Comparative Osteology of the Asian Catfish Family Chacidae, with the Description of a New Species from Burma

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ABSTRACT

The recent revision of the genus *Chaca* divided the previously monotypic genus into two species: a Malayan form (*Chaca bankanensis*) and a South Asian form (*Chaca chaca*). Our research indicates that there are two species in South Asia. The type species *Chaca chaca* is restricted to eastern India and Bangladesh while the new species *Chaca bur-* *mensis* is from the Sittang River and possibly the Irrawaddy River of Burma. Morphological evidence from the skeletal system and the integument indicate that the *Chaca burmensis* is more closely related to *C. chaca* than either is to *C. bankanensis*.

INTRODUCTION

Osteology of the siluriform catfish family Chacidae is very poorly known at present. Gauba (1970) presented the first attempt at a descriptive osteology of the head of the type species *Chaca chaca* (Hamilton, 1822). A more thorough study appeared a year later (Tilak, 1971), in which cranial and postcranial osteology were included. The two studies provide conflicting interpretations of several cranial elements. Even less well documented is the skeleton of *C. bankanensis* Bleeker, 1852, the only other species of the genus which Roberts (1982) recognized in his recent revision of the family. Kner (1858) provided a dorsal view of the neurocranium, the pectoral girdle, and premaxillae, and Chardon (1968) examined the posterior portion of the cranium and the anterior vertebral region as part of his study of the Weberian complex in catfishes. Lundberg and Baskin (1969) added

information on the caudal skeleton of this species, identified therein as *C. chaca,* then considered to be a monotypic genus.

Recent availability of *C. bankanensis* specimens through the aquarium trade prompted a more thorough study of the osteology of this otherwise rare fish in order to attempt to resolve the discrepancies in the literature of the osteology of *C. chaca.* Examination of this material indicated, however, that the osteology of *C. bankanensis* differs from both accounts of *C. chaca.* It was decided to expand the study to provide a comparison of the two species. Direct examination of the few available skeletons identified as *C. chaca* indicated the presence of yet a third species of *Chaca* from the Sittang River of Burma. Regan's (1911) comments on the relationship of *Chaca* appear to be based on this new species. His illustration clearly matches the dry skeleton from which we obtained our earliest indication of the existence of the new species.

The new species is described herein, followed by a comparative osteology of the three species. The spatial relations and form of many of the skeletal elements are typical for catfishes and, therefore, have not been discussed. Our discussion is limited to those elements about which we disagree with one or more of the published accounts or find variation among the species. Tilak (1971) provided a thorough account of the osteology of *C. chaca,* and can be consulted for those aspects of the skeleton which we do not mention here. Because of the limited material available, we are unable to provide observations on all three species for some elements.

MATERIALS AND METHODS

Measurements were taken from specimens with dividers. When meristics vary, the count for the holotype is indicated by an asterisk (*). Fin-ray counts indicate the hardened anterior rays of the pectoral fin and dorsal fin with roman numerals. Principal caudal fin-ray counts include only those rays articulating directly with the ural complex. All other rays are considered procurrent rays. Vertebral counts include five for the Weberian complex and one for the ural complex. Neurocranium length (NL) is the straight-line distance from the anterior extremity of the mesethmoid, exclusive of the cornua, to the posterior extremity of the supraoccipital. Cornua width is measured at the anterior tips of the processes.

Osteological observations are from dry skeletal preparations, cleared and stained specimens, dissections, and radiographs. Disarticulated skeletons of *Chaca bankanensis* were prepared either by poaching unpreserved specimens in water or by digestion of the flesh by trypsin, followed by manual disarticulation of the cranial elements when necessary. Disarticulated bones were stored in glycerine or allowed to dry. Illustrations were made from a single cleared and stained specimen of *C. chaca* (UMMZ 208728), a dry skeleton of *C. burmensis,* n. sp. [BM(NH) 1891-11.30:147], two dry skeletons (AMNH 77377) of *C. bankanensis,* and a single cleared and stained specimen (AMNH 40803). Radiographs were examined for indications of intraspecific variation.

Appropriate names for several catfish bones are still under debate. In recent years, the homology of several elements has been evaluated, e.g., upper shoulder girdle (Lundberg, 1975) and suspensorium (Howes, 1983). Fink and Fink (1981) reviewed the skeletal system as part of their examination of ostariophysan anatomy. Therein, they differed from both Lundberg and Howes in the interpretation of the homology of certain bones. While we recognize that conflicts in interpretations are not

settled by recency of publication, we choose here to follow the names used by Fink and Fink, when possible, for all elements of the skeletal system, due to the breadth of coverage of their work. This, however, does not imply agreement with their interpretation. It is our opinion that some, and perhaps many, of the uncertainties of the homology of ossifications can be settled only with extensive ontogenetic information, something that we do not have in *Chaca*. By following Fink and Fink, we hope to eliminate any ambiguity in meaning for a name which has more than one usage. As Fink and Fink did not include the hyoid arch elements in their study, we adopt the names of Nelson (1969) for these elements.

The following specimens of *Chaca* were examined in this study. Condition of specimens is as follows: alcoholic (A), dry skeleton (D), wet skeleton (W), radiograph only (R).

C. burmensis, n. sp.

BMNH 1891-11.30:144	A(1)
BMNH 1891-11.30:145	A(1)
BMNH 1891-11.30:146	W(1)
BMNH 1891-11.30:147	D(1)

C. chaca

UMMZ 208728	A(4), W(1)
BMNH 1870.11.30:61	R(2)
BMNH 1855.12.26	R(1)

C. bankanensis

USNM uncat.	W(1)
AMNH 77377	A(5), W(2), D(5)
AMNH 9496	A(1)
AMNH 40803	A(1), W(1)
BMNH 1848.2.11.5	R(3)
BMNH 1904.7.2.8	R(1)
BMNH 1863.12.4.117	R(1)
BMNH 1893.3.6.180-181	R(2)
BMNH 1902.12.12.22	R(1)
BMNH 1894.1.19.51	R(1)
BMNH 1911.1.30.49	R(1)
BMNH 1897.12.28.38	R(1)

DESCRIPTION

Chaca burmensis, new species
Figure 1

DIAGNOSIS: A species of *Chaca* most readily distinguished from its congeners by a great-

TABLE 1
Select Measurements of *Chaca burmensis*, New Species, Holotype BMNH 1891-11.30:144
(All measurements in millimeters.)

Total length	240.0
Standard length	203.5
Neurocranium length	43.5
Head width	71.5
Head length	71.5
Interorbital width	31.5
Snout length	11.5
Dorsal spine length	19.0

er number of serrations on the anterior edge of pectoral spines, by the absence of papillae surrounding the eye, and a temporal fossa which is bordered dorsally by pterotic and epiotic only. A large number of osteological characters which further serve to distinguish this species will be discussed in the comparative osteology and phylogeny sections, below.

MATERIAL EXAMINED: Holotype BMNH 1891-11.30:144 203.5 mm SL. Burma: Sittang River. E. W. Oates, collector. Paratypes (all presumably taken with holotype) BMNH 1891-11.30:145 170.0 mm; BMNH 1891-11.30:146 (partially disarticulated, cleared and stained specimen); BMNH 1891-11.30:147 (partially disarticulated dry skeleton).

DESCRIPTION: Meristics: dorsal fin II, 4; pectoral fin I, 4*–5; pelvic fin 6; anal fin i, 9–10*; principal caudal fin rays 11, procurrent caudal rays: upper 21–24*, lower 10–11*. Vertebrae: 33–35(34*). Select measurements of the holotype are presented in table 1.

With the small number of specimens available to us, only a few proportional measurements were judged sufficiently different to be useful in distinguishing *C. burmensis* from *C.*

TABLE 2
Select Proportional Measurements of Three Species of *Chaca*
(in hundredths of the neurocranium length)

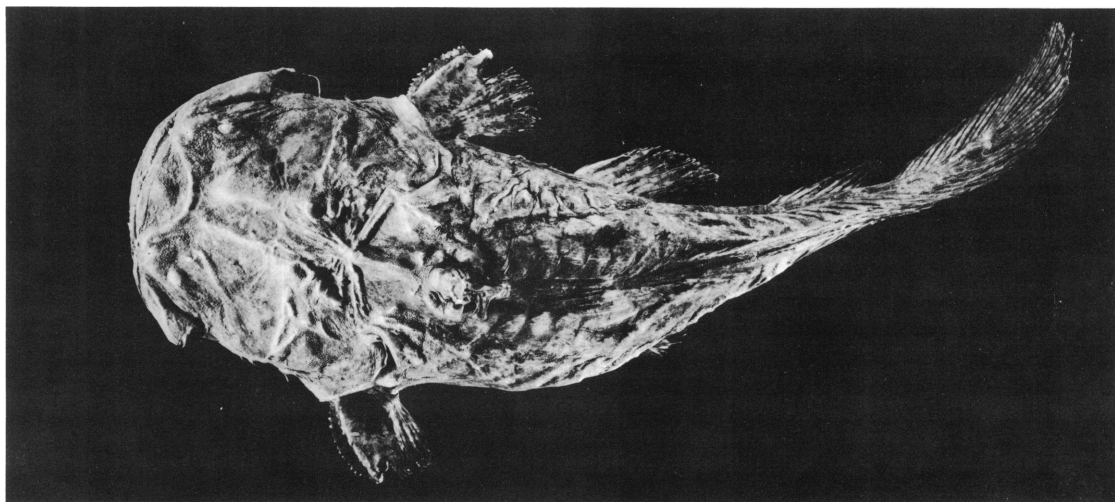|	C. chaca (n = 5)	C. burmensis (n = 3)	C. bankanensis (n = 14)
Cornua width	38–50	49–58.5	39–65.4
Maxilla length	37–38	51–59	28–81
Dorsal spine length	44–53	39–44	22–47

Fig. 1. *Chaca burmensis,* new species, Brown and Ferraris, holotype, BMNH 1891-11.30:144, dorsal view.

chaca. Comparing body parts to neurocranium length instead of the more traditional standard length or head length provided a more convenient measure and, additionally, allowed us to increase our sample size by incorporating skeletal preparations into our sample. A summary of these measurements is provided in table 2.

The pectoral spine has numerous serrae along the anterior surface, which help distinguish the species. Serrae number relates to size of the individual and ranges from 12 in the smallest paratype (NL = 20 mm) to 19 in the 40 mm NL specimen (fig. 2). In c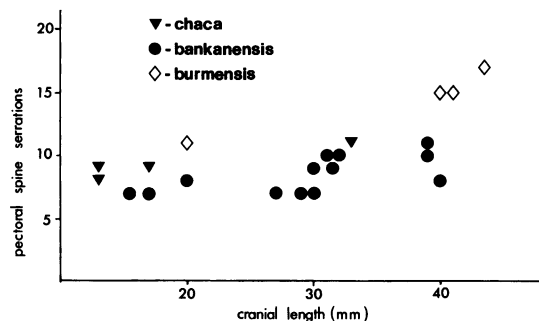omparison, no *C. bankanensis* specimen available to us has a higher serrae count, and a *C. chaca* of more than 1.5 times the neurocranium length of the smallest *C. burmensis* has only one more serrae.

Color in alcohol is light brown to tan with darker areas on head around eyes and down sides beyond dorsal fin dorsally. The venter is almost uniformly light brown except in the area of the pectoral girdle which is nearly white.

Pairs of slender, conical papillae are distributed in a line that runs above the lateral line from the level of the dorsal spine to the caudal peduncle. Some additional papillae are variously distributed along the sides of the body. On the head, flattened flaps of skin, usually branched at the tip, occur laterally in the region of the cheek and opercle. None is found along the dorsal surface of the head or immediately posterior to the eye, as in *C. chaca.* There are no flaps of skin ventrally.

ETYMOLOGY: The specific epithet is derived from the distribution of the species, as currently known.

DISTRIBUTION: All specimens examined by us are from the Sittang River, Burma. Day (1889) noted that a specimen he collected from the Irrawaddy River lacked papillae around the eye. Although we have not examined the specimen, which appears to be in the Zoological Survey of India, number F.-423 (Jayaram and Majumdar, 1964), it is likely
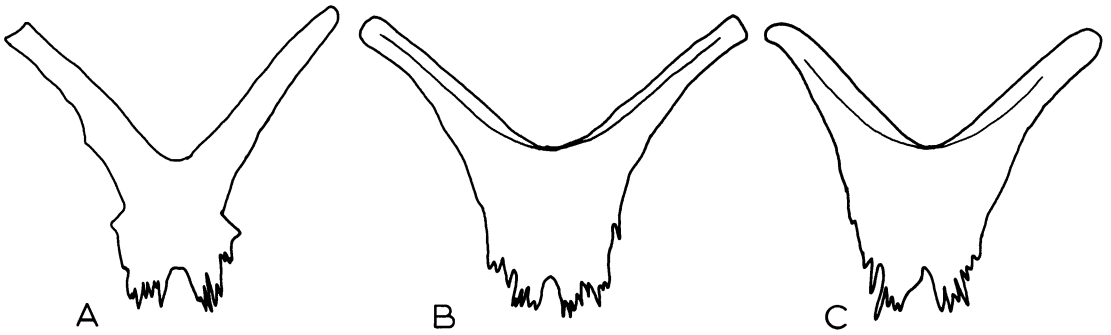

Fig. 2. Pectoral serrations as a function of neurocranium length in three species of *Chaca. C. bankanensis* (13), *C. chaca* (4), and *C. burmensis* (4).

Fig. 3. Mesethmoid of the three species of *Chaca,* dorsal view. (A) *C. bankanensis* (neurocranium length, NL, = 40 mm), (B) *C. burmensis* (NL = 41 mm), (C) *C. chaca* (NL = 33 mm).

that the fish is *C. burmensis* and that the distribution of the species includes the Irrawaddy drainage.

COMMENTS: Roberts (1982) provided a detailed summary of the superficial anatomy, proportional measurements, and nomenclatural history of *Chaca.* He correctly removed *C. bankanensis* from the synonymy of *C. chaca.* However, the decision to retain the Irrawaddy River record of *Chaca* within *C. chaca* is somewhat problematical. It appears that Roberts did not personally examine any material from that drainage, as none of the material listed is from there. There is, however, an enigmatic entry in the material examined as "Nishangara, Tarai Varei" (Zoologische Museum der Universität Hamburg 2324) which we have not been able to find in available gazeteers. Roberts commented on both of the characters which we list in the diagnosis of *C. burmensis,* papillae around the eye and pectoral spine serrations, and suggested that the observed variation is intraspecific. While we have not examined all of the specimens listed in his paper, we find that the differences we observed are consistent between the Indian and Burmese forms of *Chaca.* In addition, we have found additional skeletal differences in the length of the maxilla and dorsal spine and the shape of the posttemporal fossa, which distinguish *C. burmensis* from *C. chaca.* Because these differences serve to distinguish *C. burmensis* only from *C. chaca,* they are treated in the comparative osteology section (below) and not in the diagnosis.

The holotype of this species may be readily distinguished by its right pectoral spine which is apparently deformed. Its anterior serrations end abruptly, and the spine extends to a point. However, the serrations of the left spine decrease in size gradually to an end and the rest of the spine slopes to a point.

COMPARATIVE OSTEOLOGY

NEUROCRANIUM

ETHMOID REGION: The vomer is absent as an independent element in all species. Gauba (1970) and Tilak (1971) reported a vomer covering the ventral surface of the ethmoid, extending anteriorly into the cornua as slender strips of bone, and suturing with the parasphenoid posteriorly. While this spatial orientation is typical for the vomer, we have been unable to find an ossification separate from the mesethmoid, even in disarticulated specimens or small individuals. It is possible that the vomer is fused to the ethmoid, but in the absence of ontogenetic information which confirms this, we feel that it is more appropriate to record the element as absent.

The mesethmoid (fig. 3) projects anteriorly as two divergent cornua. Typically in catfishes, an unpaired chondral bone extends anteriorly into the snout as a median element and branches, forming two lateral or obliquely directed cornua. Dorsally, the body of the mesethmoid is split, running down either side of the anterior fontanelle to form elongate sutures with the frontals. Midventrally, the mesethmoid sutures with the parasphenoid along its entire width. The anterior cornua of the mesethmoid are as long, from the point where they diverge to their tips, as the body of the bone and its posterior projections. As
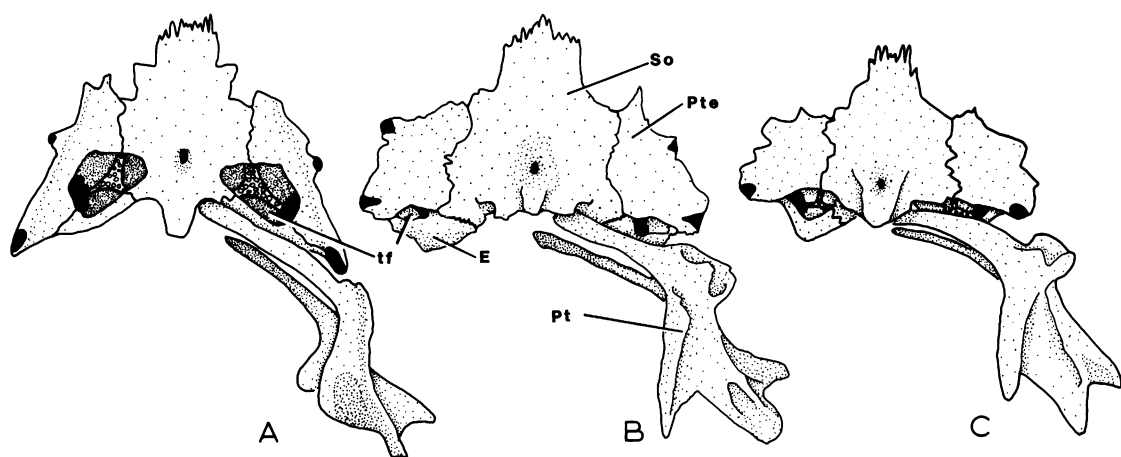
Fig. 4.   Posterior neurocranium and posttemporal of three species of *Chaca,* in dorsal view. (A) *C. bankanensis* (NL = 39 mm), (B) *C. burmensis* (NL = 41 mm), (C) *C. chaca* (NL = 33 mm). *C. burmensis* drawn and reversed. So supraoccipital, Pte pterotic, E epiotic, Pt posttemporal, tf temporal fossa.

described above, both Gauba and Tilak considered the ventral part of this element, including the projecting horns, to comprise a vomer, a determination we have been unable to verify. The anterior end of the mesethmoid in the three species varies from nearly U-shaped in *C. chaca* with more obtusely diverging cornu to the V-shaped, acute angle of divergence of *C. bankanensis. C. burmensis* appears similar to *C. chaca,* though the angle of divergence is somewhat more acute.

ORBITOSPHENOID REGION: The orbitosphenoid is a paired bone forming the anterior part of the sides and floor of the neurocranium. Both Gauba (1970) and Tilak (1971) reported a single element, fused along the ventral midline. In all specimens available to us, there are two separate elements, articulating ventrally with the parasphenoid and not each other. According to Gauba the pterosphenoid was reported to meet the prootic posteriorly. This, however, is not the case. A thin ventral arm of the sphenotic extends ventrally between the two elements, excluding the parasphenoid from the trigeminal-fascialis foramen.

OTIC REGION: The sphenotic is larger than the pterotic, not smaller as reported by Gauba (1970). A lateral process off the sphenotic forms the posterior border of the infraorbital canal.

The pterotic is the posteriormost element on the dorsolateral surface of the cranium. It articulates posteriorly with the epiotic and medially with the supraoccipital. The junction of these three elements can be clearly seen through the temporal fossa in a cleared and stained specimen of *C. bankanensis,* but the reduced size of the fossa makes similar observations nearly impossible in *C. burmensis.*

The epiotic forms the posterior part of the temporal fossa in all three species. As reported by Gauba, the epiotic of *Chaca chaca* is visible only from a posterior view of the neurocranium.

The supraoccipital forms the largest element of the neurocranium. Like the sphenotic and the pterotic, the supraoccipital is highly ornamented with numerous dorsal ridges in both *C. chaca* and *C. burmensis.* In *C. bankanensis* the surface of these bones is smoother. Of the three species, only *C. bankanensis* possesses an occipital process (fig. 4) which meets the dorsally expanded first pterygiophore posteriorly.

The exoccipital is located on the posterior and lateral surfaces of the neurocranium. In contrast to the observations of Gauba, the exoccipital does not articulate with the first vertebra. The first vertebra articulates only with the basioccipital.

The posttemporal (fig. 4) sits on the transverse processes of the complex centrum and articulates with the supraoccipital and basioccipital by way of dorsal and ventral prongs,
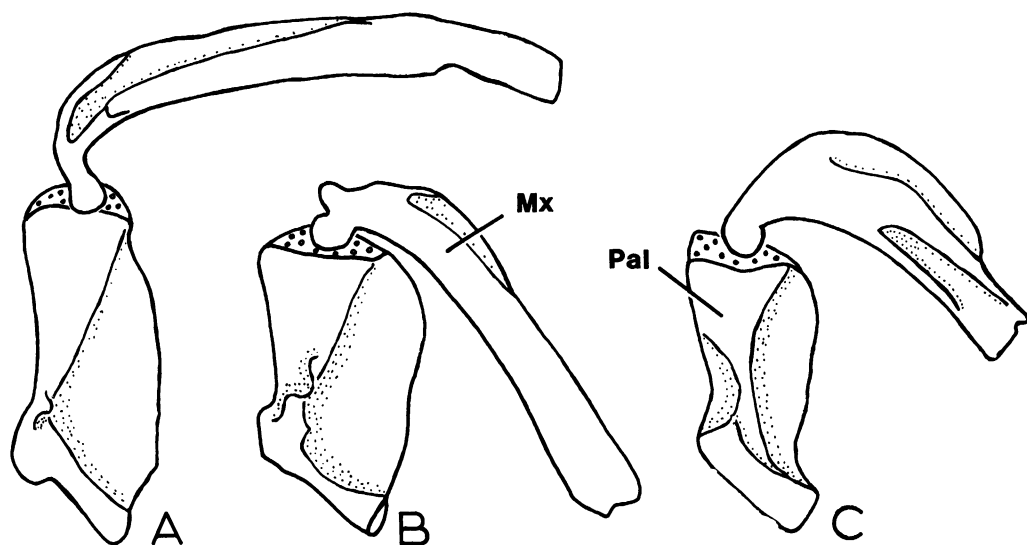
Fig. 5.   Right maxilla and palatine of three species of *Chaca,* in dorsal view. (A) *C. bankanensis* (NL = 39 mm), (B) *C. burmensis* (NL = 41 mm), (C) *C. chaca* (NL = 33 mm). Mx maxilla, Pa palatine.

respectively. In both *C. chaca* and *C. burmensis,* the dorsal body of the posttemporal is stout and heavily ridged on its dorsal surface, and bears a large knoblike projection anterolaterally and three prongs posteriorly. In *C. bankanensis,* the bone bears only two posterior prongs, and is without the anterolateral knob or the heavy ridges dorsally.

VISCERAL ARCHES

JAWS: The maxilla (fig. 5) is an elongate, anteriorly convex shaft of bone, which articulates with the cartilaginous anterior end of the palatine via paired heads. Tilak (1971) stated that the heads of the maxillae were embedded within the palatine cartilage. In fact, the bone articulates with this hyaline cartilage pad in a manner typical for catfishes. The maxilla varies in length among the three species (table 2), but is otherwise similar in form. It is conspicuously longer in large individuals of *C. bankanensis* and *C. burmensis* than in *C. chaca.* Maxillary length increases disproportionately relative to neurocranium length in *C. bankanensis.* In small individuals, maxillary length ranges from 28 to 41 percent of the length of the neurocranium. In the largest individual the maxilla is 81 percent of the neurocranium length (fig. 6).

The premaxilla has a posteriorly directed process emanating from the medial half of the tooth-bearing plate which projects obliquely medially and parallel to the ethmoid cornua. Gauba (1970) stated that the upper jaw of *Chaca* is protrusible, presumably because of this process, which superficially resembles the ascending premaxillary process in euteleosts. There is, however, no
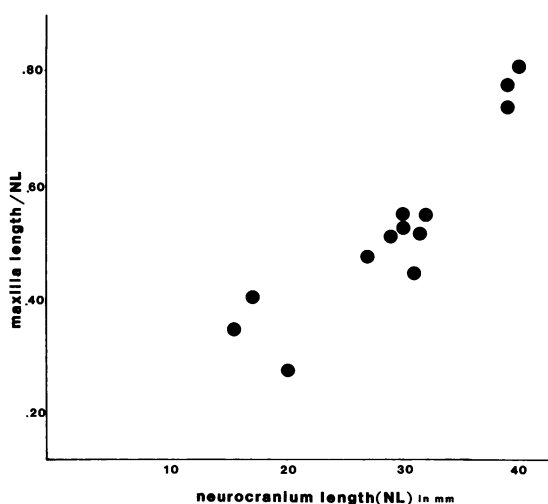

Fig. 6.   Change in length of maxilla in proportion to neurocranium length, as a function of neurocranium length.

evidence that *Chaca* can protrude the premaxilla. We have been unable to move the elements anteriorly in either alcoholic or wet skeletal specimens and the mesethmoid lacks a cartilaginous pad which is usually found along sliding joints. The premaxilla does rock slightly along a transverse axis. The articulation for this motion appears to be a fibrous joint with the mesethmoid and not, as Gauba stated, with the palatine.

SUSPENSORIUM: The palatine in *C. chaca* (fig. 5) has been described as both short and stumpy (Tilak, 1971) and a large broad bone (Gauba, 1970). Neither account appears adequately to describe the character of this bone. It consists of a perichondral core which flares anteriorly to a broadly flattened, cartilage-tipped end which articulates with the maxillary. The center of the chondral bone is constricted and the posterior portion diverges posterolaterally. The posterior end flares into an L shape, tipped with cartilage. At the apex of the angle formed by these two cones is a medial articular facet contacting the lateral ethmoid. Extending between the lateral edges of the obliquely oriented chondral shafts is a thin ossified lamina. The palatine articulates with the head of the maxilla through an anterior cartilage, with the lateral ethmoid medially, with the mesopterygoid posteroventrally, and with the metapterygoid posteriorly. As with the maxilla, the palatines in *C. burmensis* and *C. bankanensis* are longer, broader bones with more prominent (longitudinal) dorsal ridges than in *C. chaca*. Gauba stated that the palatines abut the premaxillaries anteriorly. We find no evidence to support this. The articular cartilage of the palatine is quite large, but it seems to articulate only with the maxilla.

The mesopterygoid is a tiny flat bone which lies ventral to the palatine for most of its length. The element consists of two arms, the posterior being larger than the anterior. In Tilak's illustration, the bone is called the ectopterygoid, but it is much too large and it seems to include the posterior part of the palatine. The arms of the mesopterygoid are somewhat L-shaped in *C. bankanensis* but more wedge shaped in *C. burmensis* and *C. chaca*. The mesopterygoid is ligamentously attached posteriorly to the metapterygoid in *C. bankanensis* and to both the hyomandibula and the metapterygoid in *C. chaca*. There are muscular attachments to the neurocranium along its medial edge and it is tightly bound to the posterior edge of the palatine both dorsally and anteriorly. In *C. bankanensis* the mesopterygoid does not attach to the hyomandibula. Its posterolateral face is somewhat smaller than in *C. chaca* and the placement of the metapterygoid is somewhat different in relation to the hyomandibula. Otherwise, the attachment appears to be similar to *C. chaca*. Gauba indicated that it is attached by ligaments to the palatine but has no sutural connection with the metapterygoid. Tilak stated that it is ligamentously attached to both, which appears to be the case. Neither mentioned its attachment to the neurocranium or hyomandibula.

The metapterygoid is a chondral bone which extends anteriorly from, and is both synchondrally and suturally articulated with, the quadrate. Anteriorly, the bone is attached to the mesopterygoid by an elongate ligament. The element is a flattened cone, becoming constricted anteriorly and has a laminar sheet of bone along the posterior edge. In both *C. chaca* and *C. burmensis,* the lamina sutures broadly to the hyomandibula. In *C. bankanensis,* the lamina is reduced and contacts the hyomandibula only at the base of the articular cartilage. Tilak (1971) and Gauba (1970) indicated only a short sutural attachment to the hyomandibular in *C. chaca.*

The hyomandibula is the largest bone of the suspensorium. It is irregularly shaped with many ridges along the lateral face. Posteromedially, it bears an articular face bounded fore and aft by small processes. The head and anterior process articulate with the sphenotic, the former with a facet on its lateral edge and the latter just forward to this facet. In addition, a posterior process which lacks a cartilaginous surface moves against the pterotic. Though both Gauba and Tilak noted this posterior projection, neither mentioned its connection to the pterotic.

HYOID ARCH: Hyoid and gill arch material of *C. burmensis* could not be examined for this study. Thus, all of the following observations are limited to the two remaining species.

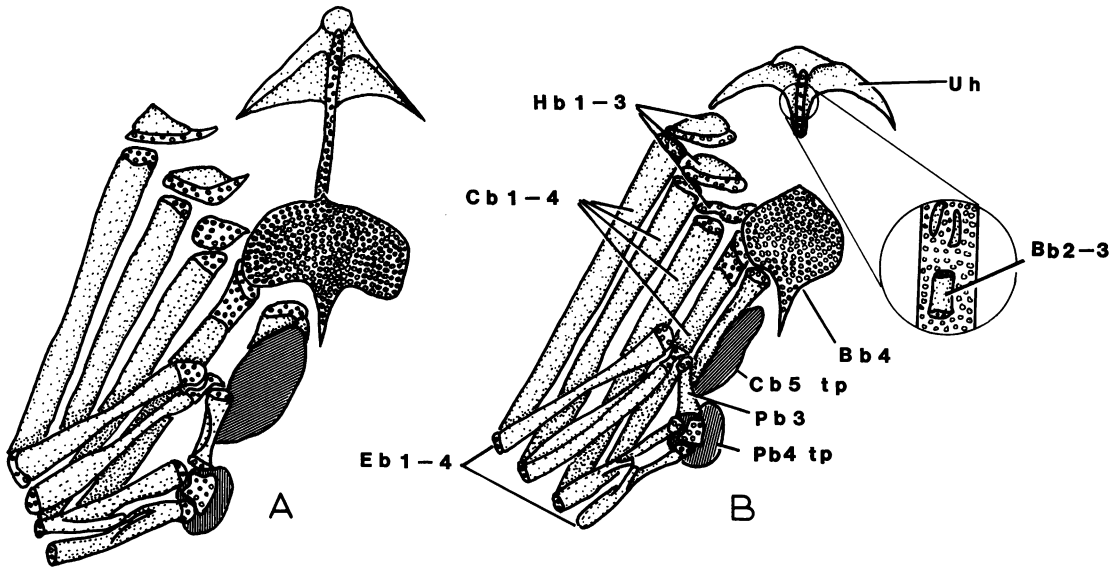The hypohyal is single, representing only

Fig. 7. Gill arches and urohyal of two species of *Chaca,* in dorsal view. Right side removed. (**A**) *C. chaca* (NL = 33 mm), (**B**) *C. bankanensis* (NL = 30 mm). Bb2–3 second and third basibranchials, Bb4 fourth basibranchial, Cb1–4 first through fourth ceratobranchials, Cb5 tp tooth plate of fifth ceratobranchial, Eb1–4 first through fourth epibranchials, Pb3 third pharyngobranchial, Pb4 tp tooth plate of fourth pharyngobranchial.

the ventral element. The dorsal hypohyal is absent. Anteriorly, the ventral hypohyals are bound together by a thick ligament, without a cartilage pad in between. The ventral hypohyal is sutured to the anterior ceratohyal along the medial surface. Tilak (1971) reported that the hypohyal bears a facet for articulation with its counterpart, and Gauba (1970) indicated the presence of a median cartilage between the hypohyals. These bones, however, do not appear to meet in either of the species and are joined together by ligaments and not cartilage.

The anterior ceratohyal is the largest element in the hyoid arch. As with the hypohyal, the anterior ceratohyal sutures to the posterior ceratohyal along the medial surface only.

Branchiostegal rays are borne on both the anterior and posterior ceratohyals. Those on the anterior ceratohyal are long and slender and 5 or 6 in number. On the posterior ceratohyal, two broad, flat, bladelike rays are found. The posterior three rays do not articulate directly with the ceratohyals but, instead, have a slender cartilaginous rod in between. Tilak correctly illustrated a gap between the rays and the hyoid arch, but did

not comment on its significance. He also reported a single branchiostegal on the posterior ceratohyal (his epihyal), but illustrated two. Our observations indicate that when the number of rays varies, it is on the anterior ossification only.

The median urohyal is a triangular ossification with a medial diamond-shaped elevated portion and two thin, pointed, obliquely directed, posterior arms. Behind the raised area, the body of this bone forms a thin recurved shelf. In *C. chaca,* the arms are longer and the posterior shelf is more extensive, when compared to the size of the elevated triangular portion, than is found in *C. bankanensis.*

BRANCHIAL ARCHES (fig. 7): The basibranchial series in *Chaca* is highly modified and has been incorrectly categorized. The first basibranchial ossification is absent, as in all catfishes. Basibranchials 2 and 3 are represented by a very thin cartilaginous rod which extends from the urohyal toward the enlarged, flattened cartilaginous plate which represents the fourth basibranchial. Gauba (1970) stated that the basibranchials were absent in the Chacidae and indicated a large cartilage plate

connecting all ceratobranchials and enveloping the hypobranchials. Tilak (1971) correctly illustrated the fourth basibranchial plate, but noted the absence of those more anterior. Interspecific variation exists both in the length of the cartilage rod and the presence of ossifications. In the one *C. chaca* available to us, a tiny, but well formed, bone is found in the position of the third basibranchial with two small nodules more anteriorly. The cartilaginous rod extends to the anterior margin of the fourth basibranchial. In three specimens of *C. bankanensis* of various sizes, there is no evidence of these ossifications. Further, the cartilaginous rod stopped far short of the fourth basibranchial in this species. The fourth basibranchial is a large, disklike cartilage, with which the ceratobranchials articulate. In the two species we examined, this element was of a characteristic shape. In *C. chaca,* it is wider than long, with a small posteriorly directed projection medially. In *C. bankanensis,* it is longer than broad with an elongate posterior projection and a shorter one anteriorly. The first two hypobranchials are ossified; the third remains unossified.

The first four ceratobranchials are slender, rodlike ossifications, noteworthy only for their lack of gill rakers. The fifth ceratobranchial bears a broad triangular tooth plate which narrows posteriorly and bears numerous small conical teeth. The size of the tooth plate varies between the species. In *C. chaca,* the plate extends broadly over the surface of ceratobranchial 5, overlapping both lateral and medial edges. In *C. bankanensis,* however, the plate does not extend to the lateral margins of the underlying rodlike element.

The first two epibranchials are bound together at their medial tips by a connective tissue sheath to the anterior end of the third pharyngobranchial. The cartilage tip of epibranchial 2 is concave, both anteriorly and posteriorly, to accommodate the broadly rounded cartilaginous tips of epibranchial 1 and pharyngobranchial 3. Epibranchial 1 is expanded medially and overlaps the second dorsally, as illustrated by Tilak.

The third and fourth epibranchials articulate medially with the cartilaginous pharyngobranchial 4. A posteromedially directed uncinate process, which is without a cartilaginous tip, originates about midway along the length of epibranchial 3 and contacts a similar, anteriorly directed process of epibranchial 4. An additional process on the third epibranchial, originating just basal to the uncinate process and directed anteriorly, is found in *C. bankanensis* only.

Pharyngobranchials 1 and 2 are absent in *Chaca.* The third pharyngobranchial is a conical bone, expanded posteriorly.

The fourth pharyngobranchial is a cuboid block of cartilage resting dorsal to the single ovoid tooth plate of the upper gill arches. Gauba identified only a single element, which he labeled pharyngobranchial and illustrated as a cylindrical element directly above the tooth plate. Tilak incorrectly identified pharyngobranchial 3 as the second, and he failed to distinguish the fourth from the epibranchial cartilages. His illustration of the third pharyngobranchial appears inverted, as the expanded end is directed anteriorly.

Caudal Skeleton

The caudal skeleton (fig. 8) of *Chaca* consists of only two separate elements. The ural complex is a single element which represents the parahypural, all hypurals, the uroneural, and the first preural and ural centra. The remaining element is a single autogenous epural. The caudal plate has a well-developed bony shelf, or hypurapophysis, following the ventral margin of the third hypural and extending nearly to the margin of the hypural plate. This form of hypurapophysis conforms to Lundberg and Baskin's (1969) type B, and appears to be the result of the fusion of the hypurapophysis of the parahypural and the secondary hypurapophyses of hypurals 1 and 2. Only Lundberg and Baskin (1969) commented on the caudal skeleton of *Chaca* previously. They reported that *Chaca* was without hypurapophyses and the epural was reduced or absent. Their observations were based, however, on a radiograph of a single specimen of *Chaca bankanensis,* a technique which we found to be exceedingly difficult to use for these characters.

There is little variation in the caudal skeleton among the species. The shape and extent of the hypurapophysis vary among individuals, but there is no obvious pattern attrib-

utable to interspecific variation. The epural, however, is distinctly different among species. In *C. chaca* and *C. burmensis* it is an elongate, flat splint between the second preural neural arch and the ural complex. In *C. bankanensis,* the element is much reduced or absent, appearing as a crescent-shaped nodule near the distal tip of the neural arch.

WEBERIAN APPARATUS

Five vertebrae are involved in the Weberian Apparatus. The first vertebra consists only of a full centrum and two pairs of posterolateral projections. Anteriorly, it contacts the basioccipital by means of the centrum alone. Dorsally, it is covered by the neural arch of the fused centrum. The posterolateral processes interdigitate with similar structures of the complex centrum to form the anterior end of the open aortic canal. These projections consist of two pairs of thin flanges which project posteriorly off the first vertebra. The dorsal pair, which varies from long and tapered to bluntly rounded, fits into a groove on the outside of the lateral plate of the complex centrum. The ventral prongs, also varying somewhat in shape but not position, form part of the medial wall of the aortic canal.

The aortic canal is a narrow trough, running the length of the first five vertebrae. Its depth decreases posteriorly as plates of bone from the complex centrum converge, meeting at the anterior border of the fifth vertebra. The canal then deepens somewhat to the posterior end of the fifth vertebra. The sides of the canal are formed by posterior and anterior projections off the first and fifth vertebrae, whose interdigitating pattern, with a series of thin plates that extend down from the body of the complex centrum, appears generally constant between individuals.

The second, third, and fourth vertebrae are fused into a single element commonly referred to as the complex centrum. Anteroventrally, a ventrolateral process of the complex centrum contacts that of the first vertebra (described above), while dorsally, neural arches extend forward as two prongs over the first centrum to contact the supraoccipital. The transverse process of the complex centrum is divided into anterior and posterior processes. The anterior portion is substan-
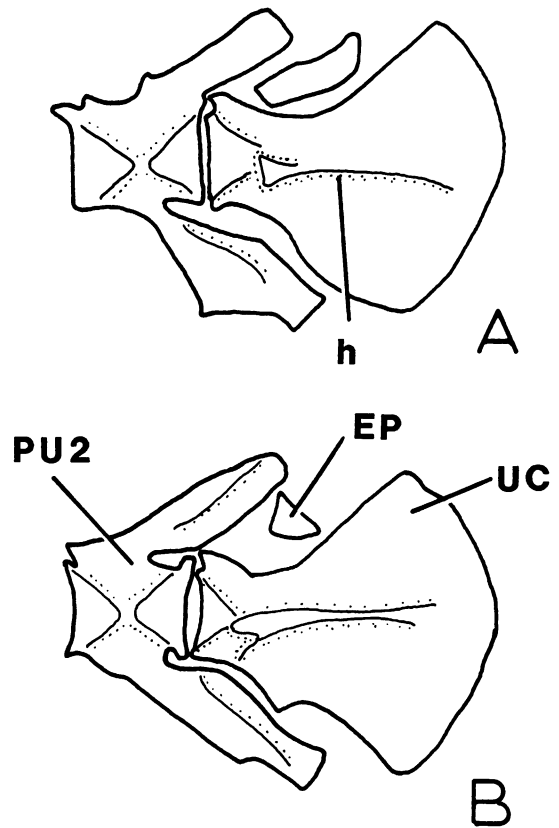

Fig. 8. Caudal skeleton of two species of *Chaca,* left side. (A) *C. bankanensis* (NL = 30 mm), (B) *C. chaca* (NL = 33 mm). UC ural complex, EP epural, h hypurapophysis, PU2 second preural centrum.

tially more massive than the posterior. Between the anterior and posterior parts, a nearly vertical lamina extends dorsally to the ventral base of the first dorsal spine-pterygiophore expansion dividing the neural arch into an anterior and posterior segment. Anterodorsally, the anterior transverse process is somewhat trough shaped and is closely associated, by a thick connective tissue sheath, to the descending arm of the posttemporal anteriorly and the main body of the posttemporal posterodorsally. Between the transverse process and the posttemporal slides the posterior prong of the posterior process of the cleithrum. Midventrally, the small, splintlike os suspensorium extends from the transverse process anteroventrally, to pass behind the posterior end of the tripus. At the
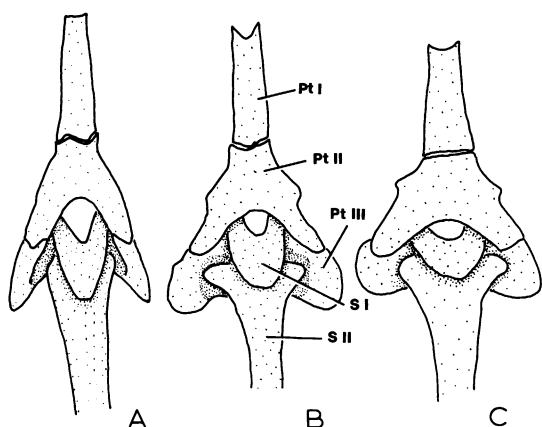
Fig. 9. Dorsal spines and pterygiophores of three species of *Chaca*, in dorsal view. (A) *C. bankanensis* (NL = 39 mm), (B) *C. burmensis* (NL = 41 mm), (C) *C. chaca* (NL = 33 mm). PtI first dorsal-fin pterygiophore, PtII second dorsal-fin pterygiophore, PtIII third dorsal-fin pterygiophore, SI first dorsal-fin spine, SII second dorsal-fin spine.

distal tip of the os suspensorium is found the expansion, called the radial nodule, which is surrounded by the transformator process of the tripus.

The fifth vertebra is a partially autogenous element. Ventral processes similar to the posterior extensions of the first vertebra extend anteriorly along the sides of the complex centrum, nearly meeting those of the first. These laminae contribute to the posterior end of the aortic canal. The fifth vertebra bears an expanded flat platelike transverse process off the neural arch, which tapers to a point posteriorly. Interdigitating sutures of the ventral and transverse processes firmly join the fifth vertebra to the complex centrum. The Weberian ossicles are as described by Tilak (1971). The claustrum is noteworthy as an unusually slender element that parallels the ascending process of the scaphium, just dorsal to the scaphium body.

Descriptions of the Weberian Apparatus of *Chaca chaca* (Tilak, 1971) and *C. bankanensis* (Chardon, 1968) are difficult to interpret. Chardon's illustrations are very accurate, but their labeling is contradictory and therefore confusing. In both the dorsal and ventral views (his figs. 145–147), the posterior part of the transverse process of the complex cen-

trum is incorrectly labeled as part of the fifth vertebra and the transverse process of the fifth is labeled as part of the sixth vertebra. In his figure 148, however, these elements are labeled correctly, though the posterior portion of the fourth transverse process is labeled as anterior. Also, he failed to illustrate the extensions of the first and fifth vertebrae onto the aortic canal.

Tilak reported cartilaginous neural arch material of the first vertebra but examination of a double-stained specimen of *Chaca bankanensis* showed no evidence of such. He also referred to the transverse processes as parapophyses and appeared to differentiate between the fourth neural spine and that of the second and third or complex centrum. He failed, however, to differentiate them clearly either in the text or his drawings. He apparently used the vertical wall of the transverse process of the complex centrum as a point of division between the two vertebrae. The os suspensorium is referred to as the dorsal lamina. He made no mention of the cleithrum's relationship with the transverse processes of the fused vertebrae and stated only that the descending limb of the posttemporal was in contact with the anterior part of the transverse process when the posterior prong of the cleithrum slides between them.

DORSAL FIN AND SUPPORTING ELEMENTS

The dorsal fin skeleton of *Chaca* is composed of two spines and four rays and their pterygiophores. Directly behind the supraoccipital, running posteriorly sits the first pterygiophore (fig. 9), a flat plate of bone, resting on the neural arch material of the complex centrum extending from the supraoccipital to second pterygiophore. This pterygiophore is Y-shaped dorsally with the top of the Y directed posteriorly. It is a relatively deep bone which sutures ventrally with the neural arch material of the complex centrum. In the notch formed by the arms of this bone sits a bifid, reduced first spine. The two elements of the spine are fused dorsally and split ventrally, running down on either side of a posterior, raised, rounded knob of the second pterygiophore. At the posterior tips of the second pterygiophore are the paired dorsal aspects

of the third pterygiophore. They form extensions of the arms of the Y of the second pterygiophore. They slant slightly inward posteriorly and drop down to suture with the neural arch of the complex centrum. Medially, the bone forms a knob on which sits the second, larger dorsal spine. The posterior portions of the third pterygiophores vary in shape between *Chaca bankanensis* and the other two forms. In *C. bankanensis,* the pterygiophores taper narrowly to a point posterodorsally and slope sharply down to meet the neural arch material of the fused vertebra. In *C. chaca* and *C. burmensis,* the posterior projections flare into rounded flat plates that slope more gradually downward medially. The dorsal aspects of the pterygiophores, like the skulls of *C. chaca* and *C. burmensis,* are more sculptured than in *C. bankanensis.*

Chardon (1968) failed to indicate the sutures between the first and second pterygiophores. He referred to the entire structure as the *bouclier* or shield. Tilak (1971) stated that the neural spine of the fourth vertebra was connected via ligaments to a nuchal plate and that there is no pterygiophore associated with the fourth vertebra. He also reported that the pterygiophore of the dorsal spine slipped between the neural arches of the complex centrum and the fifth vertebra and the lateral nuchal plates. He apparently failed to recognize two dorsal spines or that the nuchal plates were pterygiophores and were sutured to the neural arch material of the complex centrum. He reported that removal of the nuchal plates and dorsal spine would break away parts of the Weberian Apparatus. This is not the case as the two spines and their pterygiophores can be removed from the Weberian apparatus and separated from each other.

THE PECTORAL GIRDLE

Tilak's (1971) account of the pectoral girdle accurately describes the elements involved, with one exception. He noted the attachment between the pectoral girdle and rays as by a single radial. Although in both dry skeletal preparations and alizarin stained, glycerine specimens the cartilaginous first radial cannot be seen, it is present as a slender cartilaginous rod. The first branched ray is supported

by the cartilaginous radial while the remaining three or four rays articulate with the distally expanded second radial. As Tilak noted, two basal radial elements are widespread in catfishes and probably the primitive condition for the order. Often, however, the first does not ossify and is found as either a rod or ball of cartilage.

The pectoral spine of *Chaca* is unusual in possessing a shelf along the length of its posterior surface. Typically, the posterior, and sometimes the anterior, surface is armed with serrations. When serrations are absent, the spine is usually in the form of an elongate cone. In *Chaca,* the anterior surface of the spine has a single series of serrae, the density of which is useful in distinguishing *C. burmensis* from the remaining species. Posteriorly, a broad shelf, which is thinner than the core of the spine, replaces the serrations. Tilak noted that the posterior margin of this shelf is itself finely serrated. This is true for both *C. chaca* and *C. burmensis,* but the margin of *C. bankanensis* is smooth.

Roberts (1982) used pectoral fin-ray number as a distinguishing feature for the two species of *Chaca* which he recognized. *C. chaca* has five rays and *C. bankanensis* has four; *C. burmensis* may have either four or five rays.

THE PELVIC GIRDLE

The basipterygium of *Chaca* is a flat, plate-like bone, as illustrated by Tilak (1971). We have not observed any variation in either the structure of the girdle or the fin rays. All rays in this fin are branched, a condition unique in catfishes and hitherto unnoticed.

PHYLOGENY OF THE CHACIDAE

The family Chacidae is a clearly defined monophyletic group within the Siluriformes, defined by a host of characters. Among these are several characters which appear to be unique within catfishes, including: (1) anterior ray of the pelvic fin branched; (2) palatine with a lateral flexure posteriorly, behind the articular facet; (3) two obliquely oriented arms of the palatine joined together along their lateral surfaces with a lamina of bone ventrally; (4) orbitosphenoid a paired element, not meeting along the ventral midline; (5) mes-

ethmoid with two large, anterolaterally expanded cornua; (6) first three basibranchial elements greatly reduced in size; and (7) premaxilla with posteromedially directed process.

In addition, there are a number of characters found in members of the Chacidae which are clearly derived within catfishes. While these characters are not unique to the Chacidae, they are included here as presumptive synapomorphies of the family, because other taxa possessing these characters appear to be more closely related to other catfishes based on other character information. We, therefore, postulate that these characters have been independently acquired in two or more groups of catfishes, until a preponderance of the character information indicates otherwise. Thus, additional characters which define the Chacidae are: (8) Absence of an independent vomer [the vomer is also absent in the pimelodid catfish genera *Microglanis* and *Pseudopimelodus* (J. G. Lundberg and A. Bornbusch, personal commun.) and the aspredinid genus *Agmus*, personal obs.]. (9) Procurrent caudal rays expanded, forming a continuation of the caudal fin (this is seen in several catfish groups and has been used as evidence to unite the Plotosidae with the Chacidae). (10) Ural complex of caudal skeleton without separate elements, except for a single epural. A similar condition exists in the Plotosidae and at least one specimen of Aspredinidae (Lundberg and Baskin, 1969). In addition, the illustration which they present of the amphiliid *Phractura scaphirhynchura* has a fusion pattern similar to that of *Chaca,* except that the fusion between the upper and lower hypurals is incomplete. We consider this difference insignificant when compared to the joined upper hypural elements to the centrum. The single epural characteristic of catfishes remains an independent element, although reduced in one species (see below). Plotosids have either a reduced epural or have none. The joined hypurapophysis–secondary hypurapophysis in *Chaca* appears to be derived within catfishes. Among those catfishes possessing a highly fused caudal skeleton, only aspredinids share the type B condition with *Chaca.* (11) Articular facet receives the hyomandibula located only on the sphenotic

and oriented for a nearly horizontal joint between these two elements. Primitively in catfishes, the articular facet is shared among the sphenotic, pterotic, and orbitosphenoid. In those catfishes in which the synchondral contact is limited to the sphenotic, the facet is oriented in a ventral or oblique direction, not approaching the horizontal condition as in *Chaca.* (12) Gill rakers absent. (13) Fourth basibranchial element a greatly enlarged, cartilaginous pad. In most catfishes, the fourth basibranchial is a rodlike element composed of cartilage. In a number of catfish groups, however, it is expanded into a platelike element, usually with a rodlike structure beneath.

Within the Chacidae, several characters may be used to indicate relationships among the species. Although we present here only a few characters, they all indicate that *C. chaca* and *C. burmensis* are more closely related to each other than either is to *C. bankanensis.* For each character, the derived condition is followed by the species which share the condition, and the presumed primitive condition for the character.

(A) Fleshy papillae along lateral surface of body, above the lateral line, usually found in pairs. This condition is shared by *Chaca burmensis* and *C. chaca.* In *C. bankanensis* the surface of the body is smooth, or with small rounded knobs.

(B) Epural a small round nodule in *C. bankanensis.* In the other species, the epural is an elongate, slighty curved bone which extends outward from near the base of the second preural neural arch.

(C) Procurrent caudal rays branched in *C. chaca* and *C. burmensis.* In *C. bankanensis* and other catfishes, the procurrent caudal rays are typically unbranched.

(D) Laminar extensions of the metapterygoid reduced, resulting in a limited sutural contact between the metapterygoid and the hyomandibula in *C. bankanensis.* In the remaining species, a broad sutural joint exists between the two bones, a condition that is widespread, and presumably primitive in catfishes.

Not included in this list are a number of other characters. These fall into one of two categories which we choose not to include for the following reasons. The first group in-

cludes characters for which we cannot satisfactorily justify the derived state. For example, the posterolateral margins of the dorsal-fin spine pterygiophore can be readily used to divide the species into two groups: those with rounded margins (*C. burmensis* and *C. chaca*) and those with acutely pointed margins (*C. bankanensis*). As we have no sound basis for determining which of these is derived within *Chaca,* we prefer not to speculate, even though the division is congruent with our hypothesis of relationships. The second category of unused characters is that for which the observed variation does not readily lend itself to groupings. The maxilla of the three species is of a characteristic length, at least in adults (fig. 5). Elongate maxillae are quite rare in catfishes and, presumably, derived within *Chaca.* Thus, the elongate maxilla of *C. bankanensis* is considered derived, compared with that of *C. chaca.* Whether to consider the more intermediate-length maxilla of *C. burmensis* a shared derived condition with *C. bankanensis* or within the range of variation of the primitive condition for the group is more problematical. In the absence of a clearer understanding of the character, we feel it best not to use this information.

Finally, our efforts to determine the affinities of the family Chacidae within catfishes have not been successful. We noted above that *Chaca* shares a number of derived characters with members of other catfish families. However, no consistent, unambiguous pattern is apparent to us. The shared derived characters suggest possible relationships between the Chacidae and such diverse catfish families as the Aspredinidae, Plotosidae, and Pimelodidae. Selective use of characters and the use of shared primitive characters have provided the basis for diverse opinions of the relationships of the Chacidae that are currently found in the literature. We feel that it is unwise to choose among the apparent shared characters for those that truly indicate relationships. Instead, we prefer to wait until a thorough study of catfish family relationships, in which conflicting character information is subjected to the criterion of parsimony, determines the best placement of the Chacidae.

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