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Phylogeny and Paedomorphosis in an African Family of Freshwater Fishes (Gomorynchiformes: Kneriidae)

Terry G. Gnos

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Phylogeny and Paedomorphosis in an African Family of Freshwater Fishes (Gonorynchiformes: Kneriidae)

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Phylogeny and Paedomorphosis in an African Family of Freshwater Fishes (Gonorynchiformes: Kneriidae)

Terry Grande

Abstract

The freshwater gonorynchiform family, Kneriidae, lives in west and central Africa and contains some of the smallest known vertebrates. The extremely small size and paedomorphic nature of some of these species pose an interesting theoretical problem for phylogenetic analyses.

The Kneriidae is defined as monophyletic in part by the presence of lateral extensions of the mesethmoids and the articulation of the first neural arch with both the exoccipitals and supraoccipital. The family is frequently divided into two clades, one consisting of the genera *Cromeria* and *Grasseichthys*, and the other consisting of *Parakneria* and *Kneria*. *Cromeria* and *Grasseichthys* are unusually small fish that mature at only 30 and 16 mm standard length, respectively, whereas *Parakneria* and *Kneria* are substantially larger by the time they reach maturity. Three characters supporting the *Cromeria* + *Grasseichthys* clade are the lack of scales, incomplete cranial ossification, and the lack of median contact between the frontal bones. Incongruent with those three characters is a peculiarly shaped vomer shared by *Cromeria*, *Parakneria*, and *Kneria*. At first look, parsimony would seem to indicate that the *Cromeria* + *Grasseichthys* group is monophyletic. The three characters supporting that group, however, are problematic, because they all are either absence or reductive characters and could be the result of paedomorphic developmental patterns. In contrast, the vomer character suggesting a *Cromeria* + *Parakneria* + *Kneria* group is neither a loss nor a reductive character. Additional non-reductive characters are needed to better resolve the family interrelationships.

Introduction

The teleostean order Gonorynchiformes is geographically widespread, is morphologically diverse, and has a fossil record dating back to the Early Cretaceous. For many years the order was poorly defined and its monophyly in doubt (Gayet, 1986). Various gonorynchiform taxa have in the past been included in the Salmoniformes, Clupeomorpha and Elopomorpha (Regan, 1929). Gosline (1960) recognized the suborder Gonorynchoidei in which he included the Chanidae, Gonorynchidae, and Kneriidae, but he grouped these gonorynchoids within the Cypriniformes. Gosline (1960) was not convinced of the monophyly of Gonorynchoidei and gave no diagnostic characters for the taxon. He simply used it as a group of

convenience. Gosline (1960) stated that "each family within the Gonorynchoidei is so widely different that any relationship between them is difficult to comprehend" (p. 353).

Not until Greenwood et al. (1966) reexamined gonorynchiform relationships was any significant progress made. They proposed the order Gonorynchiformes with two suborders: the Gonorynchoidei (including Gonorynchidae) and the Chanoidei (including Chanidae, Kneriidae, and Phractolaemidae). Kneriidae *sensu* Greenwood et al. (1966) included two tiny (probably paedomorphic) genera, *Cromeria* and *Grasseichthys*. Gonorynchiformes was diagnosed as having an epibranchial organ, upper and lower intermuscular bones, a loosely articulated suspensorium, and one or more pairs of cephalic ribs. In 1970 Rosen

and Greenwood included the Gonorynchiformes within the superorder Ostariophysi as the sister group to the Otophysi (fishes possessing a Weberian apparatus and including all non-gonorynchiform ostariophysans). Lenglet (1974) agreed that the Gonorynchiformes and Otophysi are closely related but considered Rosen and Greenwood's (1970) findings to be premature. He considered the interrelationships within the order uncertain, and the placement of *Cromeria* and *Grasseichthys* in the Gonorynchiformes problematic because of their probable pedomorphic nature. Lenglet (1974) found that *Cromeria* and *Grasseichthys* do not share all the characters of the Gonorynchiformes and proposed that the two genera be placed within a new suborder, Cromeroidei, on the basis of a reduction in cranial osteology, lack of scales, and lack of suprapreopercle. Roberts (1973) criticized Rosen and Greenwood's (1970) classification and stated that the inclusion of the Gonorynchiformes within the Ostariophysi would render the latter paraphyletic. But later, Fink and Fink (1981) corroborated Rosen and Greenwood's placement of the Gonorynchiformes within the Ostariophysi and further diagnosed the order. Although today few ichthyologists question the monophyly of the group, many debate the relationships among its taxa. Howes (1985), in a study based on muscle characters, was unable to resolve relationships of taxa within the order.

In a study of the phylogenetic interrelationships of both Recent and fossil gonorynchiform fishes, Grande (1992) confirmed the monophyly of the order. This was based on several characters, including the loss of the orbitosphenoid bone, a reduction and separation of the pterosphenoid bones, a reduction of the parietals along with expansion of the frontal bones posteriorly, an extension of the supraorbital canal ending on the frontals instead of the parietals, the loss of teeth on the fifth ceratobranchial, lateral expansion of the first neural arch, the presence of a strong ascending process of the parasphenoid that rises high and passes in front of the prootics, the presence of cephalic ribs, and the presence of an epibranchial organ. Grande (1992) also showed that *Chanos* (a marine Indo-Pacific form) is the sister group to a group containing the Gonorynchidae plus an African freshwater clade consisting of the Phractolaemidae (*Phractolaemus*) and the Kneriidae (*Grasseichthys*, *Cromeria*, *Parakneria*, *Kneria*) (Fig. 1).

This paper will focus on the phylogenetic interrelationships of the family Kneriidae. The Kneriidae has long been a systematically problematic

group. Myers (1938) suggested that *Cromeria* (a monotypic genus) was only a larval stage of some species of *Kneria*. Howes (1985) tentatively synonymized *Parakneria* and *Kneria*, stating that "characters separating the genera *Kneria* and *Parakneria* appear to be ones of degree and on the basis of synapomorphies of the skeleton and jaw musculature the two genera should probably be considered a single genus" (p. 299). The family is thus in need of review.

Methods

Skeletal material was prepared using a modified version of Dingerkus and Uhler's (1977) method of clearing and double staining. Measurements and meristic counts were taken from all specimens examined as outlined by Hubbs and Lagler (1949). Cranial and postcranial osteological illustrations were made using a Wild M5 or M8 dissecting microscope equipped with a camera lucida.

Comparative morphological data were analyzed to assess the relationships among kneriid fishes by means of phylogenetic analysis, or cladistics (Nelson & Platnick, 1981). Character polarity was determined by outgroup comparison. Outgroups chosen for this study included *Chanos* (a generalized gonorynchiform), *Phractolaemus* (the hypothesized sister group to the Kneriidae), and *Opsariichthys* (a generalized cypriniform).

Derived character information (character matrix, Table 1) was processed using outgroup rooting, Deltran optimization, and the branch-and-bound version of PAUP version 3.0 (Swofford, 1990). These data were also analyzed using the Hennig 86 program to test the stability of my data matrix and the reliability of PAUP. Characters were optimized using a character description program, D3, version 2, by Buckup (1991). This program generates lists of character state transformations from the output produced by Hennig 86.

Materials Examined

Chanos chanos: 16 specimens (SL = 30–220 mm): AMNH 87984 (cleared & stained); ANSP 122260, 122264 (alcoholics); FMNH 97110, 3981, 10119 (cleared & stained).

Chanos cyprinella: 58 specimens (SL = 70–105

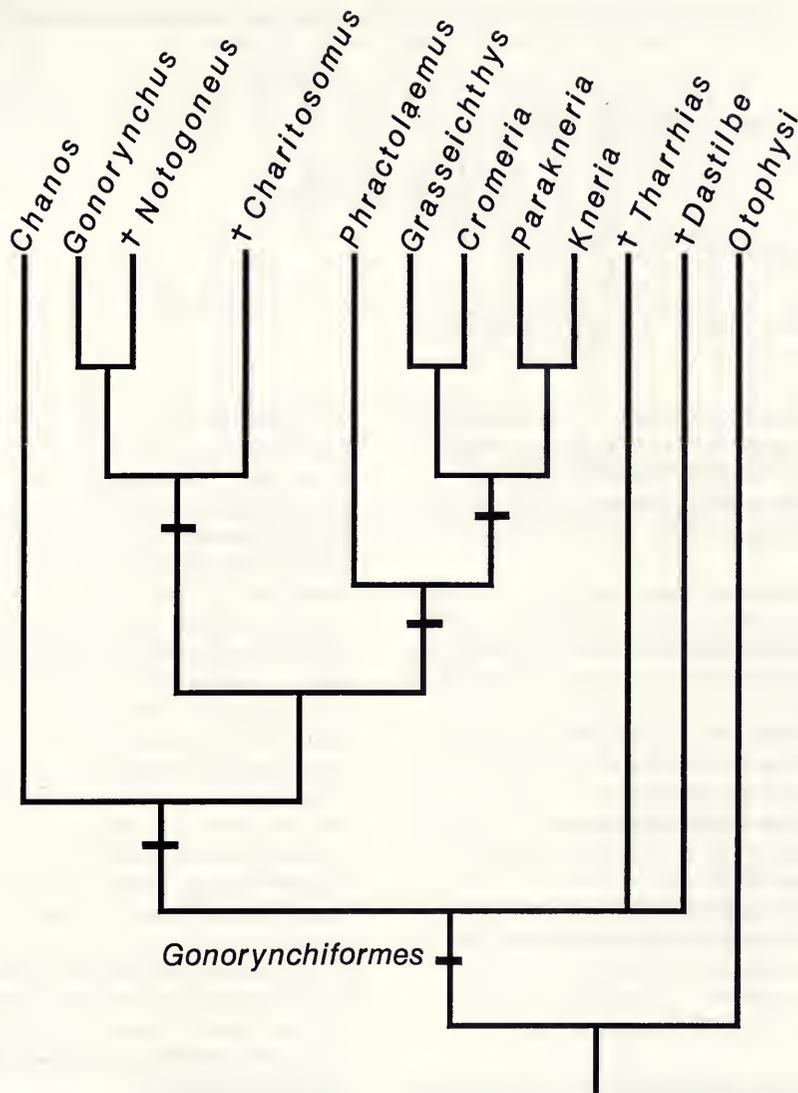


Fig. 1. Phylogenetic hypothesis of gonorynchiform relationships from Grande (1993), modified from Grande (1992). The cladogram was generated using the 3.0 version of PAUP; consistency index equals 0.83. Daggers indicate extinct taxa. Bars identify monophyletic groups.

mm): CAS 03108–03115, 05022–05075 (cleared & stained, alcoholics).

Gonorynchus sp.: 6 specimens (SL = 20–24.5 mm): CAS 60742, 60743 (cleared & stained).

Gonorynchus gonorynchus: 3 specimens (SL = 201–213 mm): AMNH 96050 SD, 96053 SD, 96057 (dried skeletons).

Gonorynchus greyi: 7 specimens (SL = 86–120 mm): AMNH 32973 (cleared & stained); SU 20781, 31874, 09178 (cleared & stained, alcoholics).

Gonorynchus mosleyi: 1 specimen (SL = 122): SU 29239 (holotype).

Phractolaemus ansorgei: 12 specimens (SL = 64.4–123.9 mm): ANSP 71873–71875 (cleared & stained, alcoholics); FMNH 63938 (cleared & stained).

Grasseichthys gabonensis: 43 specimens (SL = 15.5–20 mm): ANSP 103405 (paratypes); CAS 38524 (alcoholics); USNM 199509 (alcoholics); USNM 272934 (cleared & stained); USNM 199591 (paratypes, cleared & stained); SU 63379 (alcoholics); T 73-02-P-264–268 (cleared & stained).

Cromeria nilotica: 2 specimens (SL = 23.2–25.6 mm): T 141098–099 (cleared & stained).

TABLE 1. Data matrix from which the phylogenetic hypothesis for kneriid fishes was constructed.*

	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Grasseichthys</i>	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Cromeria</i>	1	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0
<i>Parakneria</i>	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0
<i>Kneria</i>	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1
<i>Chanos</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phractolaemus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Opsariichthys</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

* 0 = primitive condition; 1 = derived condition.

Cromeria nilotica occidentalis: 12 specimens (SL = 24–34.5 mm): SU 54641 (cleared & stained); BMNH 11.14:124–128 (cleared & stained).

Parakneria tanzaniae: 3 specimens (SL = 43.7–49 mm): BMNH 10.21:163–165 (cleared & stained).

Parakneria malaissei: 1 specimen (SL = 57.6 mm): T 164685 (male paratype, cleared & stained).

Kneria sp.: 5 specimens (SL = 51.2–53.5 mm): CAS 16150 (cleared & stained); USNM 272929 (cleared & stained).

Kneria articulata: 5 specimens (SL = 44.9–47.8 mm): BMNH 5.2:8–10 (cleared & stained); USNM 257091 (cleared & stained).

Kneria katangae: 3 specimens (SL = 34.4–35.1 mm): BMNH 1976.10.20:116–118 (cleared & stained, alcoholic).

Kneria wittei: 7 specimens (SL = 47.9–55.6 mm): FMNH 63939 (alcoholic); T 79-01-P-516–521 (cleared & stained).

Opsariichthys bidens: 2 specimens (SL = 52.5–67.1 mm): SU 68907 (cleared & stained).

For additional gonorynchiform and euteleostean material examined and used for the phylogenetic analysis of the order of Gonorynchiformes, see Grande (1992).

List of Abbreviations

ANATOMICAL—aa, anguloarticular (terminology from Nelson, 1973); bb1, basibranchial 1; bb2, basibranchial 2; bb4, basibranchial 4; bb5, basibranchial 5; bh, basihyal; boc, basioccipital; cb1, ceratobranchial 1; cb2, ceratobranchial 2; cb3, ceratobranchial 3; cb4, ceratobranchial 4; cb5, ceratobranchial 5; cha, anterior ceratohyal; chp, posterior ceratohyal; crb, cephalic rib; dent, dentary;

epo, epioccipital; exo, exoccipital; fr, frontal; hb1, hypobranchial 1; hb2, hypobranchial 2; hb3, hypobranchial 3; hh, hypohyal; hm, hyomandibula; lac, lacrimal; lat eth, lateral ethmoid; max, maxilla; mes, mesopterygoid (= entopterygoid); meth, mesethmoid; mpt, metapterygoid; n, nasal; na, neural arch; op, opercle; pa, parietal; pal, palatine; pmx, premaxilla; pop, preopercle; prot, prootic; psph, parasphenoid; pto, pterotic; pts, pterosphe-noid; q, quadrate; rat, retroarticular; rb, pleural rib; SL, standard length (taken from the tip of the snout to the posterior margin of the hypural); sn, supraneural; so, supraorbital; soc, supraoccipital; sop, subopercle; sph, sphenotic; sym, symplectic; vert, vertebrae; vo, vomer.

INSTITUTIONAL—AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; SU, California Academy of Sciences, Stanford Collection, San Francisco; T, Musee Royal de L’Afrique Central, Tervuren; USNM, Smithsonian Institution, Washington, D.C.

Results and Systematic Descriptions

One tree (Fig. 2) was found with a consistency index of 0.83. The analysis indicates that the Kneriidae forms of monophyletic group consisting of two clades. One clade consists of the genera *Grasseichthys* and *Cromeria* as sister taxa, and the other clade consists of *Kneria* and *Parakneria*. A character conflict exists, however, in that *Cromeria* shares with the *Parakneria* + *Kneria* clade a very distinctive vomer morphology (character 12). This character is therefore incongruent with the characters uniting *Cromeria* with *Grasseichthys*. This

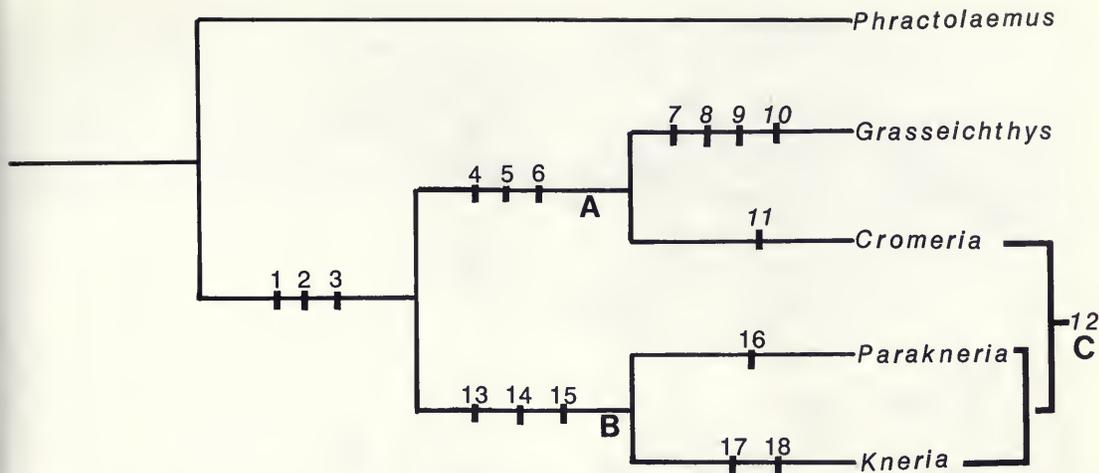


Fig. 2. Phylogenetic hypothesis of kneriid relationships showing two monophyletic groups: *Grasseichthys* + *Cromeria* and *Parakneria* + *Kneria*. Character 12 is shared by *Cromeria*, *Parakneria*, and *Kneria* and is incongruent with the characters uniting *Grasseichthys* with *Cromeria*.

character conflict will be addressed in the Discussion section.

Ostariophys Sagemehl, 1885 (*sensu* Fink & Fink, 1981)

Gonorynchiformes Berg, 1940 (*sensu* Rosen & Greenwood, 1970)

Kneriidae Steindachner, 1866 (*sensu* Rosen & Greenwood, 1970)

Four monophyletic genera compose this family: *Kneria*, *Grasseichthys*, *Cromeria*, and *Parakneria*. They are all small fishes ranging in size from 20 to 60 mm SL, known only from freshwater rivers and river basins of west and central Africa (Poll, 1933). Members of Kneriidae exhibit several interesting morphological specializations (to be discussed) thought by several researchers to be ecological adaptations (Thys van den Audenaerde, 1961). The Kneriidae, unlike other gonorynchiform families, have no known fossil record.

Members of the family Kneriidae are diagnosed by the following synapomorphies:

- (1) The angular forms a major component of the coronoid process. In *Chanos* and *Phractolaemus*, the dentary forms the coronoid process (Fig. 3).
- (2) Lateral wing-like extensions on the meseth-

moids. These extensions also support a series of nodular rostral processes (Fig. 4A). In other gonorynchiforms, there are no processes on the mesethmoids, and the mesethmoids are small with no extensions (Fig. 4B).

- (3) Articulation between the first neural arch and the exoccipitals and supraoccipital (Figs. 5, 6, and 9). In *Grasseichthys*, *Cromeria*, and *Parakneria*, the first neural arch forms an anterodorsal extension that articulates with the back of the skull. In other gonorynchiforms, the first neural arch abuts only the exoccipitals and forms no extension.

Unnamed Kneriid Subgroup A

Monophyly of the *Grasseichthys* + *Cromeria* clade is indicated by the following characters:

- (4) Absence of scales on the body. In all other gonorynchiform taxa, scales are present on the body or in some cases also covering the head (i.e., *Gonorynchus*). Interestingly, *Gonorynchus* specimens less than 25 mm SL are also devoid of scales (CAS 60742, 60743). This character is therefore problematic and indicates that the lack of scales in *Grasseichthys* and *Cromeria* may be the result of delayed or arrested development (i.e., paedomorphosis).
- (5) Absence of suprapreopercle bones. These bones are found in most other gonorynchiforms (with the exception of the Gonorynchidae) and most

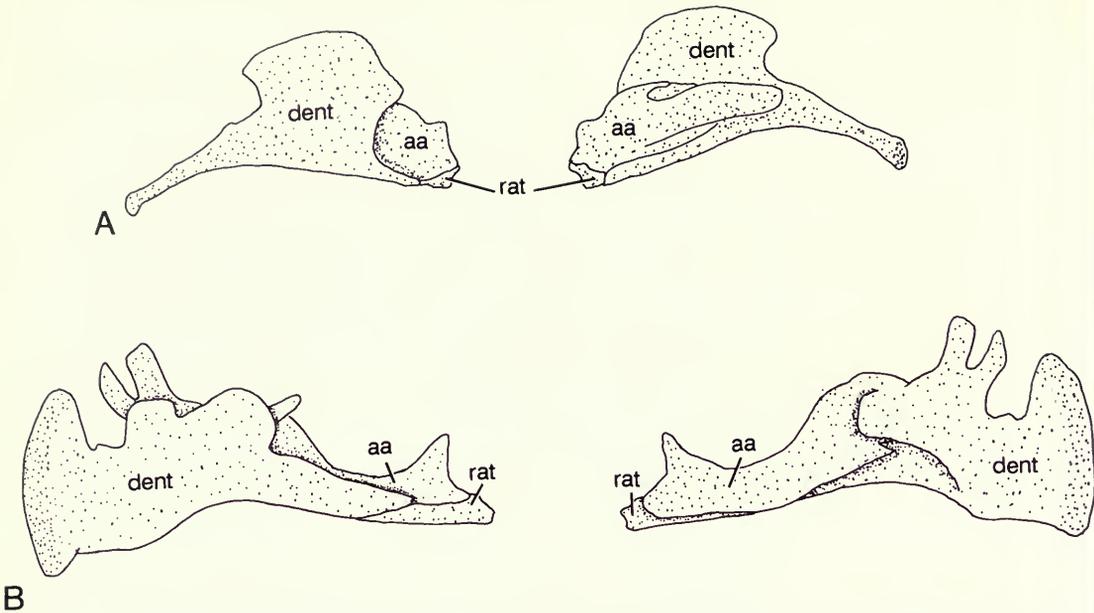


Fig. 3. Coronoid processes (arrow) of (A) *Chanos chanos*, FMNH 97110 (SL = 76.2 mm), and (B) *Kneria wittei*, T 79-01-P-516 (SL = 54.3 mm). Kneriids are diagnosed by a reduction in the size of the dentary and an enlargement of the anguloarticular.

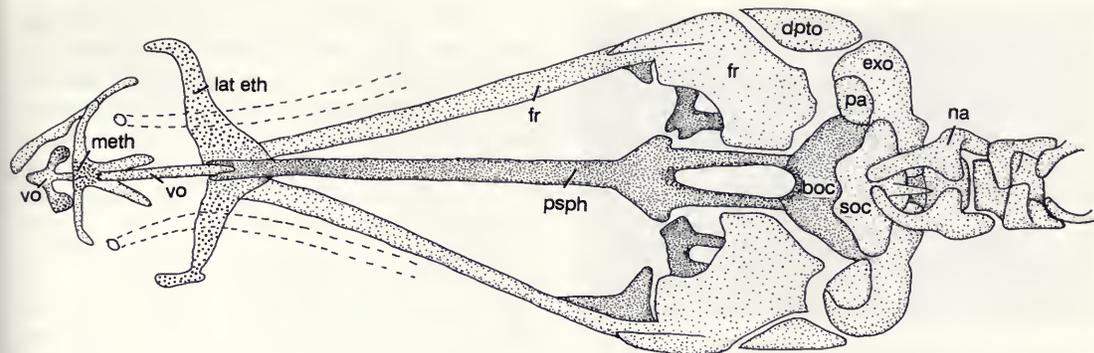
otophysans. It is hypothesized that the loss of these bones occurred independently in the Gonorynchidae, *Grasseichthys* and *Cromeria*, and that the presence of such bones is most likely an ostariophysan character.

- (6) The paired frontals are widely separated in the adults and do not contact each other medially. The frontal bones run along the sides of the skull separated by a protruding brain covered only by connective tissue and skin (Fig. 6). This condition does not occur in any other adult gonorynchiform. In all other gonorynchiforms, the skull is well ossified on the dorsal surface and the frontals either meet along the midline (i.e., *Chanos*) or are laid down as one median element (i.e., *Gonorynchus*). Once again, the separated frontal bones seen in *Grasseichthys* and *Cromeria* may be the result of an incomplete ossification process. Early ontogenetic stages observed in *Chanos* also show a separation of the frontals, and then later in development the bones articulate with each other along the dorsal midline of the skull. This character uniting *Grasseichthys* with *Cromeria* in all probability does not reflect their true phylogenetic relationships but is really the result of delayed development.

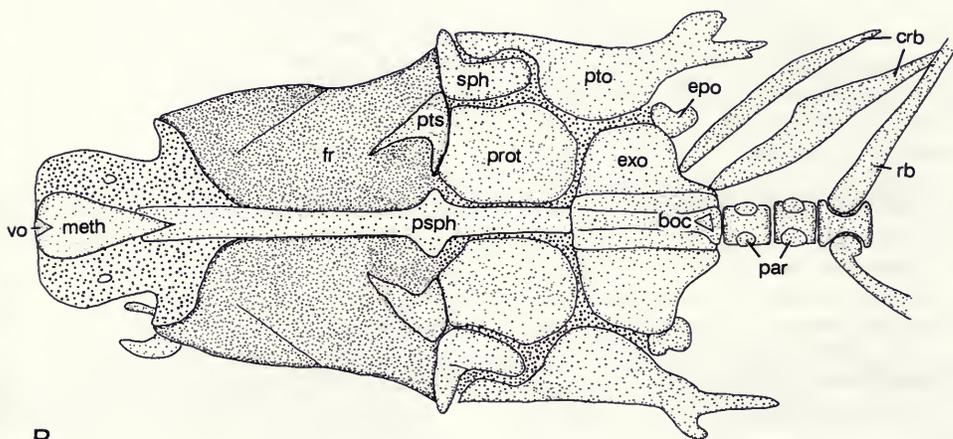
Grasseichthys Géry, 1964

The genus *Grasseichthys* is a monotypic genus consisting of only *G. gabonensis* Géry, 1964 (Fig. 7A). Although not much is known about its ecology, life history, and behavior, Géry (1964) reported that *Grasseichthys* is found in freshwater streams deep in the forests of Gabon and central Zaire. *Grasseichthys gabonensis* is the only species within the Gonorynchiformes without an epibranchial organ. Gut content analysis indicates that *Grasseichthys* feeds on small insects and is probably not an epiphytic feeder like all other gonorynchiforms.

Grasseichthys reaches an adult length of only 20 mm SL. Individuals are mature at only 16–18 mm SL. The body is elongate, compressed, and semi-translucent. Scales are absent and the myomeres are clearly visible. The mouth is small and terminal. The dorsal fin is short and inserts behind the middle of the body (predorsal length equals 56% of SL). The pelvic fins are abdominal. The pectoral base and girdle are attached to the head, and posttemporals are absent. The caudal fin is rounded, and the caudal peduncle is three times longer than high. The number of dorsal fin rays is reduced to 5 principal rays, pelvic fin rays 5–6,



A



B

Fig. 4. A. Skull of *Grasseichthys gabonensis*, τ 73-02-P-264 (SL = 18.9 mm) showing laterally extended mesethmoid extensions with nodular processes. B. Ventral skull of *Chanos chanos*, FMNH 97110 (SL = 76.2 mm) showing a reduced mesethmoid devoid of lateral processes. Anterior to left.

pectoral fin rays 4–5, and anal fin rays 5–6. The number of vertebrae is 36–37, and the number of branchiostegal rays is reduced to 2 (Table 2).

CRANIUM AND JAW ELEMENTS—The entire cranium of *Grasseichthys* is poorly ossified (Fig. 4). The frontals are separated, and it is therefore possible to look through the skull and examine the ventral elements and at the same time examine the dorsal skull bones. The mesethmoid possesses laterally extended wings, which are diagnostic for the family Kneriidae. The lateral ethmoids are extended, as in all African forms, including *Phractolaemus*. The vomer and parasphenoid are straight and the parasphenoid forks posteriorly as it meets the basioccipital. The supraoccipital and parietals are small in size, but the exoccipitals are greatly

enlarged both posteriorly and laterally, accommodating the large occipital region of the brain.

The suspensorium and cheekbones are poorly ossified (Fig. 8.) Both the ectopterygoid and metapterygoid bones are absent. The symplectic (reported by Géry, 1964, as missing) is slender and elongated, unlike that found in other kneriids.

ANTERIOR VERTEBRAE AND ASSOCIATED STRUCTURES—The first vertebra (Fig. 9) is approximately one-third the size of the rest, and its neural arch extends and articulates with both the exoccipitals and the supraoccipital. A hook-like process extends posteriorly from the ventral side of the second vertebra. The second neural arch is expanded both dorsally and posteriorly. All neural arches abut their posteriorly positioned vertebra. Only those supraneurals associated with the second and

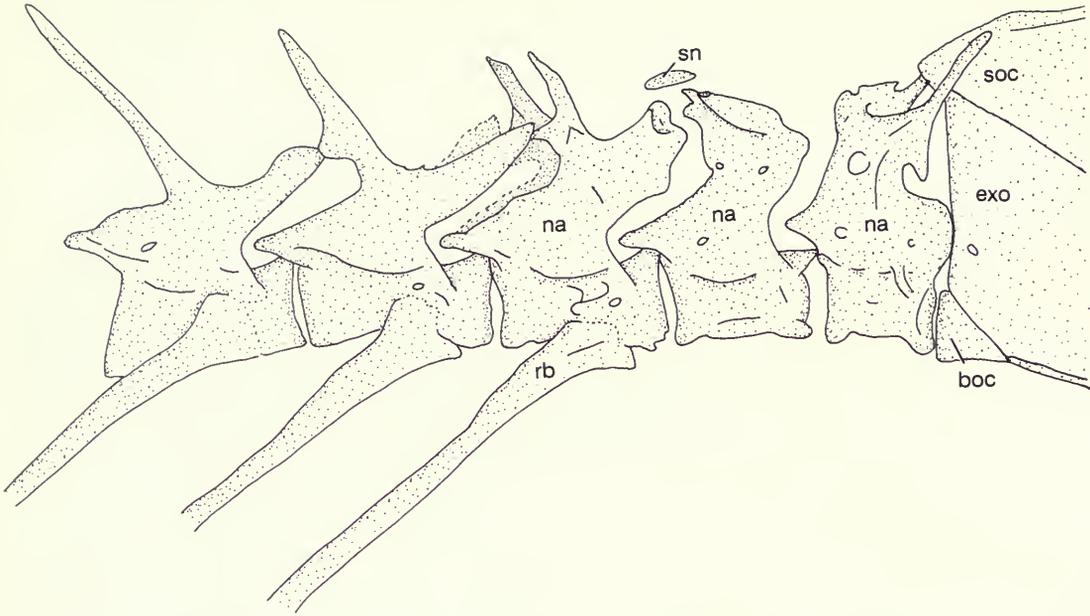


Fig. 5. Anterior vertebrae and neural arches of *Parakneria tanzaniae*, BMNH 10.21:163 (SL = 43.7 mm). Anterior to right.

third arches are present. The first pleural rib is fused with the third vertebra, and there are no intermuscular bones, including cephalic ribs.

Grasseichthys is diagnosed by the following apomorphies:

- (7) The symplectic is elongated, proportionally twice that found in other kneriids.
- (8) Absence of the ectopterygoids. Ectopterygoid bones are found in all other gonorynchiforms.

- (9) Absence of metapterygoids. All other gonorynchiforms have metapterygoids.
- (10) Absence of intermuscular bones, including cephalic ribs. This is the only gonorynchiform without intermuscular bones.

***Cromeria* Boulenger, 1901**

This pedomorphic gonorynchiform genus consists of only one species, *C. nilotica*. Two subspe-

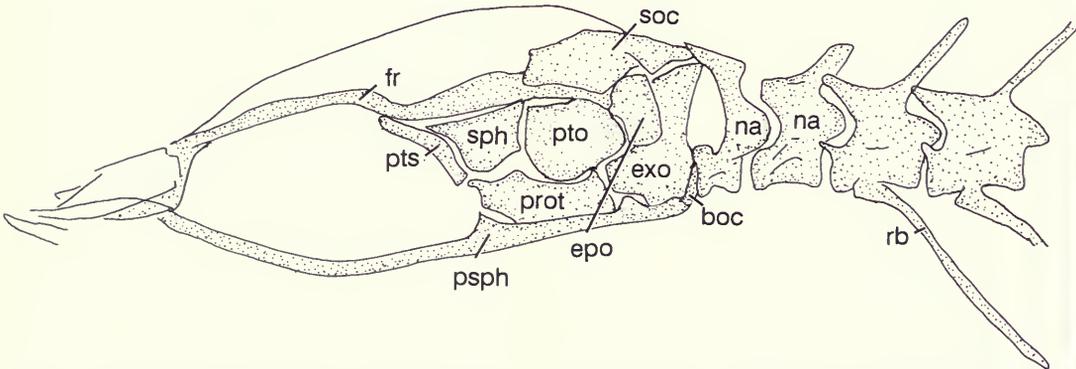


Fig. 6. Skull, anterior vertebrae, and neural arches of *Cromeria nilotica*, τ 141098 (SL = 23.2 mm) showing the separated frontal bones and a first neural arch that articulates with both the exoccipitals and supraoccipital. Anterior to left.

cies (*Cromeria n. nilotica* Boulenger, 1901, and *Cromeria n. occidentalis* Daget, 1954) have been described based on minor meristic count differences and differences in geographic distributions. *Cromeria nilotica* reaches an adult length of about 30–35 mm and is mature at about 27 mm. It is an elongate fish (Fig. 7B) with the body compressed and scaleless. The eyes are very large (8% of head length) and the otic capsule is enlarged. The mouth is small and ventrally positioned. The number of branchiostegal rays is reduced to 3. The vertebrae are small and delicate and range in number from 42 to 43. The number of principal dorsal fin rays is 7; anal fin rays, 5; pectoral fin rays, 9; and pelvic fin rays, 7 (Table 2).

Not much is known about the ecology of *Cromeria*. Géry (1964) reported that *Cromeria* is found in tributaries near sandy riverbanks of the Nile and Niger rivers (north of *Grasseichthys*' habitat). Roberts (1972) reported that *Cromeria* spends much of its time buried in the sand.

CRANIAL AND JAW ELEMENTS—Figure 10 illustrates both the dorsal and ventral skull bones in *Cromeria*. This view is possible because of the expanded frontals and the lack of ossification above a much enlarged brain, a condition also found in



Fig. 7. A. Specimen of *Grasseichthys gabonensis*, T 73-02-P-265 (SL = 20 mm). B. Specimen of *Cromeria nilotica occidentalis*, BMNH 11.14:124 (SL = 35 mm). Scale bar = 10 mm.

Grasseichthys. The anterior cranial bones are reduced in size and poorly ossified. The vomer extends beyond the mesethmoid complex and is directed ventrally (as opposed to horizontally as in *Grasseichthys*). The lateral ethmoids are extended anteriorly and are comparatively longer than those of *Grasseichthys*. The parasphenoid is a thick bone that extends to the posterior margin of the exoccipitals and does not fork at its posterior end as it

TABLE 2. Meristic counts of representative species of *Kneria*, *Parakneria*, *Cromeria*, and *Grasseichthys* for comparisons. See text for discussions. Ranges in text are wider, based on additional specimens.

	Total vertebrae	Dorsal fin rays	Anal fin rays	Pectoral fin rays	Pelvic fin rays
<i>Kneria katangae</i>					
BMNH 10.20:116	41	ii, 9	ii 8 (6 branched)	11	10 (9 branched)
BMNH 10.20:117	41	ii, 9	ii 8 (6 branched)	11	8 (7 branched)
<i>Kneria</i> sp.					
USNM 272929a	41	ii, 8	ii 8 (6 branched)	14	8 (7 branched)
USNM 272929b	41	ii, 8	ii 8 (6 branched)	14	8 (7 branched)
<i>Kneria wittei</i>					
T 79-01-P-516	42	ii, 8	ii 8 (6 branched)	16	8 (7 branched)
T 79-01-P-517	41	ii, 8	ii 8 (6 branched)	16	8 (7 branched)
<i>Parakneria malaissei</i>					
T 164685	42	ii, 8	ii 7 (5 branched)	15	9 (8 branched)
<i>Parakneria tanzaniae</i>					
BMNH 10.21:163	43	ii, 8	ii 7 (5 branched)	14	9 (8 branched)
BMNH 10.21:164	43	ii, 8	ii 7 (5 branched)	14	9 (8 branched)
<i>Cromeria nilotica</i>					
T 141098	42	i, 7	i 5 (4 branched)	9	7 (5 branched)
T 141099	42	i, 7	i 5 (4 branched)	9	7 (5 branched)
BMNH 11.14:124	43	i, 7	i 5 (4 branched)	9	7 (5 branched)
<i>Grasseichthys gabonensis</i>					
T 73-02-P-264	36	i, 5	i 5 (4 branched)	5	6 (5 branched)
T 73-02-P-265	36	i, 5	i 5 (4 branched)	4	—

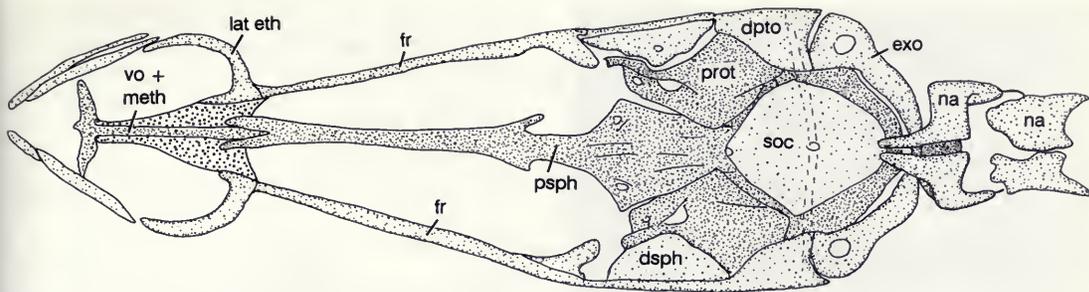


Fig. 10. Skull of *Cromeria nilotica*, τ 141098 (SL = 23.2 mm). Anterior to left.

does in *Grasseichthys*. The supraoccipital is greatly enlarged while the parietals are hardly noticeable. The exoccipitals are enlarged both dorsally and anteriorly and do not border the foramen magnum dorsally. The foramen magnum is therefore bordered only by the large supraoccipital above and the small basioccipital below.

The suspensorium and jaw bones (Fig. 11) are considerably more ossified than in *Grasseichthys* but are still quite delicate, showing size reductions in all bones except possibly the hyomandibula. The quadrate has a very distinctive shape, with an elongated forked posterior process. There is no symplectic.

ANTERIOR VERTEBRAE AND ASSOCIATED ELEMENTS—The anteriormost vertebrae in *Cromeria* are small and delicate (Fig. 6). The first neural arch articulates with both the exoccipitals and the supraoccipital. All subsequent neural arches abut each other dorsally and ventrally. There are no supra-neurals, and there is no evidence to suggest that they have fused with their corresponding neural arches. A slender cephalic rib is present bilaterally, extending from the exoccipitals to the cleithra. The first pleural rib, although more robust than the others, is slender and fused to the third vertebra.

Cromeria is diagnosed by the following apomorphy:

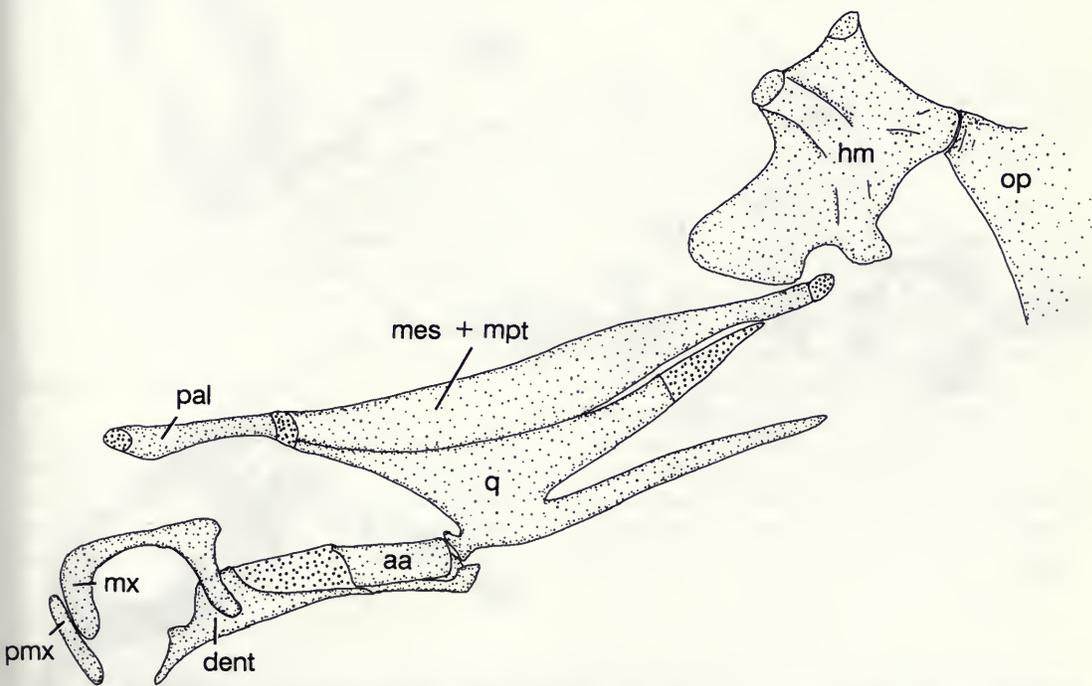
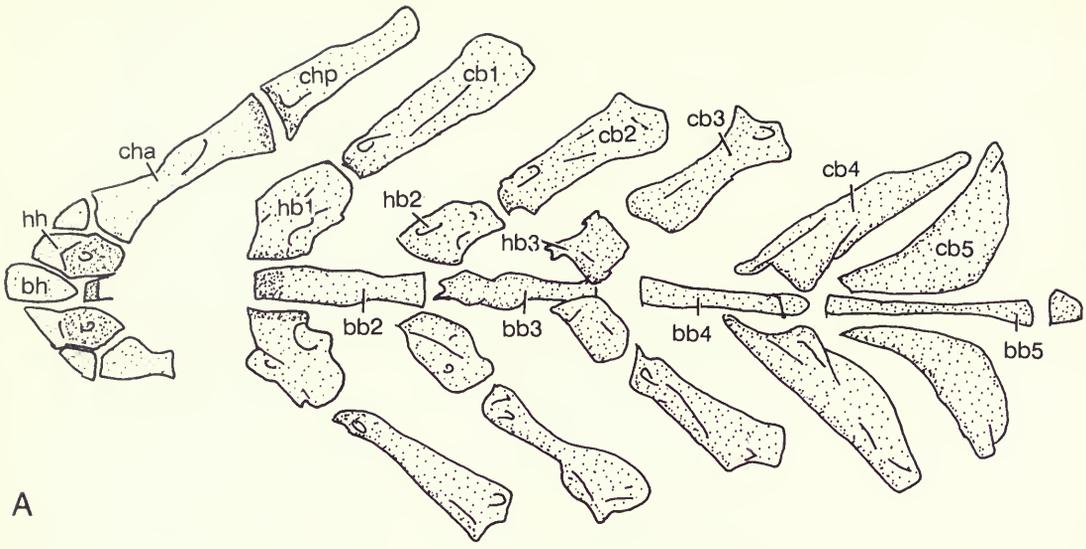
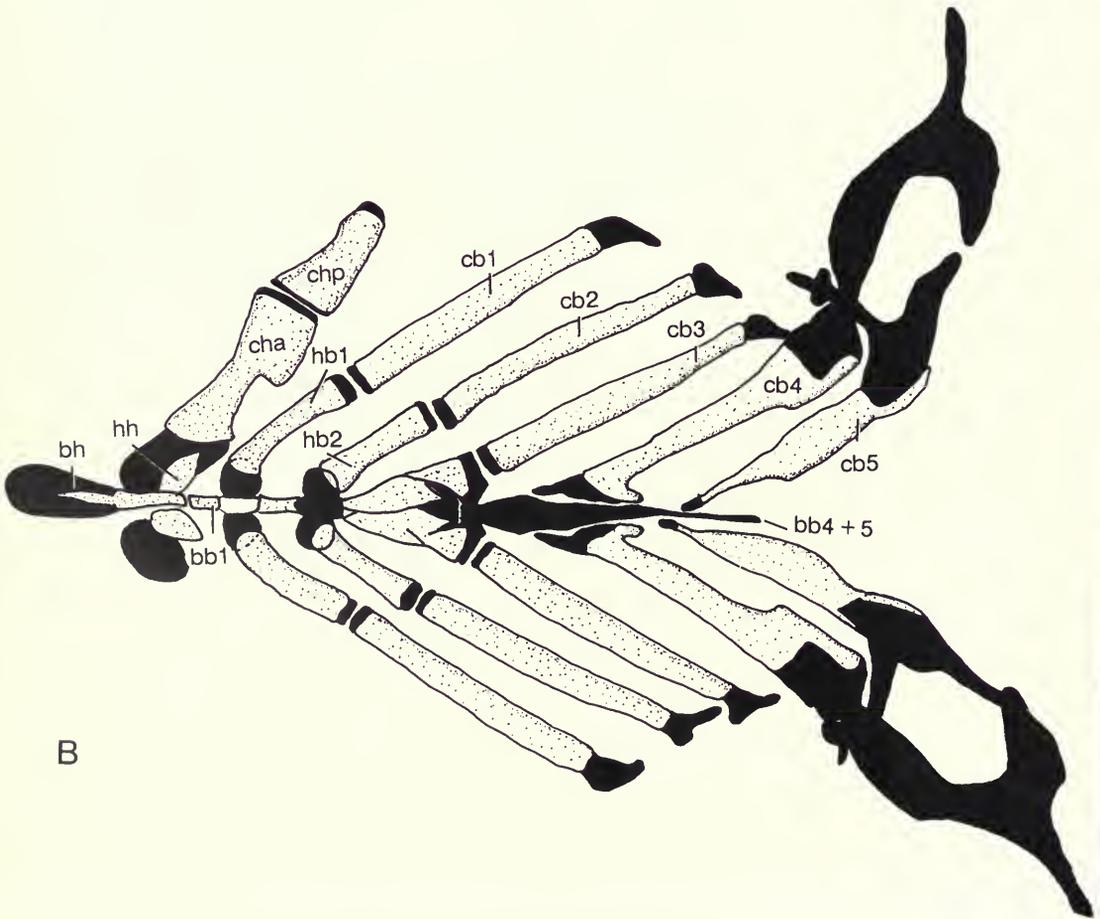


Fig. 11. Lateral view of suspensorium of *Cromeria nilotica*, τ 141098 (SL = 23.2). Anterior to left. Dark stippling indicates cartilage; light stippling indicates bone.



A



B

- (11) The presence of a distinctively shaped quadrate with an elongated forked posterior process (Fig. 11). In other gonorynchiforms this process is not present.

Unnamed Kneriid Subgroup B

The monophyly of a *Parakneria* + *Kneria* clade is indicated by the following:

- (13) The presence of ossified fourth and fifth basibranchials that lie between the enlarged ceratobranchials (Fig. 12A). In other gonorynchiforms, the fourth and fifth basibranchials are formed in cartilage (Fig. 12B).
- (14) The presence of six infraorbital bones. Other gonorynchiforms have five.
- (15) Absence of parietals. In all other gonorynchiforms, the parietals (although reduced in size) are present.

Unnamed Kneriid Subgroup C

The monophyly of a *Cromeria* + *Parakneria* + *Kneria* clade is indicated by the following synapomorphy:

- (12) Rostral extension and ventral inclination of the vomer. In these fish, the anterior part of the vomer is curved and directed ventrally. In other gonorynchiforms, the vomer is straight (*Chanos*, *Grasseichthys*, Gonorynchidae) or curved dorsally (*Phractolaemus*). This character is most likely unique among euteleosts. A character conflict therefore exists between those characters uniting *Cromeria* with *Grasseichthys* and this character uniting *Cromeria* with the *Kneria* + *Parakneria* clade.

Parakneria Poll, 1965

These small African gonorynchiforms reach an adult length of about 60 mm (Fig. 13A). The body is slender (body depth 12.6% of SL), the head is small (about 14% of SL), the eyes are positioned dorsolaterally, and the mouth is ventral. Scales

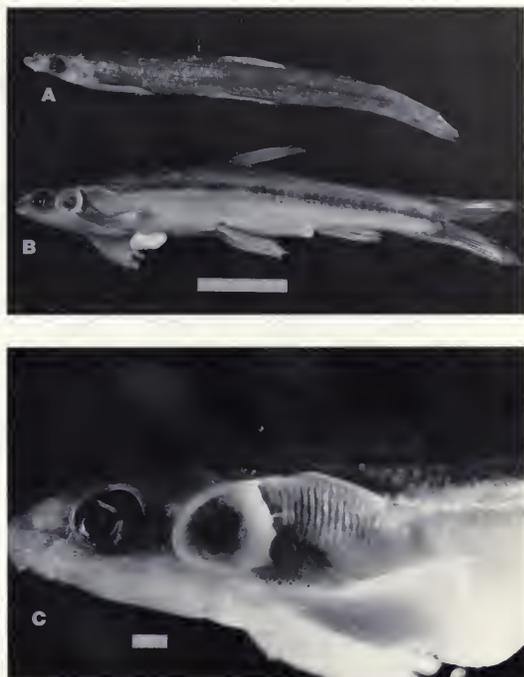


Fig. 13. A. Specimen of *Parakneria tanzaniae*, BMNH 10.21:165 (SL = 51 mm). B. Specimen of *Kneria wittei*, T 79-01-P-517 (SL = 62 mm). C. Specimen of *Kneria wittei*, T 79-01-P-517 (SL = 62 mm) showing the opercular apparatus. Scale bar = 10 mm.

cover the postcranial body. The number of branchiostegal rays is reduced to 3. The number of vertebrae ranges from 42 to 43; principal dorsal fin rays, 8–9; pectoral fin rays, 14–15; pelvic rays, 9–10; and anal rays, 7 (Table 2).

Ten species of *Parakneria* have been described from rivers in Rhodesia, Mozambique, Angola, and the Congo Basin. *Parakneria* inhabits slow-moving pools with muddy bottoms as well as fast-moving streams with waterfalls (Jubb & Bell-Cross, 1974; Penrith, 1973). *Parakneria* is believed to be an epiphytic feeder because of a developed epibranchial organ. Grande (1992) aligned *Parakneria* and *Kneria* as sister taxa (based on osteological characters), although Howes (1985) could not distinguish them on the basis of myological characters. The type species is *Parakneria damasi* Poll, 1965.

Fig. 12. A. Ventral gill arches of *Parakneria tanzaniae*, BMNH 10.21:163 (SL = 43.7 mm) showing the ossification of basibranchials 4 and 5. Cartilage is not drawn. B. Ventral gill arches of *Chanos cyprinella*, CAS 05022 (SL = 101 mm) showing cartilaginous basibranchials 4 and 5. Anterior to left.

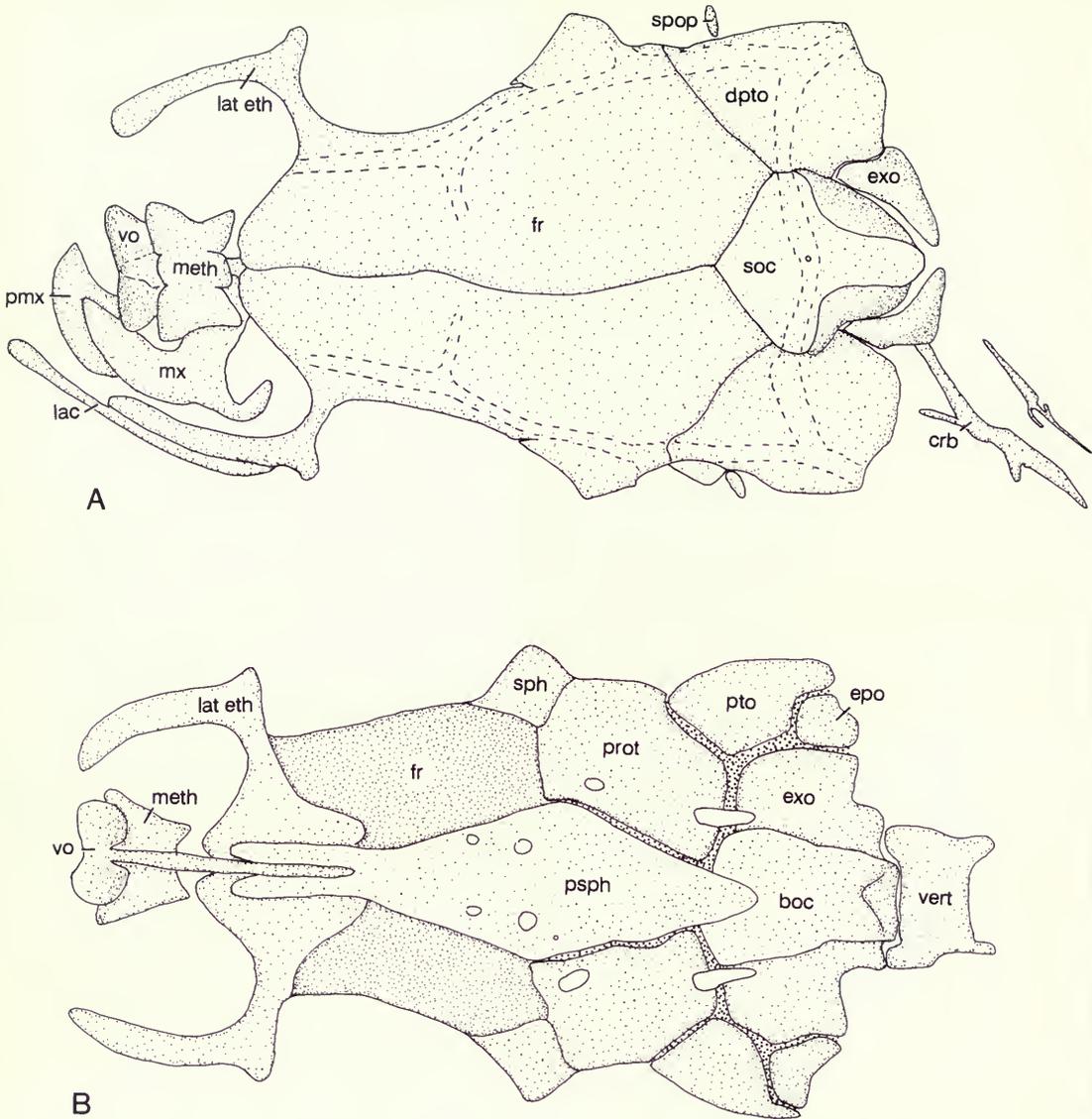


Fig. 14. Dorsal view (A) and ventral view (B) of skull of *Parakneria tanzaniae*, BMNH 10.21:163 (SL = 43.7 mm). Anterior to left. Dashed lines indicate sensory canals.

CRANIUM AND JAW ELEMENTS—The morphological descriptions presented for the genus *Parakneria* are based on examinations of cleared and stained specimens of *P. tanzaniae* and *P. malaissei* and on Lenglet's (1974) detailed osteological study of *P. thysi*. The vomer in *Parakneria* (Fig. 14A) extends beyond the butterfly-shaped mesethmoid and, as in *Cromeria*, is directed ventrally. The lateral ethmoids extend anteriorly to the anterior margin of the vomer. The lacrimals are elongated

and are at least twice as long as those of *Kneria* (character 16). The frontals extend posteriorly to the pterotics, which are larger and more rounded than those of *Kneria*. Parietals are absent in *Parakneria*, so the pterotics border the triangularly shaped supraoccipital instead of the parietals. A supraoccipital crest is present but is not forked as in *Kneria*. The exoccipitals are moderate in size (not as disproportionately large as in *Grasseichthys* and *Cromeria*) and do not border the foramen magnum from above. On the ventral surface of

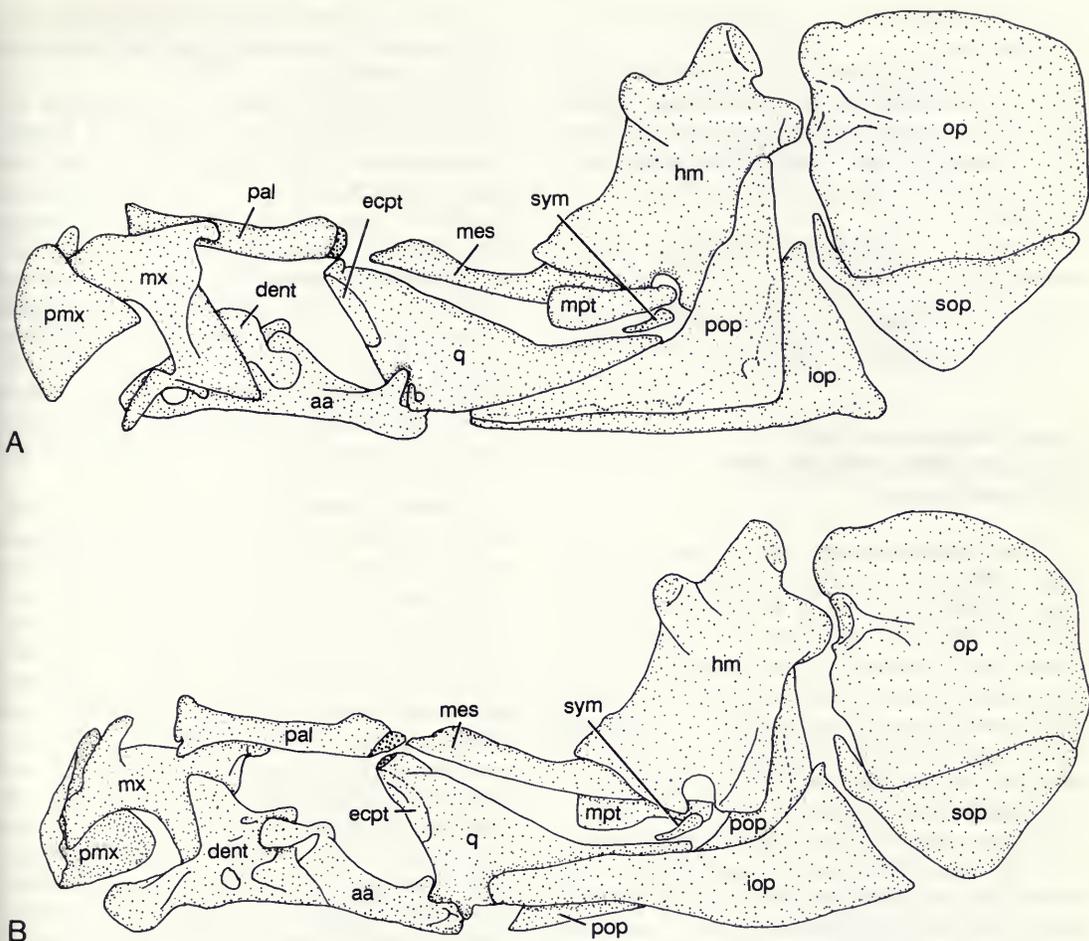


Fig. 15. Suspensoria of *Parakneria tanzaniae*, BMNH 10.21:163 (SL = 43.7). **A**, lateral view; **B**, medial view. Anterior to left.

the skull (Fig. 14B), the parasphenoid is a massive bone that terminates in a point at the anterior end of the basioccipital. The basioccipital is rectangularly shaped and squat in comparison to *Kneria*.

Among the interesting osteological features of this genus is the presence of large but thin maxilla and premaxilla bones (Figs. 15A and B). The premaxilla overlaps the maxilla and completely excludes it from the gape. The ectopterygoid is reduced in size and borders the quadrate anteriorly. The symplectic, in comparison to that of *Grasseichthys*, is greatly reduced in size (almost one-half smaller). The opercular border is partially sealed to the body wall, forming only a small passageway for water to exit the buccal cavity. The extensions of the preopercle forming the height and length of the bone (Fig. 15A) are straight and

form a right angle where they meet posteriorly. The preopercle is rounded in *Kneria*, and its extensions are of equal length. The subopercle has a prominent ascending process that rises dorsal to the level of the interopercle. One suprapreopercle is present in this genus and serves only as a sensory canal.

ANTERIOR VERTEBRAE AND ASSOCIATED ELEMENTS—The neural arch of the first vertebra is expanded and enlarged. Two dorsal processes extend from this arch and articulate with the exoccipitals and supraoccipital (Fig. 5). The second neural arch is without a neural spine. One single autogenous supraneural is present posterior to neural arch 2; no other supraneurals are present. The first pleural rib is expanded and fused with its vertebra. One large blade-like cephalic rib (Fig.

14A) extends from the exoccipital to the cleithrum on either side.

VENTRAL GILL ARCHES—In *Parakneria* (as well as *Kneria*), both basibranchials 4 and 5 are ossified (Fig. 12A). In more generalized gonorynchiforms (i.e., *Gonorynchus* and *Phractolaemus*), only basibranchials 2 and 3 are ossified; the others are cartilaginous.

Parakneria is diagnosed by the following synapomorphy:

- (16) Elongated lacrimal bone, proportionally three times the lacrimal length of *Kneria* (Fig. 14A).

***Kneria* Steindachner, 1866
(*Xenopomatischthys* Pellegrin, 1905,
Is a Junior Synonym)**

Kneria reaches an adult size of about 55 mm (Fig. 13B). It has a deeper body than its sister taxon, *Parakneria* (15% of SL in *Kneria* as opposed to 13% of SL in *Parakneria*). The head is shorter than *Parakneria*'s, the eyes are lateral, and the mouth is almost terminal. There are three branchiostegal rays. The number of vertebrae ranges from 41 to 46. The number of dorsal fin rays is 9; pectoral fin rays, 11–14; pelvic rays, 8; and anal fin rays, 8 (Table 2).

Fourteen species of *Kneria* have been described from the Congo Basin and Angola. *Kneria* constitutes the most speciose genus within the order Gonorynchiformes. Its habitat is very similar to that of *Parakneria*, as it inhabits quiet forest pools as well as fast-flowing waters (Howes, 1985). *Kneria*, like most other gonorynchiforms, is an epiphytic feeder (Roberts, 1972). The type species is *Kneria angolensis* Steindachner, 1866.

CRANIUM AND JAW ELEMENTS—Descriptions of *Kneria* are based on examinations of *Kneria* sp., *K. autriculata* and *K. wittei*. The head of *Kneria* is stout and not as elongate as *Parakneria*. The vomer is directed ventrally and extends beyond the anterior margin of the mesethmoid (Figs. 16A and B). The lateral ethmoids extend anteriorly, but they are not as long as in *Parakneria*. There are no parietals, and the pterotics are elongated posteriorly and separated by a large supraoccipital. The supraoccipital is extended laterally, and the supraoccipital crest is forked, unlike the crest of *Parakneria*. The exoccipitals are considerably larger in *Kneria* than in *Parakneria*. The parasphenoid runs along the ventral side of the cranium and ends at the anterior margin of the ba-

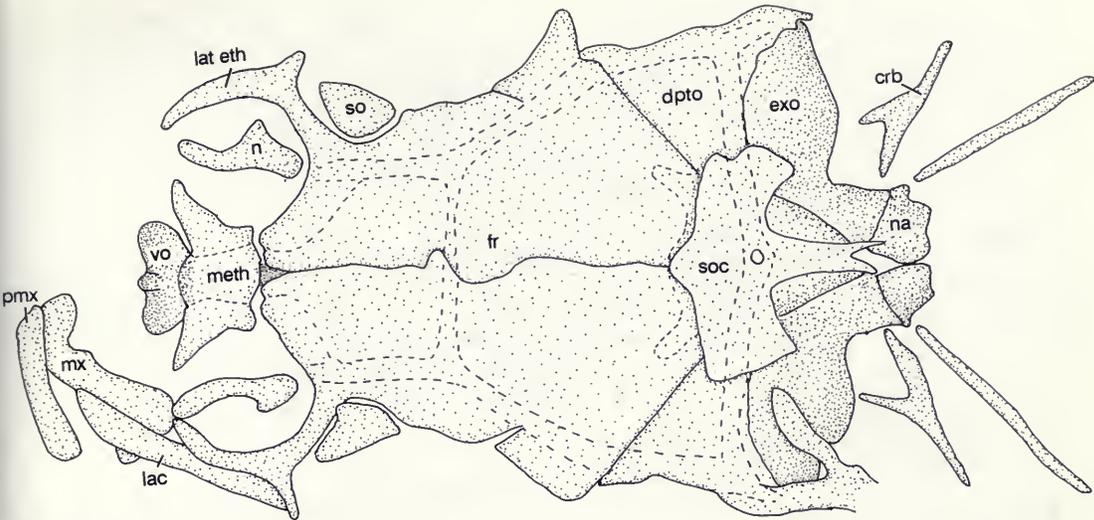
sioccipital. One large foramen is positioned almost in the center of the parasphenoid. Its function is yet to be determined.

In *Kneria*, the premaxilla and the maxilla are not as large as in *Parakneria* (Figs. 17A and B). The ectopterygoid is almost jug-shaped, larger, and more rounded than in *Parakneria*. The symplectic, like that of *Parakneria*, is very small. The height of the preopercle equals its length (in *Parakneria*, the preopercle is longer than it is high), and the interopercle appears more robust and massive than in *Parakneria*. The opercular bone is rounded and supports an opercular apparatus in males. The subopercle is small, without an ascending process as in *Parakneria*. Two suprapreopercular bones are present (compared to one in *Parakneria*) but are reduced to canals.

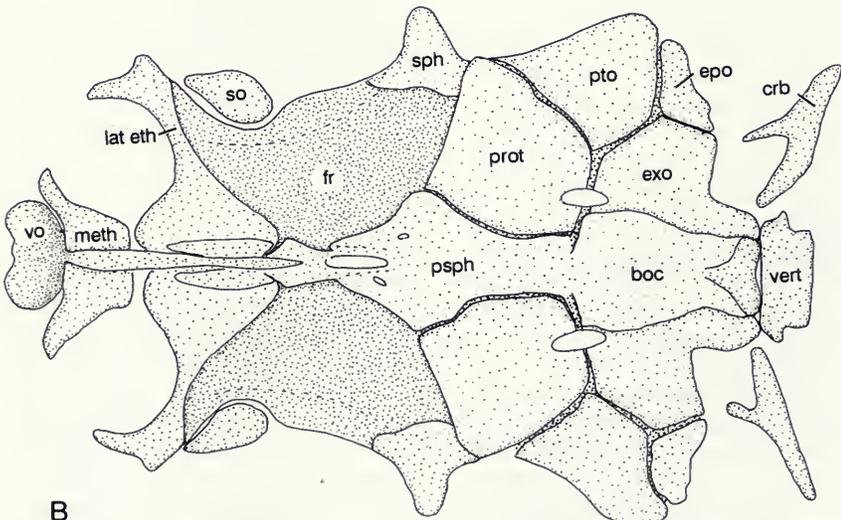
ANTERIOR VERTEBRAE AND ASSOCIATED ELEMENTS—The anterior part of the vertebral column of *Kneria* differs markedly from that of *Parakneria* (Figs. 5 and 18). The anterior vertebrae are very reduced in size and the neural arches are massive. The first neural arch abuts both the exoccipitals as well as the supraoccipital. There is, however, no anterior process extending from the arch and attaching to the skull as in *Parakneria*. There are no autogenous supraneurals, although the second supraneural is fused with the second neural arch. One large forked cephalic rib is present. According to Greenwood et al. (1966), this large rib is a fusion of two smaller ones. *Kneria* differs from *Parakneria* in the presence of enlarged and expanded epipleural ribs or intermuscular bones. These intermuscular bones branch off from the pleural ribs or from ventral processes of the first and second vertebrae. These intermuscular bones extend laterally and attach to the body wall by ligaments. The most anterior six ribs are the most modified and massive. Intermuscular bones of this nature are not found in any other gonorynchiform, and their presence distinguishes *Kneria* from *Parakneria*.

Kneria is diagnosed by the following synapomorphies:

- (17) The external opercular region in males is greatly modified, with a sucker-like apparatus directly on the opercle (Fig. 13). It has been assumed that this apparatus is used during breeding (Lenglet, 1974), even though virtually nothing is known about the fish's life history. The histological structure of this apparatus is now under investigation (Grande & Jones, in prep.). It is not known whether



A



B

Fig. 16. Skull of *Kneria wittei*, τ 79-01-P-516 (SL = 54.3 mm). A, dorsal view; B, ventral view. Anterior to left.

the males are born with an opercular apparatus or it develops at maturity. In any event, no other gonorynchiform exhibits this opercular modification.

- (18) The anterior epipleural ribs are greatly modified and enlarged (Fig. 18). These ribs are attached to the body walls. In no other gonorynchiform, male or female, are these ribs expanded in this way.

Discussion

The phylogenetic study presented here clearly shows that the family Kneriidae is monophyletic and belongs to the order Gonorynchiformes, superorder Ostariophysi. To exclude the genera *Cromeria* and *Grasseichthys* from the Kneriidae would render the family paraphyletic. Contrary to Howes (1985), *Kneria* exhibits two very interesting apo-

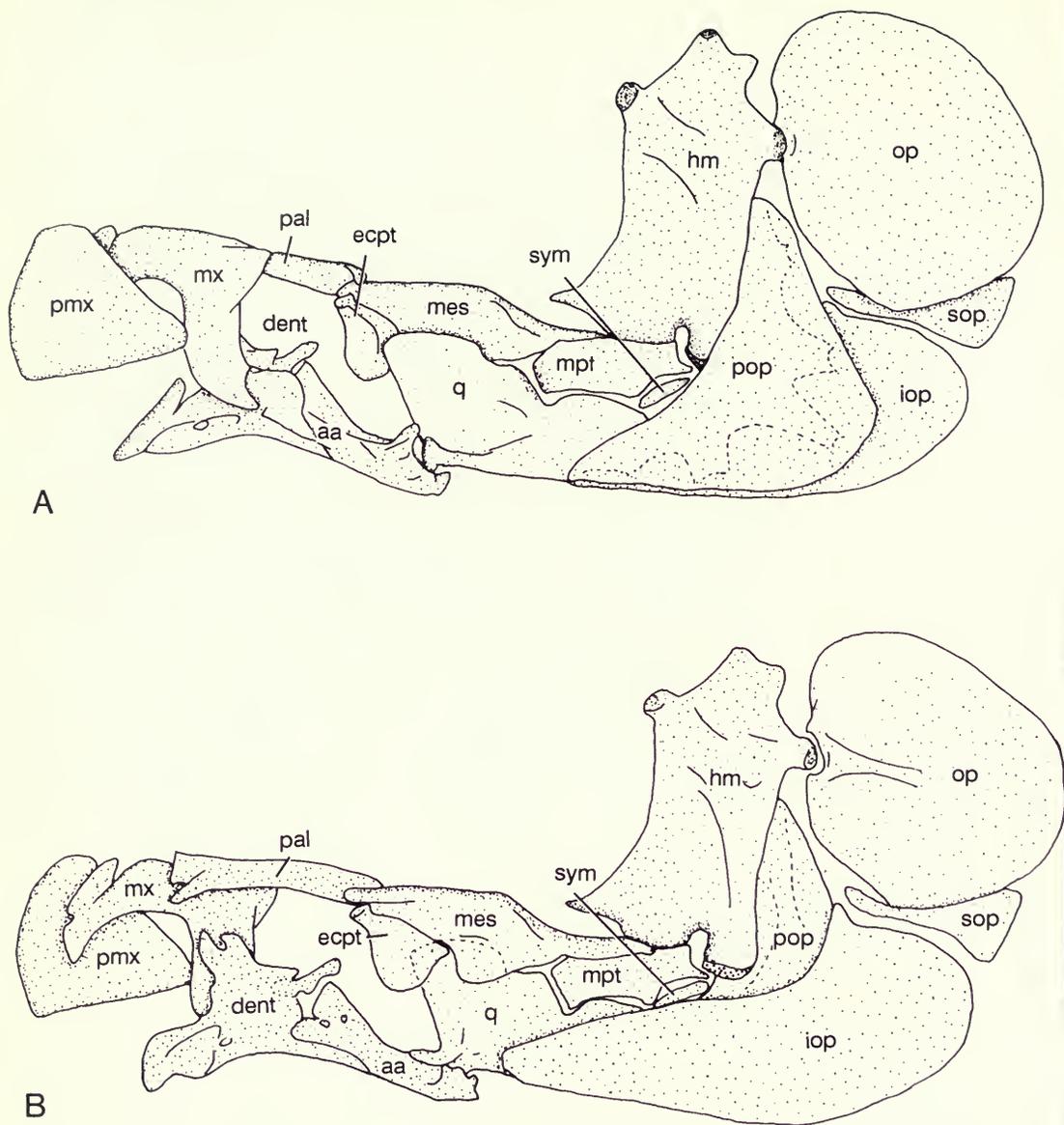


Fig. 17. Suspensoria of *Kneria wittei*, τ 79-01-516 (SL = 54.3 mm). A, lateral view; B, medial view. Anterior to left.

morphies that diagnose it as distinct among gonyranchiforms. These are the modified epipleural ribs that attach to the body wall and the sucker-like opercular apparatus found in males. These characters plus differences in cranial and postcranial morphology show that the genera *Kneria* and *Parakneria* are diagnosable taxa and should not be synonymized.

The relationship of *Cromeria* to the other kneriids is problematic. A character conflict exists be-

tween the characters uniting *Cromeria* with *Grasseichthys* (i.e., loss of scales, reduction in cranial ossification, and separated frontals) and the character that unites *Cromeria* with *Kneria* and *Parakneria* (ventral inclination of the vomer). Both *Cromeria* and *Grasseichthys* are tiny-bodied forms, and the characters that unite them are all loss or reductive characters. Such characters are likely to be the result of pedomorphic development in species as small as these. Ontogenetic stages examined

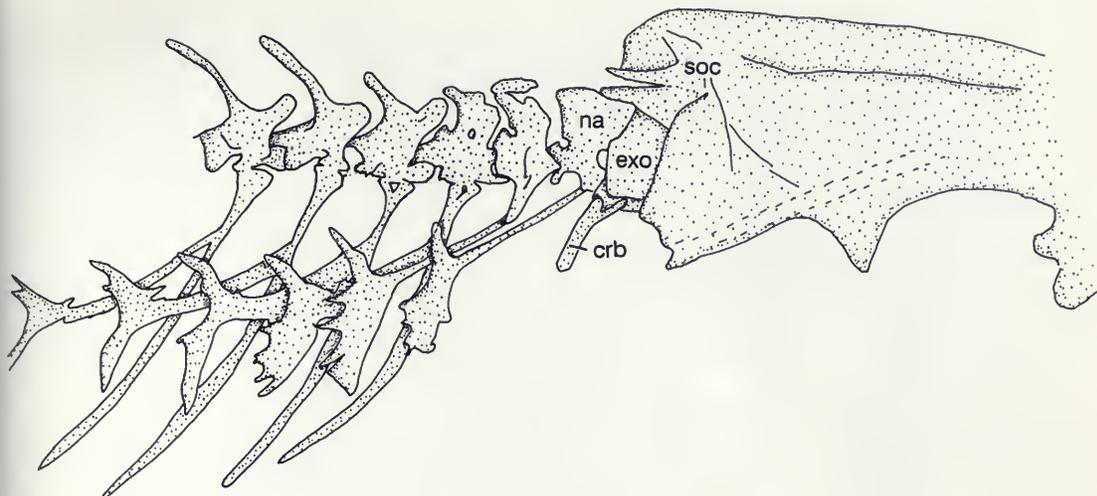


Fig. 18. Anterior vertebrae and neural arches of *Kneria wittei*, T 79-01-P-516 (SL = 54.3 mm) showing the elaborate epipleural ribs. Anterior to right.

in other gonorynchiform taxa (i.e., *Chanos* and *Gonorynchus*) showed that fishes smaller than 25 mm were also devoid of scales, the frontals were separated, and the cranium poorly ossified. Hanken (1984) demonstrated the same cranial developmental pattern as that exhibited in *Cromeria* and *Grasseichthys* (e.g., a reduction in cranial ossification, loss of many dermal bones, a separation of the frontal bones) in the paedomorphic plethodontid salamander *Thorius* (adult SL about 14 mm). He hypothesized that the limiting factor to cranial miniaturization is directly correlated to the minimum size at which the nervous and sensory structures can function. In essence, the skull shrinks around the now predominant brain and sense organs (Hanken, 1983). All extraneous bones are lost. It seems clear that the paedomorphic events that occur in *Thorius* are independent from those that occur in *Grasseichthys* and *Cromeria*, and yet the same pattern of cranial development results in all. It therefore seems that the similarities existing among those paedomorphic taxa are the result of independent paedomorphic events not reflective of a shared evolutionary history. If we assume that the characters uniting *Cromeria* and *Grasseichthys* are the result of paedomorphosis, these reductive characters could be combined as a single character (i.e., all the result of a single phenomenon—paedomorphosis). Then the choice becomes one between a group containing *Cromeria* + *Grasseichthys* (supported by the shared phenomenon of paedomorphosis) versus a group containing *Cromeria* + *Kneria* + *Parakneria* (supported by

the ventral inclination of the vomer). The value of reductive characters or losses in phylogenetic analysis has been demonstrated by Begle (1991). Those characters, however, must be unambiguous and shown to be derived reductions and losses by means of character congruence (Begle, 1991). That is clearly not the case here. The characters uniting *Grasseichthys* and *Cromeria* seem to be the result of two independent paedomorphic events, as indicated by the fact that *Cromeria* shares a unique nonreductive character with *Parakneria* and *Kneria*. Paedomorphosis is therefore obscuring the true phylogenetic relationships within this family of gonorynchiform fishes. To unambiguously solve this dilemma, additional nonreductive character information is necessary. Characters obtained from mitochondrial DNA (Grande, in prep.) and the addition of nonosteological characters to the database should help to resolve the phylogenetic relationships of *Cromeria* within the family Kneriidae.

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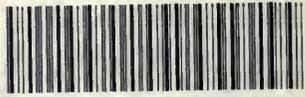
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