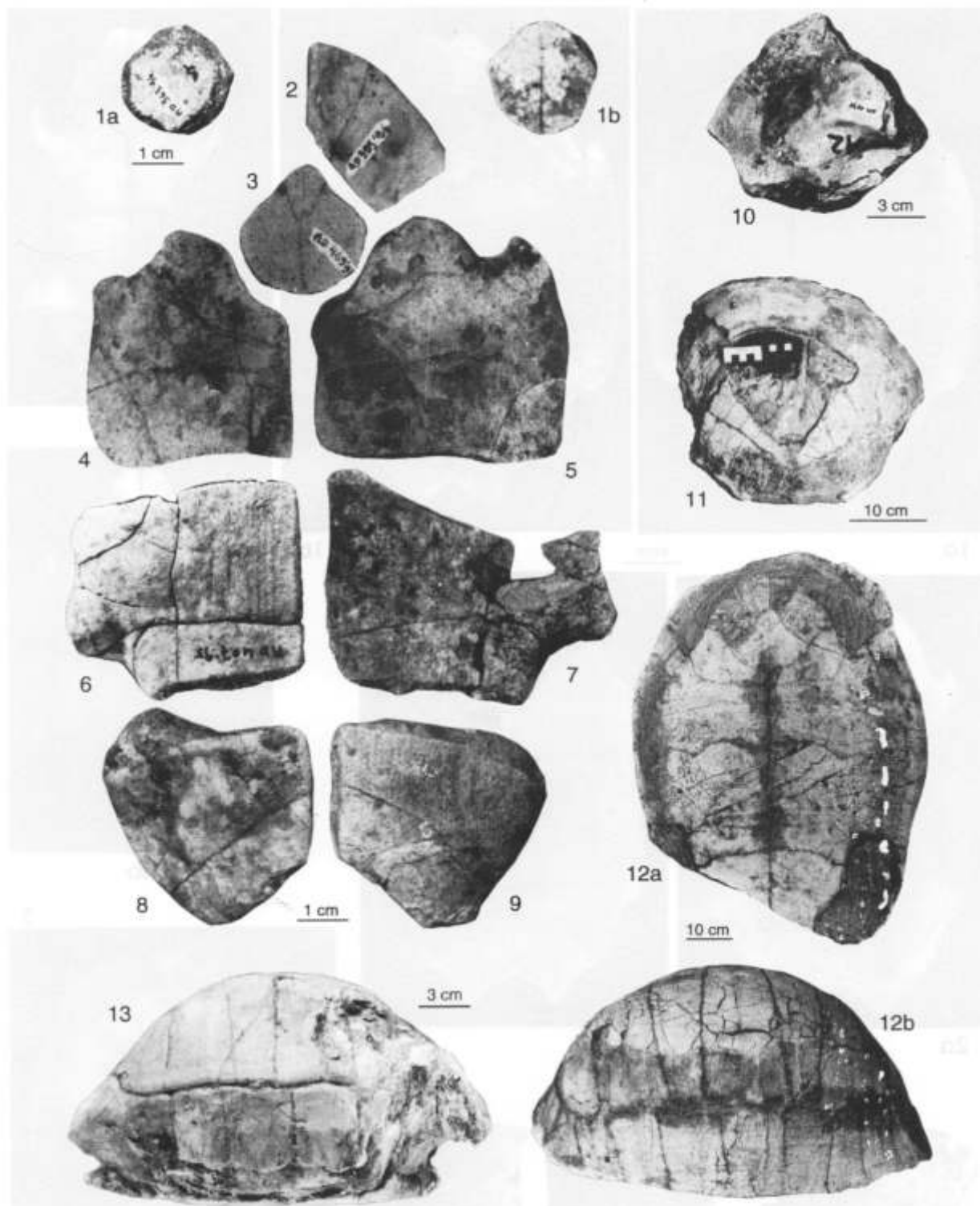


Plate IV

- Figure 1** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 363'96, entoplastron, a, b, dorsal, ventral views.
Figure 2 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 389'96, epiplastron, holotype, ventral view.
Figure 3 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 469'97, entoplastron, ventral view.
Figure 4 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 472'98, right hyoplastron, ventral view.
Figure 5 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 185'95, left hyoplastron, ventral view.
Figure 6 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 407'95, right hypoplastron, ventral view.
Figure 7 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 361'96, left hypoplastron, ventral view.
Figure 8 - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 468'98, right xiphiplastron, ventral view.
Figure 9 - *Mesochersus orangeus* left n. g. n. sp., Arrisdrift, AD 470'98, partial left xiphiplastron, ventral view.
Figure 10 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 10'98, partial left epiplastron, dorsal view.
Figure 11 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, OMS x1, carapace (probable female), posterior view.
Figure 12 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 9'93, carapace, female, a, b, ventral, left lateral views.
Figure 13 - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM 1'99, carapace, male, lateral left view.

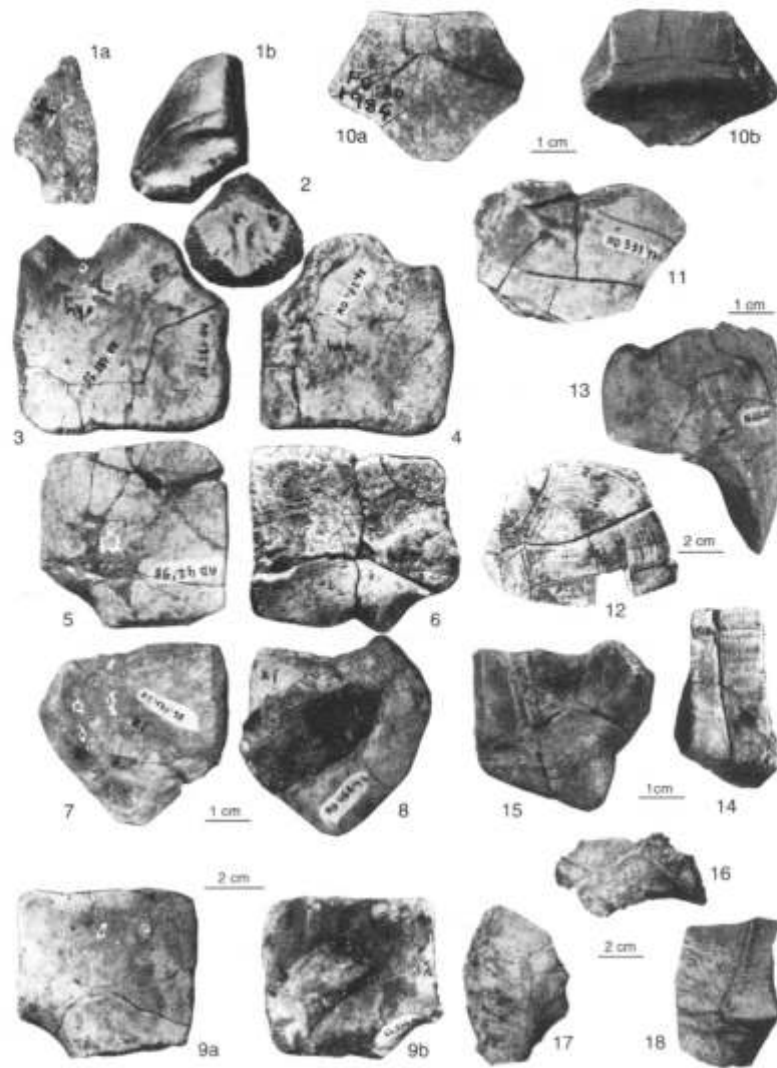


Plate V

- Figure 1** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 389'96, epiplastron, holotype, a, b, symphysis, dorsal view.
- Figure 2** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 469'97, entoplastron, dorsal view.
- Figure 3** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 185'95, left hyoplastron, dorsal view.
- Figure 4** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 472'98, right hyoplastron, dorsal view.
- Figure 5** - *Mesochersus orangeus* n. g. n. sp. Arrisdrift, AD 42'98, left hypoplastron, dorsal view.
- Figure 6** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 407'95, right hypoplastron, dorsal view.
- Figure 7** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, dorsal. AD 470'98, left xiphiplastron, dorsal view.
- Figure 8** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 468'98, right xiphiplastron, dorsal view.
- Figure 9** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 715'97, right hypoplastron with a short depression at the location of a missing inguinal scute, visible in ventral view; a, b, ventral, dorsal views.
- Figure 10** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, nuchal PQ AD 1984, a, b, dorsal, ventral views.
- Figure 11** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, nuchal, AD 533'97, dorsal view.
- Figure 12** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 207'95, young, right pleurals 1 and 2 with fragments of the neurals 1 and 2, dorsal view.
- Figure 13** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD559'98, peripherals from the left posterior bridge (6, 7 and partial 8) and fragment of hypoplastron; inferior view showing the absence of inguinal.
- Figure 14** - *Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD 339'95, young right peripheral 7, latero-inferior view showing the presence of a narrow relict inguinal scute in contact: below with the abdominal and above with the posterior part of marginal 7 and marginal 8.
- Figure 15** - ?*Mesochersus orangeus* n. g. n. sp., Arrisdrift, AD x, right xiphiplastron with a strong femoro-anal narrowing (male?), dorsal view.
- Figure 16** - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM xc, fragment of a left hypoplastron; inferior view showing the inguinal widely contacting the femoral, on the left of the photograph.
- Figure 17** - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM xd, fragment of a left hypoplastron; ventral view showing the transversal inguinal, on the right, contacting on the left: widely the abdominal (anteriorly) and less the femoral (posteriorly).
- Figure 18** - *Namibchersus namaquensis* (Stromer, 1926), Auchas, AM xe, fragment of a left peripheral 7 from the posterior part of the bridge; latero-inferior view showing the inguinal contacting: above, the marginal 8 (on the right) and only the posterior part of the marginal 7 (on the left), and, below, the abdominal (on the left).

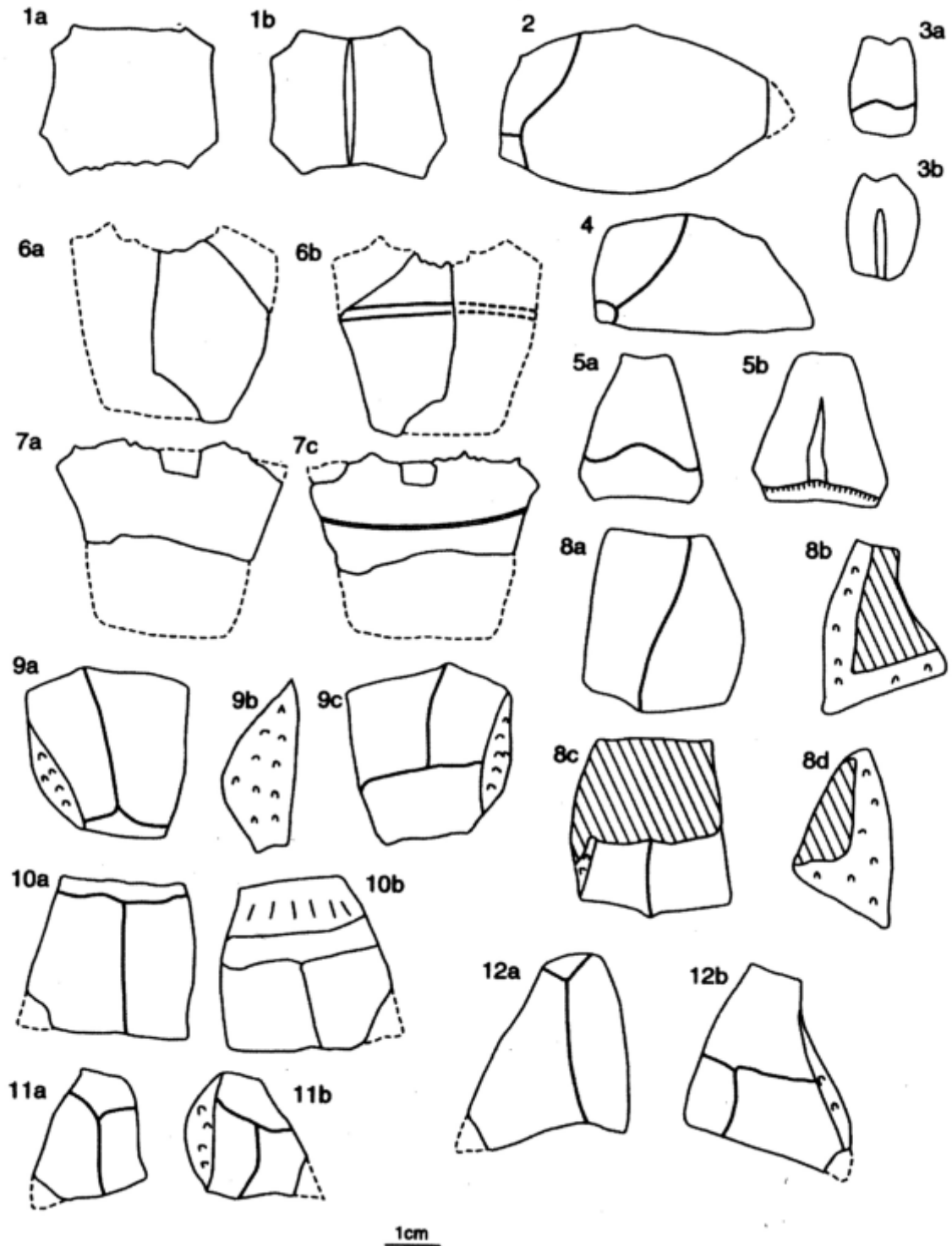


Plate. VI.

Figure 1 - *Mesochersus orangeus* n. g. n. sp., Arrisdraft. PQ AD 898, neural 2 or 4, a, b, dorsal, ventral views.

Figure 2 - *Mesochersus orangeus* n. g. n. sp., Arrisdraft. AD 606'97, right pleural 1, dorsal view.

Figure 3 - *Mesochersus orangeus* n. g. n. sp., Arrisdraft. AD 72'98, neural 1, a, b, dorsal, ventral views.

Figure 4 - *Mesochersus orangeus* n. g. n. sp., Arrisdraft. AD 563'94, right pleural 1, dorsal view.

Figure 5 - *Mesochersus orangeus* n. g. n. sp., Arrisdraft. PQ AD 1436, neural 1, a, b, dorsal, ventral views.

Figure 6 - *Mesochersus orangeus* n. g. n. sp., Arrisdraft. PQ AD 1527, pygal, a, b, dorsal, ventral views.

Figure 7 - *Mesochersus orangeus* n. g. n. sp., Arrisdraft. PQ AD 3084, pygal, a, b, dorsal, ventral views.

Figure 8 - Aff. *Psammobates-Homopus* sp., AD 592'98, bridge left peripheral (4th?), a, b, c, d, dorsal, anterior, ventral, posterior views.

Figure 9 - Aff. *Psammobates-Homopus* sp., AD 429'95, left peripheral 1, a, b, c, dorsal, proximal, ventral views.

Figure 10 - Aff. *Psammobates-Homopus* sp., AD 471'98, right peripheral 9, a, b, dorsal, ventral views.

Figure 11 - Aff. *Psammobates-Homopus* sp., AD 159'98, right peripheral 11, a, b, dorsal, ventral views.

Figure 12 - *Mesochersus orangeus* n. g. n. sp., Arrisdraft. AD 564'94, right peripheral 11, a, b, dorsal, ventral views.