

**A new species of *Nannocharax* (Characiformes: Distichodontidae)
from Cameroon, with the description of contact organs and breeding
tubercles in the genus**

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Abstract.—*Nannocharax reidi*, new species, is described from several localities in the upper Cross River basin in Cameroon. The species possesses the synapomorphies of the clade comprising *Nannocharax* and *Hemigrammocharax*. It is assigned to *Nannocharax* on the basis of its possession of a completely-pored lateral line, a feature distinguishing that questionably monophyletic genus within the clade composed of these two genera. *Nannocharax reidi* is distinguished from its congeners on the basis of a combination of meristic and morphometric features and details of pigmentation on the body. Comparative studies revealed the presence of hook-shaped contact organs on the pectoral fins of some species of *Nannocharax* and epidermal breeding tubercles on the head, body, and fins of at least one species of the genus. These observations represent the first reports of contact organs and breeding tubercles in African members of the order Characiformes. Some species of *Nannocharax* were found also to possess variably-developed fields of hook-shaped contact organs on the exposed surfaces of scales of the midlateral portion of the body posterior of the pectoral girdle. This latter feature has not been previously reported among fishes.

Species of the African distichodontid genus *Nannocharax* are relatively small-sized fishes inhabiting the Nile River and many sub-Saharan rivers, with the greatest species-level diversity of the genus occurring in West Africa and the Congo River basin. Species of *Nannocharax* share a number of distinctive modifications relative to phylogenetically-proximate taxa including transversely-flattened ventral surfaces of the head and body, a down-turned mouth, and, in many species, expanded pelvic and pectoral fins; these features apparently correlate with their habits of resting on, and feeding off of, the substrate or vegetation (e.g., *Nannocharax fasciatus*, see Géry 1977:89). The most recent comprehensive

treatment of *Nannocharax* was that of Boulenger (1909:279) who discussed seven nominal species that recent authors have assigned to the genus. Subsequent decades saw the progressive descriptions of additional species of *Nannocharax*, resulting in 24 species being recognized in the compendium of the genus by Daget & Gosse (1984:200). Two treatments of the West African species of *Nannocharax* have been published (Daget 1961, Gosse & Coenen 1990), and recent decades have seen the description of several new species of the genus from that region (Vari & Géry 1981, Coenen & Teugels 1989, Van den Bergh et al. 1995). Numerous uncertainties, nonetheless, remain concerning the species-level

diversity within *Nannocharax*. Perhaps the major question is whether the geographically widespread *N. fasciatus*, whose distributional range in West Africa reportedly extends from Guinea to Gabon (Daget & Gosse 1984:201), is a single widely-distributed species or a complex of similar species. Reid (1989:24, 56), followed by Teugels et al. (1992:43), noted that population samples of an *N. fasciatus*-like form from the upper Cross River system in Cameroon differed from the more-typical *N. fasciatus* populations from that region, but those authors deferred from pursuing the question of the identity of these samples.

Studies of the species of *Nannocharax* in the lower Guinea region encompassing Cameroon, Rio Muni, Gabon, and the coastal portions of the Republic of Congo, Brazzaville demonstrate that some populations of an *N. fasciatus*-like form from the upper Cross River represent an undescribed species that we describe herein. We also describe unusual modifications of the scales, fins, and epidermis in some species of *Nannocharax* that were discovered during our comparative studies. These noteworthy modifications are either elaborations of some body scales of a form unique to the species of *Nannocharax* within the Characiformes (and perhaps fishes), or are elaborations of the fin rays and epidermis that were previously thought to be restricted to New World members within that order.

Materials and Methods

Measurements are given as a percentage of standard length (SL) except for subunits of the head that are presented as percentages of head length. Lateral-line scale counts include all pored scales along that series, including scales located posterior to the hypural joint. In fin-ray counts, lowercase Roman numerals indicate unbranched rays, and Arabic numerals indicate branched rays. The two posteriormost anal-fin rays, which are joined at their bases, were counted as one element. Morphomet-

ric and meristic data were taken following the procedures outlined in Fink & Weitzman (1974). Counts of gill-rakers, teeth, cteni, and branchiostegal rays were taken from two specimens that were cleared and counterstained following the method of Taylor & Van Dyke (1985). Vertebral counts were acquired via radiographs and include the four vertebrae of the Weberian apparatus and the terminal centrum. Institution abbreviations are: AMNH, American Museum of Natural History, New York; CU, Cornell University, Ithaca, New York; MRAC, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; and USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Nannocharax reidi, new species

Fig. 1

Nannocharax sp. 1, Reid, 1989:24, 56 [Cameroon, upper Cross River system].

Nannocharax sp., Teugels et al., 1992:43 [upper Cross River system].

Holotype.—USNM 304046, 62.7 mm SL; Cameroon, Cross River system, collecting points on southern Munaya River draining northern Korup, on Basep River at junction with Munaya River (5°49'30"N, 9°03'30"E); collected by Gordon McG. Reid, 22 February 1988.

Paratypes.—20 specimens, 34.3–59.0 mm SL. USNM 375193, 16 specimens (2 cleared and counterstained for cartilage and bone), 34.3–59.0 mm SL; AMNH 233622, 2 specimens, 37.3–41.6 mm SL; MRAC A3-47-P-1-2, 2 specimens, 37.1–43.1 mm SL; collected with holotype.

Non-type specimens examined.—19 specimens, 33.3–44.7 mm SL. USNM 375195, 3 specimens, 34.5–38.8 mm SL; Cameroon, Many, Cross River system, collecting points on main Cross River, downstream of Mamfé, Mam River, junction with Cross (3°50'30"N, 9°14'50"E). USNM 375196, 1 specimen, 41.7 mm SL; Cameroon, Cross River system, collecting points on main Cross River below Mamfé

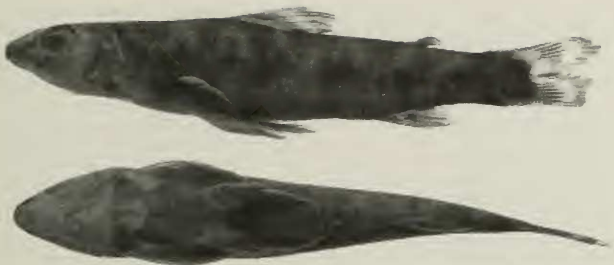


Fig. 1. *Nannocharax reidi*, holotype, USNM 304046, 62.7 mm SL; Cameroon, Cross River system, collecting points on southern Munaya River draining northern Korup, on Basep River at junction with Munaya River (05°49'30"N, 09°03'30"E); lateral and ventral views.

(5°51'25"N, 9°11'50"E). USNM 375197, 2 specimens, 36.4–44.5 mm SL; Cameroon, Cross River system, collecting points on southern Munaya River draining northern Korup, southern Munaya River, junction with Cross River (5°53'N, 9°00'E). USNM 375194, 6 specimens, 36.3–36.7 mm SL; Cameroon, Cross River system, collecting points on southern Munaya River draining northern Korup, on Basep River at junction with Munaya River (5°49'30"N, 9°03'30"E); collected with holotype. MRAC 88-053-P-0163-0168, 6 specimens, 33.3–44.7 mm SL; Cameroon, mainstream of Cross River, 5–15 km downstream of Mamfé (approximately 5°46'N, 9°17'E). MRAC 88-053-P-0170, 1 specimen, 42.4 mm SL; Cameroon, mainstream of Cross River, approximately 5 km downstream of Mamfé (approximately 5°46'N, 9°17'E).

Diagnosis.—*Nannocharax reidi* is distinguished from all congeners by the combination of: the lack of a large, dark, rounded spot extending from the posterior portion of the caudal peduncle to the basal portions of the middle caudal-fin rays; the lack of a distinct, dark, midlateral stripe extending from the snout at least to the rear of the caudal peduncle; the absence of a series of very narrow, vertical, dark bars positioned along

the lateral surface of the body; the location of the origin of the dorsal fin posterior to the vertical through the insertion of the pelvic fin; the possession of 47 to 49 scales along the lateral line, 5, rarely 6, scales dorsal of the lateral line to the origin of the dorsal fin, and 4 scales ventral of the lateral line to the origin of the anal fin; and the overall body form.

Descript on.—Morphometric values for holotype and paratypes are presented in Table 1. Body elongate, relatively wide transversely in region from rear of head to vertical through posterior terminus of base of dorsal fin and increasingly transversely-compressed posterior to latter region. Transverse widening of anterior portion of body proportionally more pronounced in larger examined individuals. Ventral region of head and body anterior to insertion of pelvic fin distinctly flattened; degree of flattening more pronounced in larger examined specimens. Dorsal profile of head gently convex from tip of snout to vertical through posterior margin of orbit, straight or very slightly convex from that point to posterior limit of supraoccipital spine. Predorsal profile of body slightly convex in all examined specimens. Dorsal profile of body slightly posteroventrally-inclined along base of dor-

Table 1.—Morphometrics and meristics of holotype and paratypes of *Nannocharax reidi*, new species, n = 21. Standard length is expressed in mm; measurements 1 to 14 are percentages of standard length; 15 to 18 are percentages of head length; mean includes holotype.

	Holotype	Paratypes	Mean
Morphometrics			
Standard Length	62.7	34.3–59.0	
1. Snout to anal-fin origin	75.6	72.1–76.3	74.3
2. Snout to pelvic-fin insertion	40.7	37.2–41.4	39.3
3. Snout to pectoral-fin insertion	23.4	23.2–26.3	24.8
4. Snout to dorsal-fin origin	43.7	42.1–45.9	44.3
5. Dorsal-fin origin to hypural joint	54.7	53.7–59.6	56.3
6. Dorsal-fin origin to anal-fin origin	35.4	32.3–36.7	34.3
7. Dorsal-fin origin to pelvic-fin insertion	20.2	17.9–20.0	18.8
8. Dorsal-fin origin to pectoral-fin insertion	26.2	23.9–27.1	25.7
9. Caudal-peduncle depth	10.2	9.8–10.4	10.1
10. Pectoral-fin length	25.2	23.9–27.2	25.6
11. Pelvic-fin length	25.4	22.4–25.6	23.8
12. Dorsal-fin length	21.9	21.5–25.4	23.7
13. Anal-fin length	17.1	15.9–17.8	16.8
14. Head length	25.8	24.5–27.5	25.8
15. Postorbital head length	37.8	37.8–44.7	42.1
16. Snout length	34.6	31.5–35.3	33.3
17. Bony orbital diameter	27.2	27.1–31.9	29.9
18. Interorbital width	21.0	16.3–20.9	19.2
Meristics			
Lateral-line scales	47	47–49	47.8
Scale rows between dorsal-fin origin and lateral line	5	5–6	5.1
Scale rows between anal-fin origin and lateral line	4	4	4.0
Predorsal median scales	10	10–12	11.2
Branched dorsal-fin rays	9	8–10	9.4
Branched anal-fin rays	6	6–8	7.0
Branched pelvic-fin rays	7	6–8	7.1
Pectoral-fin rays	14	13–15	14.1

sal fin and slightly convex from posterior terminus of base of fin to caudal peduncle. Ventral profile of head straight and slightly posteroventrally-inclined. Ventral profile of body nearly straight along prepelvic region and slightly convex from insertion of pelvic fin to caudal peduncle.

Mouth slightly subterminal. Lower jaw comparatively wide relative to condition in many congeneric species, with width of posterior portion of jaw equal to height of orbit in larger specimens. Jaw teeth elongate, bicuspid, and slightly expanded distally (see Daget 1961, fig. 4 for shape of teeth in genus), with single series of functional teeth in each jaw. Dentary with 5 or 6 teeth. Dentary teeth gradually decreasing

in size posteriorly with terminal tooth in series approximately one-half as long as tooth proximate to dentary symphysis. Replacement teeth on dentary arranged in single series within enlarged dentary replacement tooth trench. Dentary lacking segment of laterosensory canal system and movably attached to lateral surface of anterodorsal surface of angulo-articular. Contralateral dentaries immovably attached syndesmotically along medial surfaces. Premaxilla with 5 or 6 teeth of same morphology as dentary teeth. Premaxillary teeth gradually decreasing in size posteriorly with terminal tooth in series approximately one-half as long as tooth proximate to premaxillary symphysis. Premaxillary replacement teeth arranged in

single row embedded in fleshy covering of inner surface of premaxillae. Contralateral premaxillae immovably attached syndesmotically along medial surfaces; but with premaxillary complex vertically mobile on mesethmoid. Maxilla edentulous, with posterior portion of bone flat, plate-like, and extending nearly entirely under first infra-orbital bone when mouth closed. Pupil ovoid, with pronounced emargination of anterior portion of iris (see Vari & Géry 1981, fig. 2, for illustration of this condition in *Nannocharax maculicauda*). Snout and dorsal portions of upper lip and head covered with small papillae-like processes in holotype and to lesser extent in larger paratypes. Such papillae may represent intermediate developmental stages of well-developed breeding tubercles present in those regions and elsewhere on head, body, and fins in at least one congeneric species (see comments on breeding tubercles under "Contact organs and breeding tubercles in species of *Nannocharax*" below).

First gill arch with 13 or 14 gill rakers in 2 cleared and stained specimens. Branchiostegal rays 4.

Scales ctenoid (sensu Johnson 1984, Roberts 1993), with cteni formed by series of independent ossifications positioned along posterior margin of scale. Scales of lateral surface of body with 23 to 28 cteni along scale margin. Lateral-line scale series completely pored, with last scale in series horizontally elongate. Body scales extending onto base of middle rays of caudal fin in triangular pattern. Many smaller individuals with scaleless region on median portion of prepelvic region immediately posterior of ventral margin of pectoral girdle.

Largest examined specimens with lateral surface of scales in region posterior and posterodorsal to insertion of pectoral fin bearing some scattered, elongate, contact organs (sensu Collette 1977). Contact organs of scales most concentrated in region proximate to posterior margin of pectoral girdle and best developed in holotype, the largest examined specimen. Contact organs

elongate, laterally-directed, and with anteriorly-directed distal tips. Field of contact organs neither as dense as, nor as extensive as, pattern of hook-shaped processes present on that region of body in at least one congeneric species (see "Contact organs and breeding tubercles in *Nannocharax*" below).

Dorsal-rays ii,8 to 10. Distal margin of dorsal fin nearly straight. Anal-fin rays ii,6 to 8 or rarely iii,7. Distal margin of anal fin concave. Individual lepidotrichia of unbranched anal-fin rays anteroposteriorly expanded with overall form of distal portion of fin rays somewhat club-shaped; such rays proportionally more expanded in larger individuals. Anterior and lateral surfaces of first unbranched dorsal-fin ray and distal portions of second unbranched ray enveloped by overlying, thick, fleshy layer in many, but not all, specimens; fleshy covering more developed in holotype and larger paratypes. Caudal fin distinctly forked.

Pectoral and pelvic fins proportionally longer than in many congeneric species. Pectoral-fin rays ii,13 to 15. Dorsal surface of basal portions of second unbranched, and first through fifth branched rays of pectoral fin with basally-directed, hook-shaped, bony contact organs on basal one-half to two-thirds of rays in holotype, the largest examined specimen. Larger male paratypes with such contact organs developed to lesser degree, but still obvious. Hook-shaped processes on pectoral-fin rays apparently limited to mature males. Unbranched pectoral-fin rays and distal portions of first branched pectoral-fin ray with individual lepidotrichia widened, more so on distal portions of fin rays; expanded portion of fin rays consequently somewhat club-shaped. First unbranched pectoral-fin ray distinctly shorter than second ray, with second unbranched pectoral-fin ray somewhat shorter than first branched ray; latter ray longest of fin. Ventral and lateral surface of first unbranched pectoral-fin ray, and distal portions of second unbranched, and first branched, pectoral-fin rays with thick,

fleshy covering. Fleshy layer on fin rays thicker and extending farther basally along rays in larger individuals, and particularly well-developed in holotype. Tip of pectoral fin extending distinctly beyond vertical through insertion of pelvic fin in specimens of all sizes.

Pelvic-fin rays ii,6 to 8. Pelvic fin with unbranched rays and distal portion of first branched ray with individual lepidotrichia thickened, more so on distal portions of fin rays that consequently have a somewhat club-shaped form. Ventral and lateral surface of first unbranched, and distal portions of second unbranched and first branched pelvic-fin rays with thick, fleshy covering; fleshy layer also extending over dorsal surface of distal portions of ray. Fleshy layer on pelvic-fin rays thicker and extending further basally along rays in larger examined individuals. First unbranched pelvic-fin ray distinctly shorter than second unbranched ray; second unbranched ray somewhat shorter than first branched ray with medial branch of latter ray longest in fin. Tip of longest pelvic-fin ray reaching vent in smaller individuals, but falling slightly short of opening in larger specimens.

Vertebrae 36 to 38 [37 in holotype].

Coloration in alcohol.—Ground coloration light dusky-brown, with scattered dark chromatophores in holotype and paratypes; tan with fewer dark chromatophores in some more lightly-pigmented, non-type specimens. Lateral and dorsal surfaces of head with irregular field of small, dark chromatophores; chromatophore field more concentrated on upper lip, snout, and dorsal surface of head. Some larger individuals with concentration of dark chromatophores located posterior to orbit and on dorsal two-thirds of operculum. Ventral surface of head ranging from unpigmented to having scattered, small, dark chromatophores.

Body with pattern of relatively wide, irregular bars on dorsal and sometimes ventral surfaces; bars often narrowing towards midlateral region with dorsal and ventral bars variably in contact in that region. Re-

gions of contact between bars sometimes appearing as irregular, darker, midlateral patches of dark pigmentation. Smaller, more lightly-pigmented, non-type specimens with deep-lying, diffuse region of dusky pigmentation positioned along midlateral region, particularly on posterior two-thirds of body. Ventral surface of body ranging from pale with few, scattered, small, dark chromatophores in some smaller non-type specimens to dusky in holotype and paratypes. Some darker specimens with variably-shaped, unpigmented, typically scaleless area on anteroventral portion of body immediately posterior of margin of pectoral girdle.

Dorsal fin with transverse band of dark pigmentation located slightly dorsal of bases of fin rays and second, more distally-positioned, wider band of dark pigmentation extending across entire fin. Wider band of pigmentation distinctly separated from distal margin of fin anteriorly, but angling toward and reaching margin of fin along distal portions of first or second branched dorsal-fin rays. Anal fin with variably-developed patch of dark pigmentation on basal portions of anterior rays and with dark band extending from more distal portions of anterior rays across fin to its posterior margin. Caudal fin with patch of dark pigmentation situated basally and with variably-shaped and -positioned patches of dark pigmentation located on both lobes of fin. Pectoral-fin rays overlain dorsally by small, dark chromatophores; dark pigmentation most intense on lateral most fin rays, more so distally. Pelvic fin with pattern of dark chromatophores on distal portion of unbranched rays and more central sections of branched rays. Individual patches of dark pigmentation forming broad, interrupted, dark band across pelvic fin. Adipose fin dark distally in smaller, more lightly-pigmented individuals, dark throughout in larger specimens.

Coloration in life.—Photos of specimens taken soon after capture show that the species has the same pattern of dark pigmen-

tation as described above, but with the hyaline regions of head, body, and fins of preserved specimens having a rosy tint in life.

Remarks.—Vari (1979:332) noted that the monophyly of *Nannocharax* had yet to be demonstrated. That author further commented that although *Nannocharax* and *Hemigrammocharax* share a series of hypothesized synapomorphies (Vari 1979:331), the single feature that has been utilized to distinguish *Nannocharax* from *Hemigrammocharax* (the possession of a completely- versus incompletely-pored lateral line, respectively) may not serve to delimit monophyletic assemblages in light of the independent reduction in the degree of development of the lateral line in various groups of characiforms. The possession of various derived characters in a subset of the species of *Nannocharax* and *Hemigrammocharax* to the exclusion of other members of each genus (Vari & Géry 1981:1082), furthermore, apparently delimits a monophyletic lineage. That hypothesis suggests that both *Nannocharax* and *Hemigrammocharax* as now defined are non-monophyletic.

More recently, Coenen & Teugels (1989:317) documented that population samples of some nominal species within the *Nannocharax-Hemigrammocharax* clade demonstrated a continuum between distinctly-shortened and fully-developed lateral lines. Such continuity in the degree of development of the poring of the lateral-line scale series bridges the gap that purportedly distinguished *Nannocharax* from *Hemigrammocharax*, thereby casting further doubt on the utility of a complete versus incomplete lateral line as a generic delimiter for these taxa. Above and beyond the uncertainty about the naturalness of *Nannocharax* and *Hemigrammocharax*, we are also encumbered by the limitation that the phylogenetic relationships within the clade formed by these two genera are yet to be critically examined within the context of a comprehensive analysis. In the absence of such a phylogenetic study, we follow current taxo-

nomic practice and assign the new species to *Nannocharax* on the basis of its completely-pored lateral line, in conjunction with the possession of the synapomorphies for the clade formed by *Nannocharax* and *Hemigrammocharax* (see Vari 1979:331, synapomorphies 96 to 107).

Distribution.—All examined population samples of *Nannocharax reidi* were collected in the upper portions of the Cross River basin in Cameroon.

Etymology.—The specific name, *reidi*, is in honor of the collector of the specimens that served as the basis of the description of the species, Dr. Gordon McGregor Reid, of the North of England Zoological Society, who first reported that these samples might represent an undescribed form and who has contributed broadly to our knowledge and conservation of African freshwater fishes.

Ecology.—*Nannocharax reidi* was typically captured in the swiftly-flowing main-stream portions of rivers, usually in association with submerged logs and branches. In all such localities the water is clear and brown-tinged. The new species was collected together with *N. fasciatus* at the type locality and at three other localities in the upper Cross River. Those two species of *Nannocharax* were sympatric with *N. latifasciatus* at two of those sites.

Contact Organs and Breeding Tubercles in Species of *Nannocharax*

Examination of other species of *Nannocharax* revealed the presence of hook-shaped contact organs on the pectoral-fin rays and on the scales in the region of the body proximate to the insertion of the pectoral fin, along with the occurrence of breeding tubercles on the head, body, and fins of at least some species. The hook-shaped contact organs on the fin rays and breeding tubercles of these species of *Nannocharax* had been previously reported within the Characiformes only in some Neotropical members of the order. The hook-shaped contact organs on some scales

of the body in the genus are unknown in any other member of the Characiformes.

Presence of hooks on pectoral-fin rays.—In their recent analysis of the phylogenetic relationships of various groups of Neotropical characids, Malabarba & Weitzman (2003:73) enumerated a series of generic and suprageneric taxa within the Characiformes that bear hook-shaped processes on various combinations of the paired and unpaired fins, including the pectoral fin. These hook-shaped processes were termed contact organs by some authors (e.g., Wiley & Collette 1970, Collette 1977), who discussed the distribution and possible functions of these structures. In their commentary on contact organs on the fins of characiforms, Malabarba & Weitzman (2003) noted that such bony processes on individual segments of lepidotrichia were known to be present in diverse Neotropical components of the order, but were unknown in Old World characiforms, including the family Distichodontidae. Although Malabarba & Weitzman (2003) were correct that contact organs on the fins had not been previously reported for Old World characiforms, we found that larger, apparently male, individuals of *Nannocharax reidi* have a series of hook-shaped, distally slightly anteriorly-bent bony processes arranged in a single series along the dorsal surface of the basal one-half to two-thirds of the medial rays of the pectoral fin. As is the case with many Neotropical characids, each lepidotrichium of the pectoral-fin rays with a hook-shaped contact organ bears a single such process.

The extent of the field of hook-shaped contact organs on the pectoral-fin rays differs both among specimens of *N. reidi* and between species of *Nannocharax*. In *N. reidi*, the hook-shaped processes on the dorsal surface of the pectoral-fin rays are more highly-developed in larger individuals, but even at their maximum observed degree of development these structures are limited to the basal one-half to two-thirds of the second unbranched and first through fifth branched pectoral-fin rays. Mature males of

N. rubrolabiatus (MRAC 95-022-P-001-007), in contrast, have hook-shaped contact organs on a greater number of fin rays (second unbranched through eighth branched) and have these processes nearly to the distal tips of the fin rays. The presence of these hook-shaped contact organs on the pectoral fin in specimens of *N. rubrolabiatus* is correlated with other apparently breeding-associated modifications of the scales and fins (the presence of hook-shaped contact organs on the lateral surface of the scales in the region medial to the pectoral fin and the possession of epidermal breeding tubercles distributed over the head, body, and fins; see discussion of next two characters). This correlation of apparently sexually-dimorphic features in conjunction with the relatively few examined specimens of the species of *Nannocharax* that demonstrate these modifications indicate that the hook-shaped contact organs on the pectoral-fin rays of *N. reidi* and *N. rubrolabiatus* may be restricted to mature males only during the height of the breeding season.

Hook-shaped processes on scales.—The holotype and larger male paratypes of *Nannocharax reidi* possess a form of contact organ (sensu Wiley & Collette 1970, Collette 1977) involving an elaboration of the scales in the region of the body medial to the adpressed pectoral fin that is apparently unique not only within the Characiformes, but perhaps throughout bony fishes. The typical form of the scales among members of the Distichodontidae (sensu Vari 1979) is a laterally-unelaborated, relatively flat ossification with the posterior margin of the main body of each scale bearing a series of smaller, independent ossifications (see Vari 1979, figs. 38b and c), that form a distinctly-serrate posterior margin to the scale. These independent ossifications, which constitute true cteni (sensu Johnson 1984, Roberts 1993:70), vary both in number and form across the members of the Distichodontidae, but such elaborations, nonetheless, are nearly invariably limited to the posterior margin of the scale. The single ex-

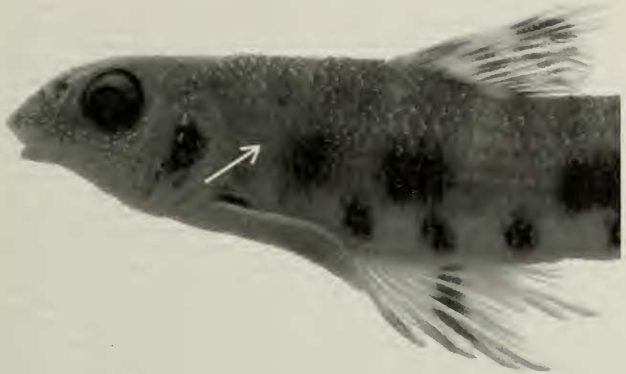


Fig. 2. *Nannocharax rubrolabiatus*, MRAC 95-022-P-001-007, 56.1 mm SL; showing breeding tubercles on the head, anterior two-thirds of the body, and dorsal, pectoral, and pelvic fins. Arrow indicates the midlateral region of the body lacking breeding tubercles, but with hook-shaped contact organs on the lateral surface of the scales.

ception to that generality that we have discovered, involves the form of the scales on the portion of the body medial to the pectoral fin in some species of *Nannocharax*. In larger specimens of *N. reidi* the scales of the portion of the body medial to the basal portion of the pectoral fin (see description above), particularly those scales in the region of the body immediately dorsal to the posteriorly-directed process of the cleithrum, have the cteni along their posterior margins complemented by hook-shaped processes arising from the lateral surface of the scales. These scale processes have the form of moderately elongate spines with slightly anteriorly-directed distal hooks. Although such processes are obvious in the larger examined specimens of *N. reidi*, they nonetheless are somewhat scattered across, and fail to completely cover, the lateral surface of the involved scales.

A dramatically greater degree of development of such contact organs in the region

of the body posterior to the insertion of the pectoral fin characterizes mature males of *Nannocharax rubrolabiatus* (Fig. 2). Contrary to the situation in all other examined distichodontids, males of *N. rubrolabiatus* lack distinct cteni along the posterior margins of the scales on the anterior portion of the midlateral surface of the body. More strikingly, the specimens in this population sample have the lateral surface of the scale variously covered by fields of laterally-directed, elongate, hook-shaped contact organs with anteriorly-curved distal tips. Continuity between the fields of hook-shaped processes of adjoining scales varies across the portion of the body with such lateral elaborations of the scales. Those scales positioned closer to the posterior margin of the pectoral girdle have patches of contact organs that together with those of adjoining scales form a nearly uninterrupted, brush-like expanse continuing approximately five scales posteriorly from the

posterior margin of the pectoral girdle and extending dorsally to the horizontal running through the dorsal margin of the opercular opening. Farther posteriorly, the hook-shaped processes on the lateral surface of the scales are restricted to the posterior one-half of the exposed portion of the scale and, thus, form discrete patches of such contact organs, with these patches distinctly separated from each other. These posteriorly-positioned scales with separate patches of contact organs on their lateral surfaces also differ from the more anterior scales characterized by the possession of such processes in retaining independent, variably posteriorly-directed cteni along at least a portion of the posterior margin of the scale. Such cteni are, however, often somewhat more laterally-directed than are the homologous ossifications in other members of the Distichodontidae.

We are unaware of any laterally-positioned, hook-shaped contact organs of a comparable morphology on the body scales, elsewhere either within the order Characiformes or among other groups of fishes. The only other report of an African freshwater fish with laterally-directed hook-shaped processes on the scales involves the gonorhynchiform *Phractolaemus ansorgei*, an ostariophysan that is phylogenetically distant from the Characiformes. *Phractolaemus* differs significantly from *Nannocharax* in the distribution, morphology, and number of such hook-shaped processes per scale (see Thys van den Audenaerde 1961a, fig. 2; 1961b, fig. 2) and the elaborations of the scales in the two genera, thus, are appropriately considered to be non-homologous. As a consequence of their apparent unique morphology, the presence of the dense patches of hook-shaped processes on the anterior portion of the midlateral scales of *Nannocharax* is a likely synapomorphy for at least a subunit of that genus, albeit one perhaps restricted to fully mature, sexually-active males during the height of the breeding season.

Breeding tubercles.—The presence of

epidermal breeding tubercles has been reported in a number of New World members of the Characiformes including the families Characidae, Parodontidae, and Lebiasinidae (Wiley & Collette 1970:164–167, Collette 1977:236–241), but not within any of the African families within that order, an apparent absence that included the Distichodontidae. One series of *Nannocharax rubrolabiatus* (MRAC 95-022-P-001-007) examined during this study has, however, very well-developed epidermal breeding tubercles distributed over the head, body and fins (Fig. 2). The degree of development of the tubercles correlates somewhat, albeit not absolutely, with the size of the specimens. The smallest specimen in the lot (45.5 mm SL) has both fewer tubercles than most of the larger conspecific individuals captured with it and, furthermore, those tubercles are proportionally less-developed than those in larger specimens. In larger, apparently male, individuals of *N. rubrolabiatus*, the breeding tubercles are broadly distributed in large numbers across the snout and the dorsal and lateral surfaces of the head (Fig. 2). On the ventral surface of the head, the tubercles are arranged in discrete rows along the ventral surfaces of the branchiostegal rays. Scales on the surface of the body have one to four tubercles, other than those scales medial to the pectoral fin whose surfaces are covered with the hook-shaped contact organs (described in the previous section and indicated by white arrow of Fig. 2). When present, the tubercles on the scales are positioned toward the posterior margin of the scale, and when three or four tubercles occur on an individual scale, these structures are arranged in an arch paralleling the posterior margin of the scale. The size and number of tubercles tend to be reduced on the scales of the ventrolateral portion of the body. An extensive series of tubercles occurs, however, on scales of the prepelvic region of the body, with a less concentrated field of tubercles present in the region from the insertion of the pelvic fin to the origin of the anal fin.

Breeding tubercles are present on all fins of *Nannocharax rubrolabiatus* with the exception of the adipose fin. The tubercles on the caudal fin are less developed than those on the remaining fins, being apparent solely as small, raised areas along the basal and middle portions of the caudal-fin rays. Tubercles are present on all of the dorsal-fin rays with the exception of the first unbranched and last branched rays. At their maximum degree of development, such breeding tubercles extend along nearly the entire length of each dorsal-fin ray. Some larger examined specimens of *N. rubrolabiatus* have indications of poorly-developed breeding tubercles on the basal portions of the second unbranched anal-fin rays, with better-developed tubercles present on all but the terminal branched anal-fin ray. The pectoral fin has tubercles on the dorsal surface of the unbranched rays, but tubercles are absent on the portions of the second unbranched through eighth branched rays with anteriorly-directed, hook-shaped contact organs. The ventral surface of the pectoral fin has at most a few tubercles distributed along the unbranched rays, but such structures are completely absent in some individuals. Variably-developed series of tubercles extend along the length of the ventral surfaces of each of the branched pectoral-fin rays. The pelvic fin has a series of tubercles arranged along the dorsal surface of the branched rays, and along the ventral surfaces of the last unbranched fin ray and all of the branched fin rays with the exception of the medialmost branched ray.

Our comparative studies failed to reveal any comparably well-developed breeding tubercles in the other examined species of *Nannocharax*. Larger examined specimens of *N. reidi* do, however, have a pattern of small, papillae-like processes on the upper lip, snout, and dorsal surfaces of the head that have an arrangement comparable to the pattern of the breeding tubercles that occur in those regions in most examined specimens of *N. rubrolabiatus*. It will be necessary to examine additional population

samples of *N. reidi* captured during the height of the breeding season in order to determine whether the papillae-like processes present in that species would develop into the distinctly larger breeding tubercles that typify the examined sample of *N. rubrolabiatus*. Broader comparative studies would possibly also yield insight in the range of the distribution of breeding tubercles across the species of *Nannocharax*.

Comparative material examined.—*Nannocharax altus*: MRAC 78-22-P-801-804, 4 specimens, Republic of the Congo, Mayala, Niola Creek.

Nannocharax fasciatus: USNM 303754, 5 specimens; USNM 303756, 2 specimens; USNM 303811, 1 specimen; USNM 303847, 3 specimens; USNM 303867, 2 specimens; USNM 303908, 4 specimens; USNM 303995, 2 specimens; USNM 304081, 3 specimens; USNM 375192, 5 specimens; Cameroon, upper Cross River system.

Nannocharax intermedius: CU 80570, 2 specimens, Gabon, Motoboi Village, Kinéné Creek; CU 90276, 3 specimens, Gabon, Okolville; MRAC 91-79-P-202-206, 4 specimens, Gabon, Riviere Loukénini; MRAC A2-006-P-0826-0828, 3 specimens, Gabon, Ivindo basin, Balé Creek.

Nannocharax maculicauda: USNM 224524, 3 paratypes; Gabon, upper Ivindo River (1°20'N, 13°12'E); CU 80621, 1 specimen, Gabon, Woleu-Ntem, Ngomo River (1°42'N, 11°38'E).

Nannocharax parvus: CU 80148, 19 specimens, Gabon (0°34'S, 10°12'E). CU 80163, 1 specimen; CU 80185, 2 specimens; CU 80184, 3 specimens; Gabon, Bi-roundou Creek (2°13'S, 11°28'E). CU 80191, 1 specimen, Gabon, Mimboubou Creek, near Franceville (1°38'S, 13°31'E). CU 80279, 5 specimens, Gabon, Okolville. CU 80607, 6 specimens, Gabon, stream at Okolville (1°29'S, 13°31'E).

Nannocharax rubrolabiatus: MRAC 95-22-P-001-007, 7 specimens, Cameroon, Sanaga River basin, Mi River (6°12'N, 14°23'E).

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