

SIRENID SALAMANDERS AND A GYMNOPHIONAN AMPHIBIAN FROM THE CRETACEOUS OF THE SUDAN

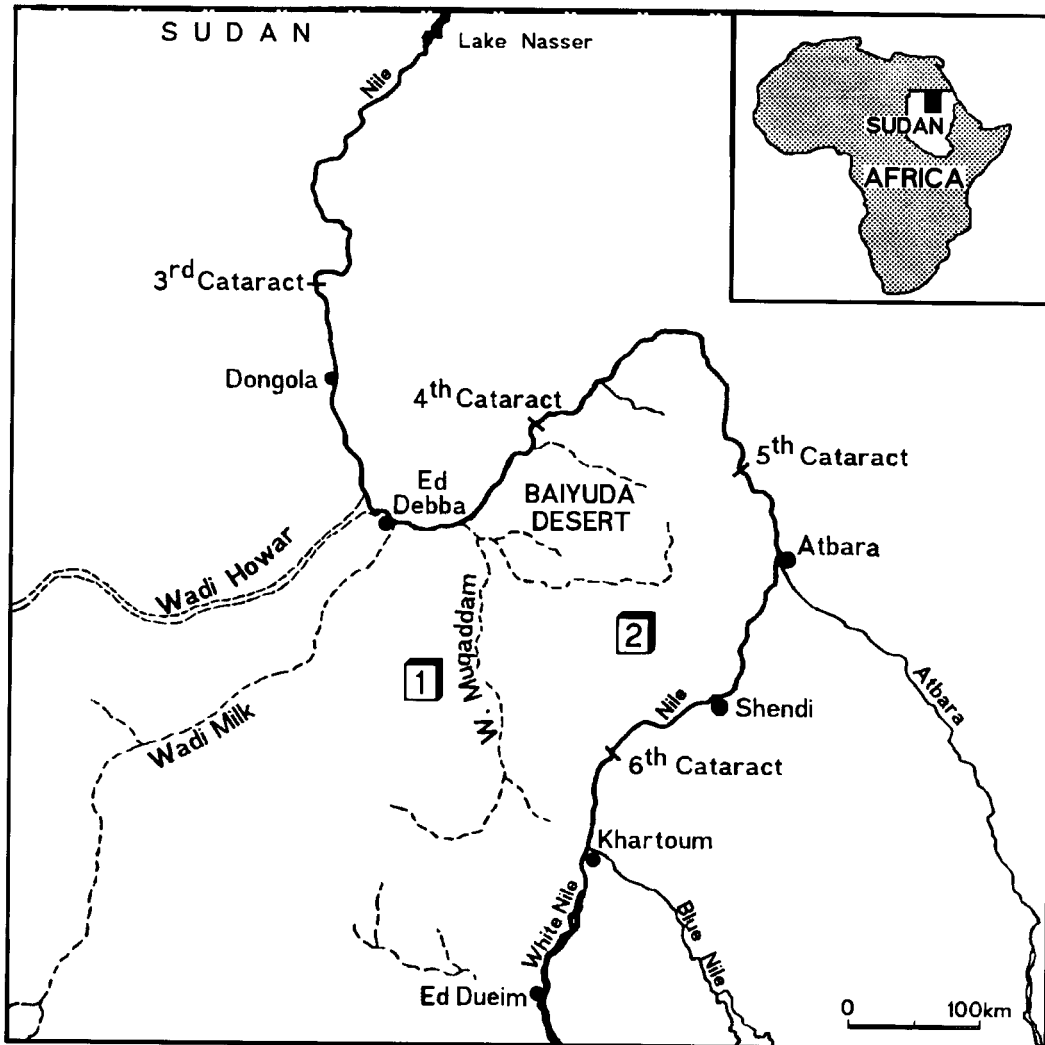
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ABSTRACT. A vertebrate assemblage from the Cenomanian of Wadi Milk, northern Sudan, includes material of all three major groups of lissamphibian, namely frogs, salamanders and gymnophionans, of which the latter two groups are described in this work. The productive horizons in the Wadi Milk Formation are lacustrine and the vertebrates are represented by isolated elements. The salamander material is described as *Kababisha humarensis* gen. et sp. nov. and *Kababisha sudanensis* gen. et sp. nov. and is referred to the family Sirenidae. *Kababisha* is the earliest sirenid genus, the first sirenid to be recognized outside North America, and is only the second fossil salamander genus to be reported from the African Plate, *Ramonellus* from Israel being the first. It is suggested that the recently described *Noterpeton*, from the Maastrichtian of Bolivia, is also a sirenid and that the *Noterpetontidae* is a junior synonym of the Sirenidae. The gymnophionan is represented by four trunk vertebrae and is strictly indeterminate within the Gymnophiona, although the vertebrae bear a non-derived resemblance to those of the dermophine Caeciliidae found in Africa. It is the oldest gymnophionan material from Gondwana, the first fossil gymnophionan from Africa and the earliest gymnophionan with holospondylous vertebrae.

THE Mesozoic record of lissamphibians (frogs, salamanders and gymnophionans) from the African Plate is extremely limited. The Lower Cretaceous (Hauterivian–Barremian; Buffetaut and Rage 1993) of Israel has produced assemblages of pipid frogs (Nevo 1968), pipid tadpoles (Estes *et al.* 1978), and an enigmatic salamander, *Ramonellus* (Nevo and Estes 1969). Four frog taxa, as yet undescribed, have been reported from the Lower Cretaceous of Cameroon (Brunet *et al.* 1988), and two anuran skulls, also undescribed, have been found in the Lower Cretaceous of Malawi (Jacobs *et al.* 1990). The Upper Cretaceous (Coniacian/Santonian; Moody and Sutcliffe 1991) of Niger has yielded two pipid frogs (de Broin *et al.* 1974; Báez and Rage 1988). A second Gondwanan salamander has been reported from this locality (de Broin *et al.* 1974) and a vertebra figured (Rage *et al.* 1993) but has not been fully described. Most recently, a diverse amphibian assemblage (including gymnophionans, salamanders and frogs) has been recovered from the lower Upper Cretaceous (Cenomanian) of the Sudan (Werner 1993a, 1993b, 1994a, 1994b). The frog material is being studied separately by Dr A. Báez and one of the authors (CW) and will be described elsewhere. The salamander and gymnophionan material provides an important contribution to our knowledge of the Cretaceous faunas of Gondwana and is described here.

GEOLOGICAL AND STRATIGRAPHICAL SETTING

The amphibian fossils described here were collected from the Wadi Milk Formation, which is widespread in the northern Sudan. The Wadi Milk Formation is dominated by deposits of braided river and sandy braided-meandering river systems, which interfinger locally with sediments of meandering rivers, flood plains and lakes (Bussert 1993a, 1993b). The vertebrate-bearing locality is situated 200 km north-west of Khartoum (Text-fig. 1) and lies at the base of the exposed part of the Wadi Milk Formation. The fossil-bearing horizons consist of fine-grained smectite-rich layers. They were deposited in a fluvio-lacustrine environment and overprinted by soil formation processes



TEXT-FIG. 1. Map of the Sudan showing the position of the vertebrate-bearing localities referred to in this work.

reflecting a warm climate with seasonal rainfall patterns (Bussert 1993a, 1993b). In these layers, continental vertebrate remains occur in abundance as scales, teeth and disarticulated skeletal elements. A rich fish fauna is present, collected material including the freshwater shark *Asteracanthus aegyptiacus*, a new rajiform batoid (one tooth), polypterids, lepisosteids, osteoglossids (represented by many scales), characiforms (represented by teeth) and the lungfish *Protopterus humei*, *P. protopteroideus*, *P. sp. nov.* and *Neoceratodus tuberculatus* (represented by toothplates; Werner 1993b). The tetrapod assemblage includes amphibians (pipid frogs, and the salamander and gymnophionan material described here), testudinates (at least three erymnochelyines represented by carapace and vertebral fragments; Werner 1993b), snakes (at least seven species, represented by vertebrae; Werner and Rage 1994), lizards (rare elements), crocodiles (long- and medium-snouted species of mesosuchian; Werner 1993b) and dinosaurs (vertebrae and teeth of sauropods, ornithopods and theropods; Werner 1994a). The assemblage is dominated by freshwater fish, aquatic amphibians and amphibious reptiles, reflecting the lacustrine facies from which it was

collected. Terrestrial elements, such as lizards and dinosaurs, are rare, and no mammalian material has been recovered.

A combination of palaeobotanical (Lejal-Nicol 1987), palynological (Schrank 1990; Schrank and Awad 1990) and lithological correlation (Wycisk 1991) indicates an Albian to Cenomanian age for the Wadi Milk Formation. The vertebrate assemblage resembles the Cenomanian assemblage from Bahariya Oasis in Egypt (Werner 1991) and is closely similar to that from the later, Coniacian/Santonian Ibecten Formation of Niger (Moody and Sutcliffe 1991). This tends to support a Cenomanian rather than an Albian age for the basal layers of the exposed part of the Wadi Milk Formation.

To date, only two salamander atlantes, Vb-820–Vb-821, and other fragmentary vertebrae (uncatalogued) have been recovered from the neighbouring Shendi Formation, which represents a lateral time equivalent of the Wadi Milk Formation. In this fluvial-dominated sequence, which crops out west of the Nile town of Shendi (Text-fig. 1), vertebrate-bearing channel deposits occur locally. The new fossils of the Shendi Formation have yet to be studied in detail, but a preliminary report on its vertebrate content has been given by Werner (1993b).

MATERIAL

Most of the amphibian material was obtained by screening the residue of about seven tons of sediment from the Wadi Milk Formation. The technique of collection of Sudanese microvertebrates was described in detail by Werner (1994a). Only a few amphibian specimens were collected by eye from the weathered surface of the vertebrate-bearing horizons.

All amphibian bones are preserved as isolated, and often fragmentary, elements. The Sudanese specimens described and figured here are stored in the collection of the Special Research Project 69 of the Technical University of Berlin (TUB-SFB-69) catalogued as Vb-659 to Vb-661, Vb-781 to Vb-809 and Vb-813 to Vb-821.

SYSTEMATIC PALAEOONTOLOGY

LISSAMPHIBIA Haeckel, 1866

CAUDATA Scopoli, 1777

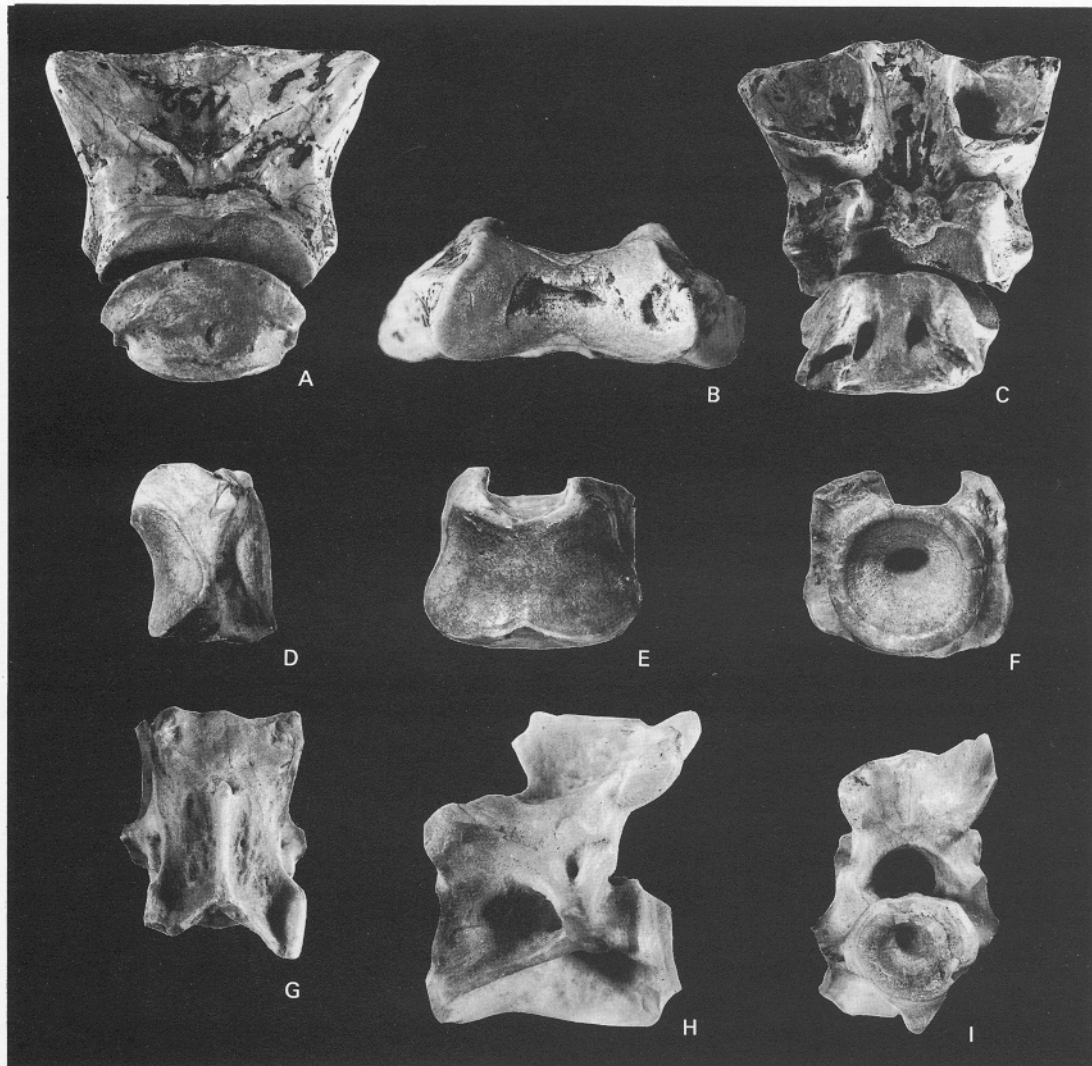
Family SIRENIDAE Gray, 1825

Genus KABABISHA gen. nov.

Type species. *Kababisha humarensis* sp. nov.

Derivation of name. The generic name *Kababisha* refers to the nomadic people, the Kababish, who occupy the Northern region of the Sudan.

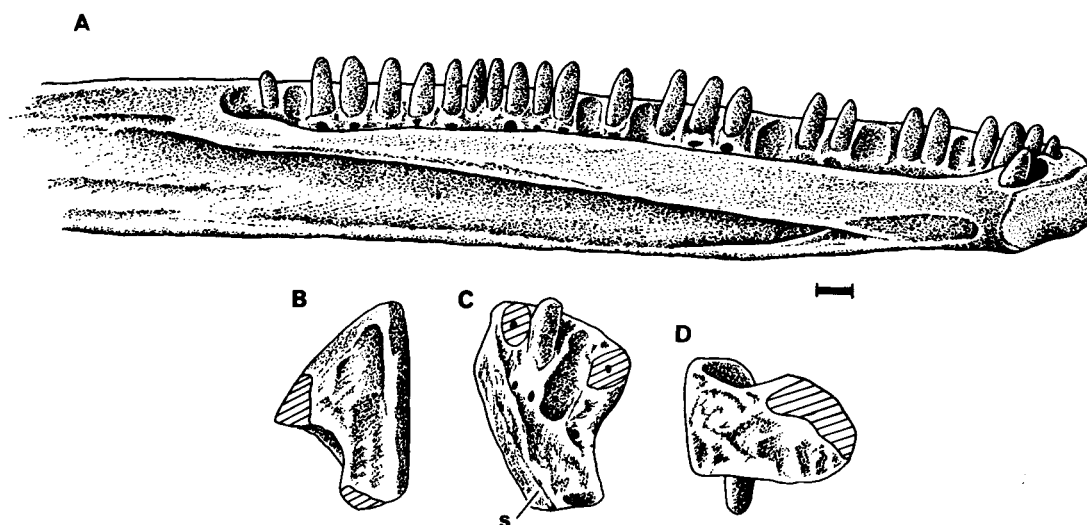
Diagnosis. Neotenous sirenid salamanders ranging in size from estimated skull lengths of less than 10 mm up to over 100 mm. Teeth non-pedicellate, thick-walled, conical (tips not preserved), showing 'zahnreihe'-type replacement. Dentary elongate, extending well beyond tooth row; deep subdental ridge faceted posteriorly for angulosplenic (or splenic if separate); lateral groove deepening posteriorly; lateral sensory nerve foramina absent; symphyseal surface compressed dorso-ventrally; symphyseal tooth position lying lingual to main tooth row. Premaxilla narrow, lacking alary process. Exoccipitals and parasphenoid fused into a composite structure; continuous, strap-like, U-shaped occipital surface; dorsal concavities for ear capsule; vagus foramina large. Atlas anteroposteriorly short but deep; no tuberculum interglenoideum; cotyles fused to form a smooth continuous, dorsoventrally concave surface closely complementing the occipital surface (Text-fig. 2B, E); strong neural spine; posterodorsal spinal nerve foramina present, posteroventral vascular pits present. Trunk vertebrae typically without spinal nerve foramina; parallel-sided neural arches bearing woven sculpture, steeply inclined zygapophyses and low neural spines; small aliform



TEXT-FIG. 2. *Kababisha humarensis* gen. et sp. nov.; Wadi Milk Formation, Sudan. A, C, fused basicranial-exoccipital element, Vb-788, and holotype atlas centrum, Vb-791, in A, dorsal; and C, ventral views; $\times 1.5$. B, fused basicranial-exoccipital element, Vb-788, in posterior view; $\times 2$. D-F, holotype atlas centrum, Vb-791, in D, left lateral; E, anterior; and F, posterior views, $\times 2$. G-I, trunk centrum, Vb-802, in G, dorsal; H, left lateral; and I, posterior views; $\times 2.5$.

processes visible on some vertebrae; rib bearers absent, transverse processes flange-like lacking rib facets and supported by accessory flanges; deep anterolateral fossae; vertebrarterial canal piercing the transverse process in an anteroventral direction; neural canal relatively small; midventral keel. Caudal vertebrae elongate, most bearing double ventral keel; narrow centrum; reduced transverse processes with faceted triangular surface; some (probably all) caudals with posterior spinal nerve foramina.

Remarks. The atlas and trunk central are present as two morphological types, treated here as two species. In *Kababisha humarensis*, represented mostly by large specimens, the vertebral centra are



TEXT-FIG. 3. *Kababisha humarensis* gen. et sp. nov.; Wadi Milk Formation, Sudan. A, reconstruction of left dentary ramus in medial view based largely on Vb-782, Vb-784 and Vb-785. B-D, Vb-787, left premaxilla in B, dorsal; C, ventromedial; and D, anterior views. Abbreviation: s, sutural surface. Scale bar represents 1 mm.

amphicoelous, with a deep anterior cotyle and a shallower posterior cotyle which is infilled to a varying degree by what appears to be a layer of calcified material. In this form, the calcified layer always lies within the posterior cotyle. It does not bulge backwards except in some posterior trunk vertebrae. However, in *Kababisha sudanensis*, mostly represented by small specimens, the infilling layer typically forms a thick bulging rim which forms a partial condyle (with a pit at the centre). These vertebrae are thus functionally procoelous, a very unusual condition in salamanders, which typically have either opisthocoelous or amphicoelous centra (for further discussion of the significance, see below). In the tail, all vertebrae show this procoelous condition and are not determinate at specific level.

We cannot be absolutely certain that the two morphologies represent two species. *K. sudanensis* rarely attains the size of *K. humarensis*, but the vertebrae are more heavily ossified in the smaller form and the atlas vertebrae of both forms are distinct over a range of sizes. These features suggest that the former is not simply an ontogenetic stage of the latter, but might be a progenetic dwarf species. Nevertheless the two morphologies might represent two morphs (sexual or paedomorphic/non-paedomorphic) within a single species, although we know of no present-day analogy for this.

Kababisha humarensis sp. nov.

Text-figures 2-3, 4A-E, 6F-J, 7A, C, 8A-G, 9A-C, E-F

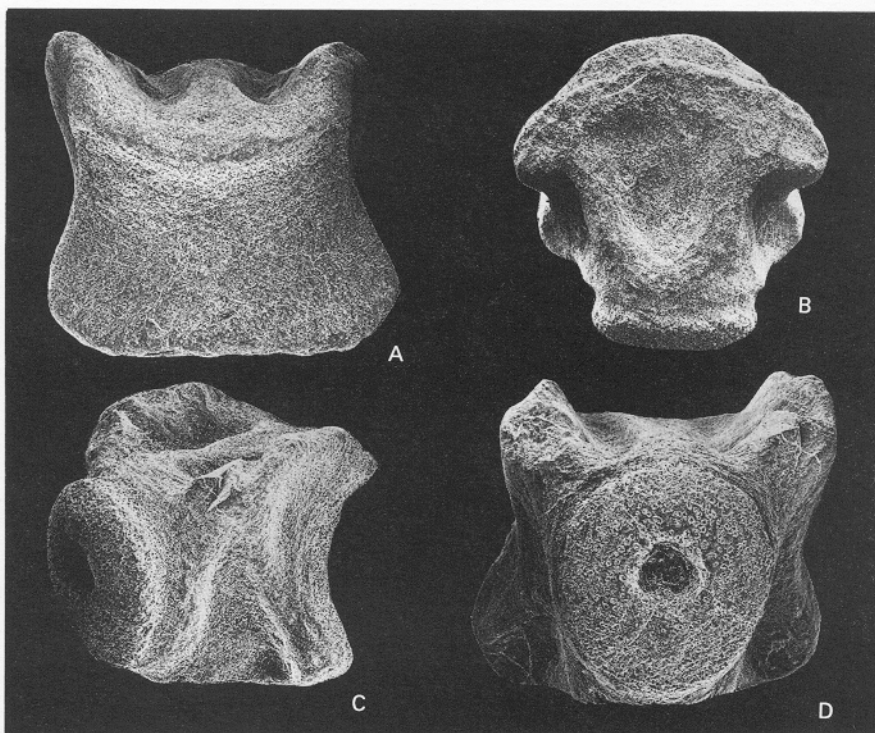
Holotype. TUB-SFB-69 Vb-791, an atlas centrum (Text-fig. 2A, C-F).

Derivation of specific name. The specific epithet relates to Humar Hill (549 m) which is situated 25 km south-east of the vertebrate-bearing locality.

Diagnosis. Large (skull length up to at least 100 mm) *Kababisha* with amphicoelous presacral vertebrae in which the depth of the posterior cotyle is only slightly reduced by calcified infilling. In ventral aspect, the atlas centrum has a width:length ratio of 1.5 and there is only a faint suggestion of a three-lobed structure to the ventral surface.



TEXT-FIG. 4. *Kababisha humarensis* gen. et sp. nov.; Wadi Milk Formation, Sudan. A-C, left dentary, Vb-782, in A, occlusal; B, lingual; and C, labial views; A, $\times 9$; B-C, $\times 7.5$. D, dorsal surface of neural arch of trunk vertebra, Vb-806, showing characteristic sculpturing; $\times 8.5$. E, atlas neural arch, Vb-800, in left lateral view; $\times 5.5$. F-G, *Kababisha* sp. indet. Wadi Milk Formation, Sudan. Caudal vertebra, Vb-808, in F, ventral and G, left ventrolateral view; $\times 10$.



TEXT-FIG. 5. *Kababisha sudanensis* sp. nov.; Wadi Milk Formation, Sudan. A–D, Vb-801, atlas centrum in A, anterior, $\times 23$; B, ventral, $\times 22$; C, right posterolateral, $\times 21$; and D, posterior view, $\times 25$.

Type horizon and locality. Wadi Abu Hashim member of the Wadi Milk Formation at Wadi Abu Hashim, c. 200 km north-west of Khartoum, Sudan. Map reference: $31^{\circ} 8' 7''$ E, $16^{\circ} 41' 7''$ N. The stratigraphical position of this exposure within the Wadi Milk Formation is yet to be established. The Wadi Milk Formation is assigned to the Cenomanian.

Paratypes. Vb-782, left dentary (Text-fig. 4A–C); Vb-788, fused basicranial-exoccipital element (Text-fig. 2A–C); Vb-800, atlas vertebra; Vb-802 (Text-figs 2G–I, 9A–C), Vb-803 (Text-fig. 7F–G), Vb-813 (Text-fig. 8A–E) trunk vertebrae; Vb-806, trunk neural arch (Text-fig. 4E).

Referred material. Vb-783, Vb-785–Vb-786, posterior regions of right dentaries; Vb-784, middle region of a small left dentary; Vb-787, left premaxilla (Text-fig. 3B–D); Vb-789–Vb-790, fused basicranial-exoccipital elements; Vb-792 (Text-fig. 6F–J), Vb-794, Vb-795 (Text-fig. 7A, C), Vb-796, atlas vertebrae; Vb-804, large trunk vertebra; Vb-807, trunk vertebra. In addition, there are further uncatalogued specimens of most elements in the collections of the TUB-SFB-69.

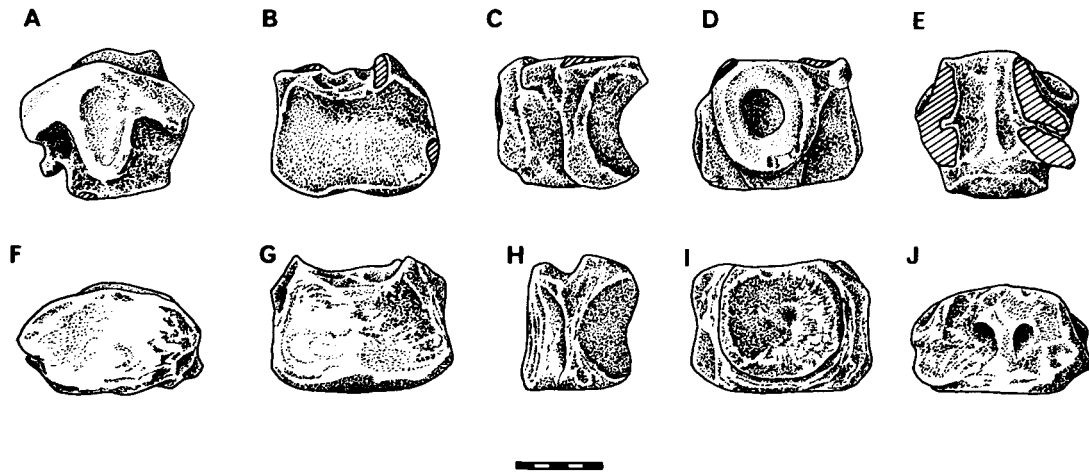
Description

Kababisha humarensis is represented principally by dentaries, fused basicranial-exoccipital elements and vertebrae, which are the commonest lissamphibian remains in the Wadi Milk microvertebrate assemblage. The atlas and trunk vertebrae are diagnostic, the fused basicranial-exoccipital elements are associated by fit with the atlas centra and the other cranial elements are associated on the basis of size.

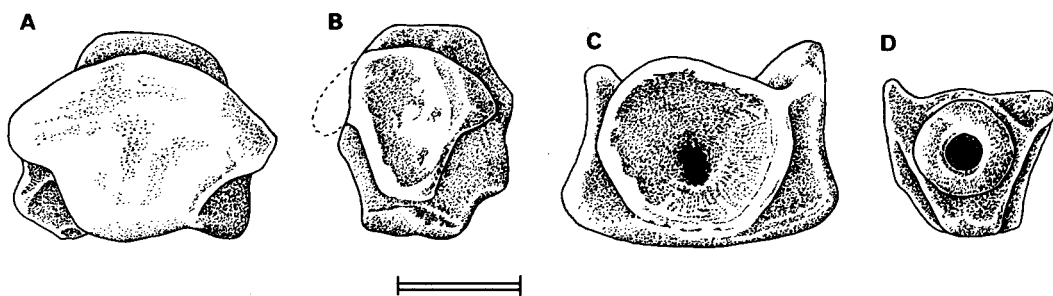
Premaxilla. One specimen of a left premaxilla, Vb-787 (Text-fig. 3B–D), is associated tentatively with *Kababisha* on the basis of size, tooth structure and implantation. It bears four teeth, one of which is almost complete (no tip) and has a slender conical form. There is a strong midline symphysis, but no alary process. The dorsal

surface is concave but the medial border is upturned so that together the united premaxillae formed a low ridge between the two nares.

Braincase and occiput. The exoccipitals are fused into a single median structure which almost certainly incorporates part of the parasphenoid (a similar, but usually still tripartite, structure is found in the living *Cryptobranchus* and *Necturus* and is formed in this way; a comparable fused structure in gymnophionans is termed the os basale). The bone is unusual, however, in that the occipital surfaces have merged across the midline to form a single, strap-like, dorsoventrally compressed surface (Text-fig. 2B) which fits closely against a corresponding surface on the atlas (Text-fig. 2E). The dorsal surface contains a pair of deep anterodorsal depressions which probably housed part of the ear capsule, and is notched posterolaterally by the vagus foramina. Only large specimens of this element have been found (i.e. belonging to *K. humarensis*). By comparison with skulls of extant sirenids, the smallest specimen, Vb-789, belonged to a skull of about 50 mm length; the largest, Vb-790, to a skull closer to 120 mm long.



TEXT-FIG. 6. *Kababisha* spp.; Wadi Milk Formation, Sudan. A-E, Vb-793, a large atlas of *Kababisha sudanensis* sp. nov. For comparison with F-J, Vb-792, a large atlas of *Kababisha humarensis* gen. et sp. nov. A, F, ventral; B, G, anterior; C, H, right lateral; D, I, posterior; and E, J, dorsal views. Scale bar represents 5 mm.

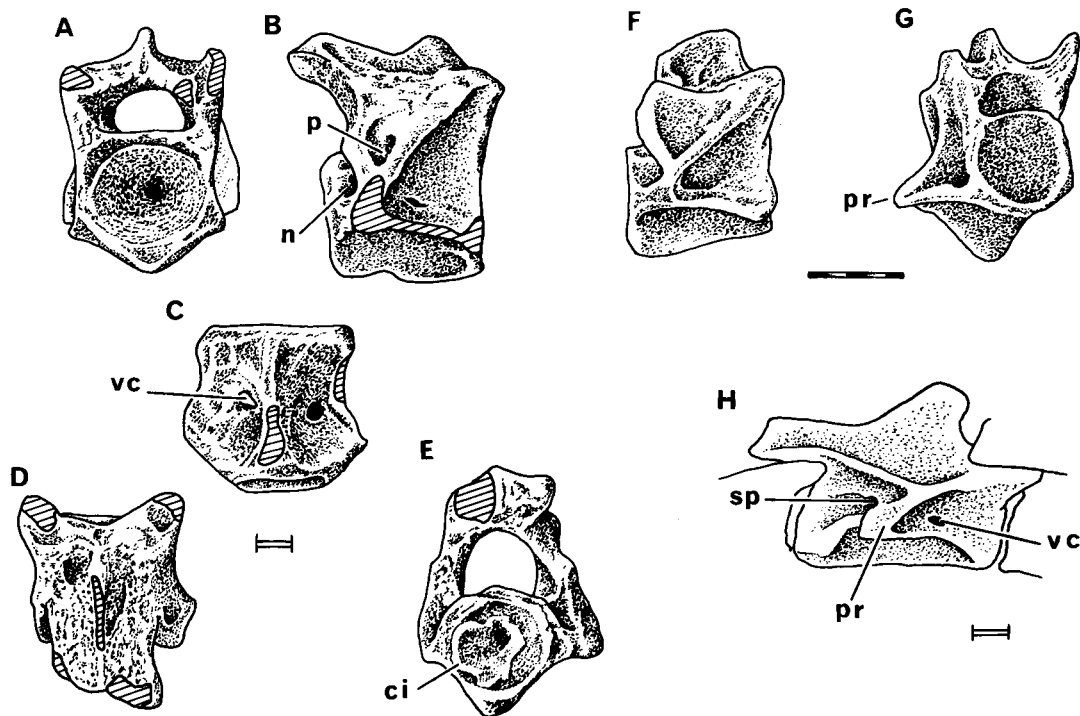


TEXT-FIG. 7. *Kababisha* spp.; Wadi Milk Formation, Sudan. A, C, Vb-795, a small atlas of *Kababisha humarensis* gen. et sp. nov. For comparison with B, D, Vb-799, a small atlas of *Kababisha sudanensis* sp. nov. A-B, ventral; C-D, posterior views. Scale bar represents 1 mm.

Dentary. The dentaries are mostly large and robust (Text-figs 3A, 4A-C). The symphysis is broad and dorsoventrally compressed. Behind it, the ramus of the dentary constricts slightly before widening again, so creating a waisted effect. The subdental ridge deepens anteriorly. Posteriorly, it bears a ventral facet for either a splenial

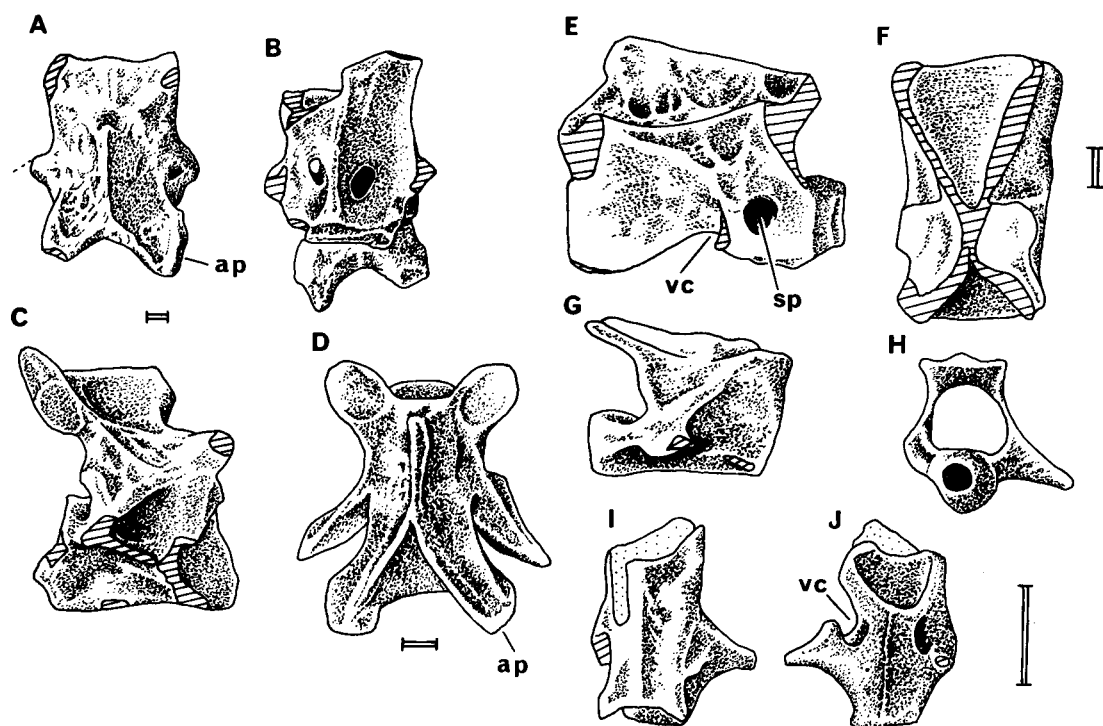
or an angulosplenial (the condition of these elements, whether separate or combined, is unknown); anteriorly it constricts the Meckelian groove and then closes it for a short distance immediately next to the symphysis. The teeth are robust, thick-walled and show no sign of pedicely; the crowns are broken. Gaps in the tooth row suggest a primitive tetrapod 'zahnreihe' pattern of replacement. Behind the symphysis, and set anteromedial to the tooth row, there are one or two tooth positions (of which only one is filled by a mature tooth). This is a constant feature of all dentaries and suggests the presence of an anterior enlarged symphyseal tooth on each ramus. The dentary continues for some distance beyond the tooth row with no step in the upper border; the shape of the posteroventral border is unclear. The lateral surface of the jaw is smooth (no sensory nerve foramina) except for a broad groove which begins as a shallow feature a short distance from the symphysis but deepens posteriorly into a distinct channel.

Atlas. The atlas is short by comparison with subsequent vertebrae. In *K. humarensis*, the atlas is very short, the anteroposterior length of the centrum being about two-thirds of its width. The anterior face is deep with a confluent articular surface which wraps around it. There is thus no interglenoid tubercle. The posterior surface contains a deep notochordal pit with a thick rim. The ventral surface is flat with a slight trefoil structure (Text-fig. 6F) which is more pronounced in small specimens (Text-fig. 7A); the dorsal surface bears deep vascular foramina. The largest atlantes average 10–12 mm in cotyle diameter. There are, however, small atlantes of *K. humarensis* (e.g. Vb-795, Text-fig. 7A, c; Vb-796) with a cotyle diameter of 2 mm.



TEXT-FIG. 8. A–G, *Kababisha humarensis* gen. et sp. nov.; Wadi Milk Formation, Sudan. Vb-813, anterior presacral vertebra in A, anterior, B, right lateral, C, ventral, D, dorsal and E, posterior views; Vb-803, anterior presacral vertebra in F, right lateral and G, oblique anterolateral views. H, *Siren lacertina*, Recent, North America; UCL Zoology W10, posterior trunk vertebra in right lateral view for comparison with B and F. Abbreviations: ci, calcified infilling; n, notch for spinal nerve exit; p, pit; pr, lateral process; sp, spinal nerve foramen; vc, vertebrarterial canal. Scale bars represent 1 mm (A–E, H) and 5 mm (F–G).

One atlas of *K. humarensis*, Vb-800 (Text-fig. 4E), has part of the neural arch preserved. The neural canal is subtriangular with a tall broad spine. Posterolaterally, the arch is perforated on each side by a spinal nerve foramen for the second spinal nerve; ventrally there are vascular pits.



TEXT-FIG. 9. A-C, *Kababisha humarensis* gen. et sp. nov.; Wadi Milk Formation, Sudan. Vb-802, posterior trunk vertebra in A, dorsal; B, ventral; and C, right lateral views. D, *Siren lacertina*, Recent, North America; UCL Zoology W10; trunk vertebra in dorsal view for comparison with A. E-F, *Kababisha* sp. indet.; Wadi Milk Formation, Sudan. Vb-805; incomplete anterior caudal vertebra bearing spinal nerve foramen in E, left lateral and F, ventral views showing natural fracture of the centrum, demonstrating the notochordal canal and the posterior position of the constriction. G-J, *Kababisha sudanensis* sp. nov.; Wadi Milk Formation, Sudan. Vb-815, immature trunk vertebrae in G, right lateral; H, posterior; I, dorsal, and J, ventral views. Abbreviations: ap, aliform process; sp, spinal nerve foramen; vc, vertebrarterial canal. All scale bars represent 1 mm.

Trunk vertebrae. A series of trunk vertebrae is associated with the atlantes on the basis of size, bone type and the detailed structure of the centra. Like the atlas elements, the vertebrae vary in size in broad but not exact correspondence to that of the two species. They are notochordal with a constriction posterior to the midpoint of the centrum, and are essentially amphicoelous. The anterior cotyle is deep in all specimens. In *K. humarensis*, the posterior cotyle is made shallower by a variable amount of calcified material (Text-figs 2I, 8E) but is almost always a cotyle although the rim may bulge slightly in some posterior trunk vertebrae (Vb-802).

The vertebrae bear flange-like transverse processes which vary in size from small flanges to more distinct processes but were not rib-bearing (no articular surfaces). However, few of the transverse processes are complete and it is possible that ribs were borne on a few vertebrae at the anterior end of the column. Each process is supported by accessory crests which run obliquely from the anterior and posterior zygapophyses (Text-figs 2H, 8B, 9C). This arrangement creates deep anterolateral and smaller posterolateral fossae. An anteroventral vertebrarterial canal perforates the transverse process. The neural spines are low but the zygapophyses are steeply angled. In some vertebrae (e.g. Vb-802, Text-fig. 9A-C), small aliform processes extend the arch beyond the posterior zygapophyses. The centra bear strong ventral keels. Well-preserved specimens often show a woven bone pattern on the neural arch (Text-fig. 4D).

Typical trunk vertebrae do not bear spinal nerve foramina. The smaller posterolateral fossa usually has a pit at its base, but these pits do not communicate with the spinal canal in the trunk region (but see below). Notches at the back of the neural arch pedicle suggest that the nerves exited intervertebrally.

Kababisha sudanensis sp. nov.

Text-figures 5, 6A-E, 7B, D, 9G-J

Holotype. TUB-SFB-69 VB-793, an atlas centrum (Text-fig. 6A-E).*Derivation of specific name*. From Sudan, the country of origin.*Diagnosis*. Small *Kababisha* with functionally procoelous presacral vertebrae in which there is a posterior condyle produced by extreme calcification of the rim of the posterior cotyle. In ventral view, the atlas has a length:width ratio of about 1.0 and bears a pronounced trefoil-shaped ridge pattern on its ventral surface.*Type horizon and locality*. Wadi Abu Hashim member of the Wadi Milk Formation at Wadi Abu Hashim, c. 200 km north-west of Khartoum, Sudan. Map reference: 31° 8.7' E, 16° 41.7' N. The stratigraphical position of this exposure within the Wadi Milk Formation has yet to be established. The Wadi Milk Formation is assigned to the Cenomanian.*Referred material*. Vb-797, Vb-798, Vb-799 (Text-fig. 7B, D), Vb-801 (Text-fig. 5), atlas vertebrae; Vb-815 (Text-fig. 9G-J), Vb-816, trunk vertebrae.*Description**Atlas*. The atlas is short by comparison with subsequent vertebrae, but the centrum has a length roughly equal to its width, so appearing roughly square in ventral aspect. As in *K. humarensis*, the anterior face is deep with a confluent articular surface which wraps around it. There is thus no interglenoid tubercle. The centrum is proportionally slightly longer than in *K. humarensis*, and at the posterior end, the infilling and rim development of the notochordal pit has increased to the extent that it bulges from the back of the centrum to give the appearance of a posterior condyle. The ventral trefoil pattern is also more marked and has a central concavity (Text-figs 5B, 6A, 7B). The size difference between *K. humarensis* and *K. sudanensis* is, for the most part, extreme. The largest *K. humarensis* atlantes average 10–12 mm in cotyle diameter while the largest atlas of *K. sudanensis* (Vb-793, Text-fig. 6A-E) has a cotyle diameter of only 7 mm, most being much smaller.*Trunk vertebrae*. The trunk vertebrae are notochordal with a constriction posterior to the midpoint of the centrum. The anterior cotyle is deep in all specimens. In *K. sudanensis*, the calcified infilling bulges out of the posterior cotyle to form a thickened rim. The notochordal canal remains open but is restricted. The effect, in the small vertebrae of *K. sudanensis* is to produce a posterior condyle (procoely), an almost unique condition in salamanders where vertebral centra are either opisthocoelous or amphicoelous. However, the condition in the large specimens of *K. humarensis* suggests that the procoely of the generally smaller *K. sudanensis* is simply a modification of amphicoely rather than a fundamentally different vertebral type. Naylor (1978) described some species of *Ambystoma* as being 'pseudoprocoelous', with the posterior cotyle smaller in diameter (i.e. with more infilling) than the anterior one. Given that the vertebrae from Wadi Milk are much larger than those from some living *Ambystoma* it seems likely that the condition in *K. sudanensis* is merely an exaggerated type of 'pseudoprocoely'. In all other significant respects they resemble those of *K. humarensis*.Vb-815 is a small trunk vertebra (Text-fig. 9G-J), almost certainly from an immature animal. It resembles typical vertebrae of *Kababisha* in the presence of wing-like lateral processes and vertebralarterial foramina, but differs in the complete absence of a neural spine and the weak zygapophyses. Like the vertebrae of *K. sudanensis*, however, the posterior cotyle of the notochordal canal is restricted by a bulging rim.*Kababisha* sp. indet.

Text-figures 4F-G, 9E-F

Material. Vb-805 (Text-fig. 9E-F) and Vb-814, anterior caudal vertebrae with spinal nerve foramen; Vb-808 (Text-fig. 4F-G) and Vb-809, caudal vertebrae.

Description

Caudal vertebrae. Typical caudal vertebrae are smaller than trunk vertebrae with a narrow centrum and a longer neural spine. The ventral surface of the centrum bears paired flanges. In all collected caudal vertebrae (mostly small), the condition of the centrum is like that of the procoelous trunk centrum in *K. sudanensis*, with a perforated posterior condyle. The flange-like transverse process remains, but the accessory crests are weaker. The tips of the transverse processes appear faceted, presumably in relation to muscle attachment. The few identified caudal vertebrae have spinal foramina (e.g. Vb-805, Vb-808 and Vb-814), but the distribution of these within the caudal series is unknown. The spinal nerve foramen opens through the pit at the base of the posterolateral fossa and it is possible that secondary closure has occurred in the presacral series. The presence of a procoelous condition in all caudal vertebrae implies three possibilities.

1. That all collected caudal centra belong to *K. sudanensis* which has similarly procoelous trunk vertebrae. This would be morphologically tidy, but unusual in that all other elements of *K. sudanensis* are much rarer than those of *K. humarensis* in this assemblage.

2. That the caudals belong to the commoner *K. humarensis* which would thus have procoelous caudals in contrast to its amphicoelous trunk vertebrae. This would imply that the procoely arose in the caudals of this genus and extended to the trunk in the more derived *K. sudanensis*.

3. That the caudal vertebrae belong to both taxa and are indistinguishable, with the same general conclusion as alternative 2. Alternatives 2 and 3 receive some support from the observation that some posterior trunk vertebrae of *K. humarensis* (Text-fig. 9A-C) show slight development of the rim of the posterior condyle. These alternatives cannot be resolved with the material to hand so the caudal vertebrae are treated as entirely indeterminate within the genus.

SYSTEMATIC POSITION OF *KABABISHA*

Kababisha exhibits an unusual combination of characters, a mixture of sirenid, unique and primitive character-states.

Character-states supporting relationship to the Sirenidae

1. Non-pedicellate teeth: not found in most adult salamanders but widespread in caudate larvae and persist in the pedomorphic adults of the families Proteidae and Sirenidae (Means 1972) and the extinct family Batrachosauroididae (Estes 1981).

2. Dentary without lateral sensory foramina but with deep lateral groove: occurs in *Habrosaurus* (Estes 1964, fig. 34 and p. 78) and *Siren* (pers. obs.).

3. Interglenoid tubercle reduced to absent (in the fossil sirenid *Habrosaurus* Estes 1964, fig. 37, the cotyles are also confluent, although the condition is less specialized than that of *Kababisha*).

4. Vertebrae with vertebrarterial canals including a dorsoventral passage, accessory anterior and posterior crests, and deep anterolateral fossae: configuration characteristic of at least some vertebrae in *Siren* (pers. obs.).

5. Trunk vertebrae with strong ventral keels: occurs in *Siren* and *Habrosaurus* (Estes 1964, fig. 37) but also in the Batrachosauroididae (e.g. *Opisthotriton* Estes 1964, fig. 38) and may be a widespread primitive feature.

6. Anterior presacral zygapophyses steeply inclined: occurs in all vertebrae of *Kababisha* and in some anterior trunk vertebrae of later sirenids (Naylor 1978) but not most vertebrae.

7. Relatively small spinal canal in trunk: occurs in *Siren* (pers. obs.) and *Habrosaurus* (Estes 1964, fig. 37c).

8. Transverse vertebral processes not rib-bearing on most if not all trunk vertebrae. In the extant eel-like Sirenidae and Amphiumidae, bicipital ribs are present on only a few anterior vertebrae. In sirenids, only presacrals 2-9, sometimes termed the 'cervicals' have rib-bearers (*Habrosaurus* in Estes 1964, *Pseudobranchius* in Goin and Auffenberg 1955, p. 508, *Siren* in Goin and Auffenberg 1955, fig. 3B and in Holman 1985, fig. 1). The remaining vertebrae lack any trace of rib-bearers (e.g. *Siren* and *Pseudobranchius* spp. in Goin and Auffenberg 1955, figs 1-2, c). Other salamanders have rib-bearers on all the post-atlas trunk vertebrae.

9. Caudal transverse processes with faceted tips: occurs in *Siren* (pers. obs.).

10. Paired tall crests on ventral surface of caudal vertebrae: occurs in *Habrosaurus* (Estes 1964, fig. 37B) and *Siren* (pers. obs.).

11. Caudal vertebrae small in relation to trunk vertebrae: occurs in *Habrosaurus* (Estes 1964, fig. 37) and *Siren* (pers. obs.).

12. In some vertebrae, the neural spine is weakly bifurcated posteriorly to give small aliform processes posteriorly. This bifurcation can be seen as a weak expression of the characteristic configuration of *Habrosaurus*, *Siren* and *Pseudobranchus* in which the neural spine is strongly bifurcated.

Character-states apparently unique to Kababisha within the Caudata

13. The sculpture on the neural arches. We have seen this in no other salamander.

14. Confluence of occipital condyles (in the living *Siren lacertina*, there is a near contact of the condyles).

Primitive character-state

15. The form of the premaxilla. Extant sirenids have a long slender lateral nasal process. There is no evidence of this in *Kababisha*.

Ambiguous character-states

16. The presence of symphyseal teeth. This is typical characteristic of temnospondyl amphibians and stem-tetrapods, but has not previously been reported in any salamander, living or extinct. This could be argued to be a retention of a primitive character lost in all other salamanders including stem-salamanders, other sirenids and more derived salamanders. Such teeth are unknown in any lissamphibian, so if the Lissamphibia are accepted as monophyletic in relation to archaic amphibians, it might be argued that the loss of symphyseal teeth occurred at the base of the Lissamphibia and that this presence represents a derived reversal and hence an autapomorphy for *Kababisha*.

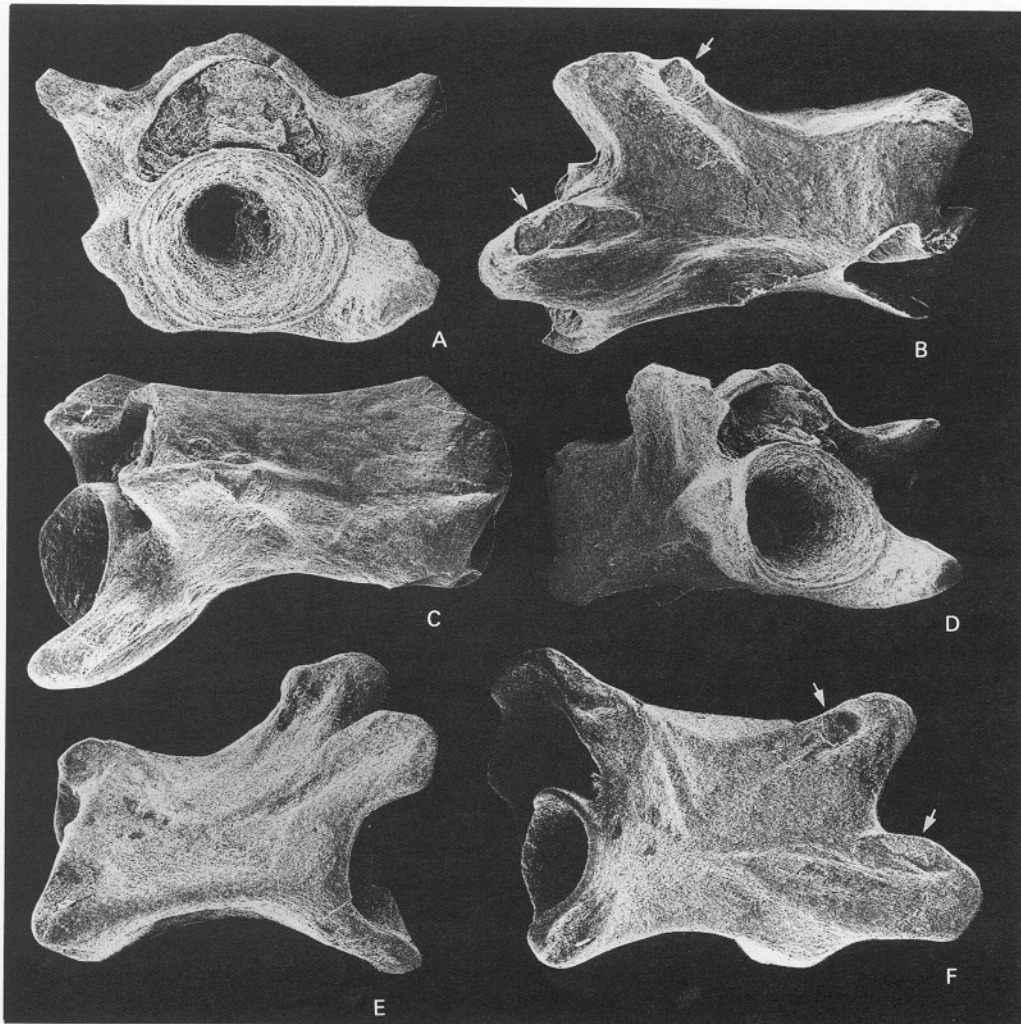
17. Vertebrae primitively amphicoelous (with the assumption that the functional procoely in *K. sudanensis* is a derived condition and an exaggeration of the slight calcification in *K. humarensis*).

18. Except for the atlas and some or all of the tail, all spinal nerves exit intervertebrally. This may be a result of secondary closure. This is more primitive than the condition in the extant sirenids, in which intravertebral foramina occur on all vertebrae except the second (Edwards 1976). This is generally accepted to be convergent with the condition in salamandrids, and implies a separate history of transition from the primitive absence of post-atlas intravertebral foramina to the modern sirenid condition, within the Sirenidae. The condition in *Kababisha* can be argued to be a transitional condition between the primitive urodele condition and that of modern sirenids. It supports the interpretation of *Kababisha* as a primitive sirenid but does occur convergently elsewhere in the Caudata. In *Siren*, the foramina are small and open from the vertebral arterial canal. This is not the case in *Kababisha*.

Characters 1–12 suggest that *Kababisha* is a member of the family Sirenidae. Not all are unique to the Sirenidae but several appear to be. Characters 13–14 are unique specializations of the genus and Character 15 is a primitive feature which other sirenids lack. Characters 16–18 are characters in which there are problems of convergence or polarity interpretation. *Kababisha* thus appears to be a primitive offshoot of the Sirenidae which has acquired some unique specializations.

SYSTEMATIC POSITION OF *NOTERPETON BOLIVIANUM*

Rage *et al.* (1993) described a new and unusual salamander, *Noterpeton bolivianum*, from the Upper Cretaceous (Maastrichtian) of Bolivia. Like the small *Kababisha sudanensis*, *Noterpeton* has procoelous vertebrae with a posterior condyle and all the vertebrae have this construction. Since this



TEXT-FIG. 10. *Gymnophiona incertae sedis*; Wadi Milk Formation, Sudan. A–D, Vb-659; trunk vertebra in A, anterior, $\times 36$; B, left lateral, $\times 30$; C, left dorsolateral, $\times 33$; D, right anterolateral views, $\times 30$. E–F, Vb-660; trunk vertebra in E, right ventrolateral; and F, right posterolateral views, $\times 30$.

is such an unusual condition in salamanders, Rage *et al.* (1993) created a new family of Gondwanan salamanders, the Noterpetontidae, based on *Noterpeton*. To this family, they tentatively referred several poorly preserved vertebrae from the Cretaceous (Coniacian/Santonian) of Niger. They noted that, in other respects, noterpetontid vertebrae were sirenid-like.

The condition of the vertebral centra in the two species of *Kababisha* suggests that *Noterpeton* is a more derived form of the same lineage and should be accommodated within Sirenidae. In *Kababisha humarensis*, the atlas and trunk vertebrae are typically amphicoelous with only a slight thickening of the rim of the posterior cotyle. This is more pronounced in very large specimens and suggests a progressive calcification of this cotyle in this species. In the otherwise similar *Kababisha sudanensis*, the atlas and trunk vertebrae show a highly exaggerated development of the same phenomenon, with the calcification of the rim of the posterior cotyle producing a protruding condyle even in small specimens. This suggests that this type of procoely can develop differentially in otherwise similar forms and is not such a profoundly different condition from amphicoely as to

merit family-level separation. Naylor (1978) named a similar phenomenon 'pseudoprocoely' in *Ambystoma*, in which he found it occurring in some species of that genus but not others. We suggest that the procoelous condition in *Noterpeton bolivianum* is not a profound feature meriting family-level separation of this form, but is simply a derived development of the procoely produced by calcification seen in *Kababisha sudanensis*. We suggest therefore that *K. humarensis*, *K. sudanensis* and *N. bolivianum* form a Gondwanan subset of the Sirenidae showing progressive development of procoely. Consequently, *Noterpeton bolivianum* should be transferred to the Sirenidae, and the Noterpetontidae treated as a junior synonym of the Sirenidae. The relationship of *Kababisha* to the somewhat younger salamander from Niger has yet to be determined but they appear to be extremely similar.

GYMNOPHIONA Rafinesque, 1814

Family *Incertae sedis*

Text-figure 10

Material. Four trunk vertebrae: Vb-659 (Text-fig. 10A–D and previously figured by Werner 1994b, fig. 2); Vb-660 (Text-fig. 10E–F), Vb-661 and Vb-781.

Horizon and locality. Wadi Abu Hashim Member of the Wadi Milk Formation at Wadi Abu Hashim, c. 200 km north-west of Khartoum, Sudan. Map reference: 31° 8·7' E, 16° 41·7' N. The Wadi Milk Formation is assigned to the Cenomanian.

Description. The vertebrae are about 2 mm in length, amphicoelous and elongated with a low spineless neural arch, midventral keel and strong anteroventral parapophyses. The prezygapophyses are widely spaced with nearly horizontal facets: the postzygapophyses are broken away in most specimens. The rib facets are double, with one lying below the prezygapophysis and one flush on the shoulder of the parapophysis (Text-fig. 10B, F).

Systematic position. Three of these vertebrae (Vb-659–661) were reported briefly and one figured by Werner (1994b, fig. 2) in which they were identified simply as gymnophionan vertebrae. Unfortunately, more detailed comparative study with the vertebrae of living forms has not permitted more precise identification although one constraint can be put on the identity of the material.

The living African gymnophionans are placed in two families, the highly derived monophyletic family Scolecomorphidae, found only in Africa, and the probably paraphyletic Dermophinae, a subfamily of the Caeciliidae, found in Africa and South America. The dermophines probably represent a middle grade of organization within the Gymnophiona and are not characterized by unique features. The Wadi Milk gymnophionan could, in principle, belong to either group or to some other lineage no longer found in Africa. Unfortunately, this small sample of gymnophionan material includes only trunk vertebrae. Taylor (1977) has shown the atlas and anterior trunk vertebrae of gymnophionans to be of some taxonomic value but these are not represented here. However, a limited survey of caecilian trunk vertebrae in the collections of The Natural History Museum, London, suggests that the Scolecomorphidae possess a derived character lacking in caeciliids and in the Wadi Milk material. In *Scolecomorphus kirki* (BMNH 93.10.26.97), each trunk vertebra parapophysis bears a posteriorly directed process to which the head of the rib attaches. In all other gymnophionans examined, the ventral rib head meets a facet which lies along the side of the parapophysis. The latter condition is also the condition in the Wadi Milk vertebrae and may be seen in Vb-659 (Text-fig. 10B) and Vb-660 (Text-fig. 10F). If the extended process proves to be a consistent feature for all scolecomorphids, then its absence would tend to exclude the Wadi Milk caecilian from the Scolecomorphidae, or at least the crown-group Scolecomorphidae. The Wadi Milk vertebrae show no features which would exclude them from the Dermophinae.

DISCUSSION

The microvertebrate assemblage from the Cenomanian Wadi Milk Formation of the Sudan contains representatives of all three lissamphibian groups, namely frogs, salamanders and gymnophionans.

Anura

The anuran material from the Wadi Milk Formation will be described elsewhere (Báez and Werner in prep.) but appears to comprise two types of frog, one of which is a pipid. The anuran family Pipidae is known only from the African Plate (including Israel) and South America (Buffetaut and Rage 1993). The earliest known pipids are from the Lower Cretaceous of Israel (*Cordicephalus* and *Thoraciliacus*, Nevo 1968; and *Shomronella*, Estes *et al.* 1978). Pipids are also known from the Upper Cretaceous of both Argentina and Niger (*Saltenia*; Báez 1981). The pipids from Wadi Milk may be closely related to the slightly younger frogs from Niger, but detailed comparison is needed.

Caudata

The salamander family Sirenidae is represented by two extant genera, *Siren* and *Pseudobranchus*, and, until now, by one extinct genus, *Habrosaurus*. Living sirenids are restricted to south-eastern and central North America and north-eastern Mexico. *Siren* first appears in the Middle Eocene of Wyoming and has thus been more widespread over North America than it is now. Fossil *Pseudobranchus* is known certainly only from the Plio-Pleistocene of Florida although *Siren miotexana* from the Miocene of Texas may also be a *Pseudobranchus* (Estes 1981). *Habrosaurus* occurs in deposits of Campanian to Upper Palaeocene age (Estes 1981) in Montana and Wyoming and was, until the recognition of the African material, the oldest recorded sirenid. Yadagiri (1986) reported sirenid material amongst an assemblage of microvertebrate material from the Lower Jurassic Kota Formation of India, but the figured fragments are not diagnostically urodelan.

Thus, the recognition of *Kababisha* as a sirenid not only extends the stratigraphical range of the group back to the Cenomanian but also extends the geographical range to Africa, and more generally, to Gondwana. Furthermore, the vertebral structure of *Kababisha* suggests that the Bolivian genus *Noterpeton* and the undescribed Niger material (Rage *et al.* 1993) are also *Kababisha*-like sirenids.

The systematic position of sirenids in relation to other salamanders has long been debated. Most recent analyses (e.g. Milner 1983; Duellman and Trueb 1986; Larson and Dimmick 1993), suggest that the sirenids are the sister-taxon to all other living salamanders and represent the most primitive surviving salamander lineage. As pointed out by Milner (1983), this implies that they diverged from the other salamanders prior to the cryptobranchoid-neocaudate dichotomy corresponding with the late Jurassic separation of Laurasia into Euramerica and East Asia by the Turgai Straits. Milner argued that the sirenid stem must have been present from the Mid Jurassic prior to the major subdivision of Pangaea, and hence that early sirenids could be expected to be more widespread than the Cenozoic and living forms and might be expected across Laurasia. A range extension southwards into Gondwana was less to be expected. The fundamentally Laurasian distribution of the living and fossil Caudata (with the well-documented exceptions of the South American bolitoglossine plethodontids and the North Africa salamandrids), still indicates that the group arose and diversified in Laurasia in the mid-Mesozoic as argued by Milner (1983). The presence of the sirenids *Kababisha* and *Noterpeton* and the enigmatic *Ramonellus* in Gondwana in the Mesozoic shows that one or two lineages underwent temporary range extensions into Gondwana in the mid-Mesozoic and that a subclade of sirenids (*Kababisha* and *Noterpeton*) diversified there with the development of procoelous vertebrae as one visible trend within the group. The alternative hypothesis, that sirenids were initially Gondwanan and only later extended their range into North America, implies that the stem lineage of the Caudata was Gondwanan, and there is no supporting

evidence for this, all stem-caudates being known from the Mesozoic of Laurasia (Evans and Milner in prep.).

Gymnophiona

The four gymnophionan vertebrae provide the earliest record of this group in Gondwana, the earliest record of gymnophionan vertebrae of modern aspect, and the first record of a fossil gymnophionan from Africa. The only older gymnophionan material is the stem-gymnophionan *Eocaecilia* from the Lower Jurassic Kayenta Formation of Arizona (Jenkins and Walsh 1993), which has more primitive vertebrae with distinct pleurocentrum and intercentrum. The only other records of fossil gymnophionans are single vertebrae from the Palaeocene of Brazil (Estes and Wake 1972) and of Bolivia (Rage 1991). The presence of living *Gymnophiona* across South America, Africa, the Seychelles and India suggests that they were widespread by the late Jurassic–early Cretaceous prior to the break-up of Gondwana (Duellman and Trueb 1986, p. 485) and so their presence in Africa in the Cenomanian had been theorized.

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